



Original Article

Fish populations forming transient spawning aggregations: should spawners always be the targets of spatial protection efforts?

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Grüss, A., and Robinson, J. Fish populations forming transient spawning aggregations: should spawners always be the targets of spatial protection efforts?. – ICES Journal of Marine Science, 72: 480–497.

Received 3 March 2014; revised 24 July 2014; accepted 25 July 2014; advance access publication 28 August 2014.

Many coral reef fish form transient spawning aggregations at sites located a few to hundreds of kilometres from their normal residence areas. Reef fish spawning aggregations (“FSAs”) are often heavily exploited, which make them targets for management with marine reserves. We used a per-recruit model to compare the long-term conservation (impacts on female spawning-stock biomass-per-recruit (SSBR) and female : male sex ratio, SR) and fisheries effects (impacts on yield-per-recruit, YPR) of spawning reserves vs. normal residence reserves for two data-poor populations from Seychelles with contrasting life history traits and sexual modes: the *Siganus sutor* population of the main granitic islands, which has a fast life history and is gonochoristic and the *Epinephelus fuscoguttatus* population of Farquhar Atoll, which has a slow life history and is protogynous. Overall, our results suggest that normal residence reserves are more effective at improving both the SSBR and YPR of *S. sutor*. In contrast, the protection of a substantial fraction of spawning sites is preferable for *E. fuscoguttatus* to ensure the reproductive output of this protogynous population through normalization of SR and maintenance of high SSBR. Neither spawning reserves nor normal residence reserves improved the YPR of *E. fuscoguttatus*. However, yields of *E. fuscoguttatus* may increase on the long term via recruitment subsidy if a substantial fraction of spawning sites is protected. This may occur only if the population was recruitment limited in the absence of reserves and increases in SSBR compensate for lost opportunities caused by the area closures. Sensitivity analyses revealed that the relative effects of spawning reserves and normal residence reserves relate more to the change in catchability occurring with FSA formation than to life history traits. Thus, normal residence reserves should be preferred over spawning reserves for *S. sutor* essentially because its catchability at spawning sites is low relative to many other aggregation-forming populations. *S. sutor* therefore suffers higher fishing mortality in normal residence areas than at FSA sites. Our study demonstrates that spawning reserves are not always the most effective tool for balancing conservation and exploitation objectives for FSA-forming populations, and that this measure should ideally be weighed against other management options.

Keywords: fisheries management, marine reserves, modelling, reef fish spawning aggregations, resource conservation, targeted marine reserves, transient spawning aggregations.

Introduction

Many coral reef fish form transient spawning aggregations (“FSAs”) at sites located a few to hundreds of kilometers from their normal residence areas (Domeier and Colin, 1997). Most

aggregation-forming species show strong fidelity to FSA sites, such that FSAs represent bottlenecks in their life history (e.g. Domeier and Colin, 1997; Sadovy and Eklund, 1999; Nemeth et al., 2007). Slow life history, the spatial and temporal predictability

of FSAs and the substantial increase in catchability that usually occurs when fish aggregate act in concert to render aggregation-forming populations highly vulnerable to fishing (e.g. Coleman *et al.*, 2000; Sadovy and Domeier, 2005; Rhodes *et al.*, 2011). Moreover, fishing often selects for larger, older individuals at FSA sites, which can lead to reduction in the reproductive output of aggregative populations (Sadovy, 1996; Rhodes and Warren-Rhodes, 2005). Further impacts of fishing are added in the case of protogynous populations (i.e. populations that mature first as female then change into males), which can suffer declines in the relative number of males because males are generally larger than females and reside for longer periods at FSA sites (Coleman *et al.*, 1996; Koenig *et al.*, 1996). Significant bias in the female : male sex ratio (SR) of protogynous populations may lead to reduced egg fertilization and reproductive failure (e.g. Coleman *et al.*, 1996; Fitzhugh *et al.*, 2006), and to the disruption of the sex change process (e.g. Koenig *et al.*, 2000). Consequently, the protection of FSAs using marine reserves, places where fishing and other extractive activities are prohibited year-round, has been widely advocated (Johannes, 1997; Koenig *et al.*, 2000; Rhodes and Warren-Rhodes, 2005; Sadovy de Mitcheson *et al.*, 2013).

Spawning reserves protect adults, including the largest, most vulnerable individuals, and allow for the persistence and stability of the mating process (Bohnsack *et al.*, 2004; Muñoz *et al.*, 2010; Sadovy de Mitcheson *et al.*, 2013). Therefore, they have the ability to maintain or recover spawning-stock biomass and mating to levels that ensure recruitment success (Bohnsack *et al.*, 2004; Russell *et al.*, 2012). Spawning reserves also reduce biases in female : male SR in protogynous aggregative populations, potentially increasing egg fertilization rates (Beets and Friedlander, 1999; Koenig and Coleman, 2013). Moreover, spawning reserves have been advocated to improve fisheries yields by enhancing yield-per-recruit (YPR; exploitable biomass) via an increase in the mean body size of the fish population and via “recruitment subsidy”, i.e. by enhancing the supply of eggs and larvae to adjacent fished areas (Russ, 2002; Roberts, 2012; Sadovy de Mitcheson and Colin, 2012). While the conservation benefits of spawning reserves are widely recognized, evidence is limited with respect to their fisheries benefits (Sale *et al.*, 2005; Grüss *et al.*, 2011).

To date, three models have explored the impacts of marine reserves for FSA-forming populations (Heppell *et al.*, 2006; Ellis and Powers, 2012; Grüss *et al.*, 2013). Heppell *et al.* (2006) and Ellis and Powers (2012) developed an age-structured, population model to evaluate marine reserve effectiveness for the gag grouper (*Mycteroperca microlepis*; Epinephelidae) population of the north-eastern Gulf of Mexico, an overexploited fish population for which a large amount of data are available. Importantly, Heppell *et al.* (2006) found that protecting all FSA sites was less effective for population growth than other management measures, including the implementation of marine reserves in normal residence areas (“normal residence reserves”) and fishing effort reduction. On the other hand, spawning reserves helped female : male SR normalization, while normal residence reserves did not (Heppell *et al.*, 2006). Grüss *et al.* (2013) designed an age-structured, per-recruit model to assess the impacts of protecting a fraction or all FSA sites for two data-poor populations from Seychelles with contrasting life history traits and sexual modes: the shoemaker spine-foot rabbitfish (*Siganus sutor*; Siganidae) population of the main granitic islands, which has a fast life history and is gonochoristic and the brown-marbled grouper (*Epinephelus fuscoguttatus*; Epinephelidae) population of Farquhar Atoll, which has a slow

life history and is protogynous. For a wide range of fishing effort levels, spawning reserves for both populations generally improved female spawning-stock biomass-per-recruit (SSBR), though benefits were often small, while increases in YPR were not achieved or were negligible.

The FSAs of *S. sutor* in the main granitic islands of Seychelles support a small-scale and socio-economically important trap fishery (Robinson *et al.*, 2011), whereas the FSAs of *E. fuscoguttatus* at Farquhar Atoll have historically contributed to the production of salted fish for local markets (J. Robinson, personal observation). Since these fisheries were first documented (Robinson *et al.*, 2004, 2007), the opinion of stakeholders has diverged with regard to their management. Conservationists have often advocated for the use of spawning reserves, whereas fishers have argued that the FSAs of *S. sutor* and *E. fuscoguttatus* can be fished sustainably and that other management options are required for these fish populations. In the case of *S. sutor*, it has been argued by fishers that existing marine reserves, covering >30 km² of shallow reefs and lagoons around the main granitic islands, already provide protection to *S. sutor* in its normal residence areas. This debate therefore highlighted a critical question, namely: are normal residence reserves more beneficial for the long-term conservation and exploitation of *S. sutor* and *E. fuscoguttatus* than spawning reserves?

A theoretical framework was used to inform the ongoing debate in Seychelles based on modifying the model developed by Grüss *et al.* (2013). We compared the long-term, equilibrium conservation (impacts on female SSBR and female : male SR) and fisheries effects (impacts on YPR) of normal residence reserves to those of spawning reserves for the *S. sutor* population of the main granitic islands and the *E. fuscoguttatus* population of Farquhar Atoll. With regards to *S. sutor*, we aimed to determine the relative benefits of spawning and normal residence reserves in terms of both female SSBR and YPR. With regards to *E. fuscoguttatus*, the effectiveness of spawning reserves and normal residence reserves in reducing bias in female : male SR was the primary consideration, given that ensuring reproductive output through SR normalization is a prerequisite for long-term conservation and fisheries benefits (Coleman *et al.*, 1996; Fitzhugh *et al.*, 2006; Ellis and Powers, 2012). In this paper, we (i) describe the modifications introduced to the model designed by Grüss *et al.* (2013), (ii) apply the model to *S. sutor* and *E. fuscoguttatus* for a range of reserve scenarios, and (iii) carry out sensitivity analyses to evaluate the influence of critical parameters (spawning-site catchability and life history traits) on our results.

Material and methods

The model we used is based on that developed in Grüss *et al.* (2013). Therefore, we provide only a short description of the model, since its structure, parameterization and underlying assumptions are detailed in Grüss *et al.* (2013).

Two life stages are represented in the model for gonochoristic populations (juveniles and adults), and three for protogynous populations (juveniles, adult females and males). The adult stage is decomposed into spawners and non-spawners. Adults are present at FSA sites only during the spawning period, whereas juveniles are absent from these sites. All larvae produced at FSA sites enter a common pool from which they settle uniformly over space (“mixed larval pool”; Hart, 2006; Kaplan, 2009). Fish are assumed to recruit into fisheries at or before the age of sexual maturity, with the rationale that reef fisheries traditionally select for a wide range of fish sizes and that many FSA-forming species mature at

a late age (Sadovy, 1994; Sadovy and Eklund, 1999; Rhodes and Tupper, 2008). All life stages are subjected to the same natural mortality rate. Finally, for protogynous populations, sex change is assumed to take place at a fixed age.

Mortality rates

In the absence of marine reserves, the mortality rates given in Grüss *et al.* (2013) also apply here. However, mortality rates in the presence of marine reserves are changed in this study by (i) the consideration of normal residence reserves and (ii) the introduction of polymorphism in spawning behaviour in the model to account for the fact that only a fraction of adults is faithful to FSA sites in some aggregative populations, as was recently shown for *S. sutor* (Bijoux *et al.*, 2013b).

We considered the effects of protecting a fraction of normal residence areas relative to the effects of protecting a fraction or all FSA sites. Moreover, we made the following assumptions regarding fishing effort redistribution following reserve creation: (i) the fishing effort previously in reserves disappears; (ii) when a fraction of FSA sites is protected, pre-reserve fishing effort is fully redistributed to non-protected FSA sites; (iii) when all FSA sites are protected, the fishing effort previously in reserves is fully redistributed to normal residence areas; and (iv) when normal residence areas are protected, pre-reserve fishing effort is fully redistributed to non-protected normal residence areas. Thus, a total of six reserve scenarios were explored (Table 1).

Status quo

In the absence of marine reserves (under the “status quo”), the total mortality rate of adults of a gonochoristic population (Z_{mat}) and of males of a protogynous population (Z_m) is

$$Z_{\text{mat}} = Z_m = M + (1 - C_s)q_{\text{ns}}E + C_sq_sE, \quad (1)$$

where M is the natural mortality rate (in year⁻¹), C_s is the fraction of the annual fishing effort that is directed towards FSAs, q_{ns} is the

catchability in normal residence areas, q_s is the catchability at FSA sites, and E is the total annual fishing effort (in year⁻¹).

Males of a protogynous population often spend more time at FSA sites than females (e.g. Rhodes and Sadovy, 2002; Rowell *et al.*, 2012; Bijoux *et al.*, 2013a). Therefore, the total mortality rate of females of a protogynous population (Z_f) is given by:

$$Z_f = M + (1 - C_s)q_{\text{ns}}E + C_fC_sq_sE, \quad (2)$$

where C_f is the fraction of the spawning period that females spend at FSA sites.

Finally, under the status quo, but also when a fraction of spawning sites is protected, or when all FSA sites are protected while pre-reserve fishing effort disappears, the total mortality rate of juveniles (Z_j) is

$$Z_j = M + (1 - C_s)q_{\text{ns}}E. \quad (3)$$

Fraction of FSA sites in reserves

When only a fraction, C_r , of FSA sites is protected, given that we assume a mixed larval pool, the total mortality rate of adults must be split into two parts to distinguish between individuals that are faithful to spawning sites and individuals that are unfaithful to spawning sites. For example, for a gonochoristic population, the total mortality rate of adults becomes:

$$Z_{\text{mat}} = C_bZ_{\text{mat}}^b + (1 - C_b)Z_{\text{mat}}^{\text{nb}}, \quad (4)$$

where C_b is the fraction of adults that is faithful to FSA sites and Z_{mat}^b and $Z_{\text{mat}}^{\text{nb}}$ are the total mortalities of the fraction of the adult population that is, respectively, faithful and unfaithful to FSA sites.

When pre-reserve fishing effort disappears, the adult subpopulation constituted of individuals faithful to FSA sites decomposes itself into two subpopulations, one that is fully protected while spawning, and one that remains fully exposed to fishing while spawning. Therefore, for gonochoristic populations:

$$Z_{\text{mat}}^b = C_rZ_{\text{mat}}^{\text{br}} + (1 - C_r)Z_{\text{mat}}^{\text{bnr}}, \quad (5)$$

where $Z_{\text{mat}}^{\text{br}}$ and $Z_{\text{mat}}^{\text{bnr}}$ are the total mortalities of the fraction of the faithful adult subpopulation spawning at, respectively, protected and non-protected FSA sites; and C_r is the fraction of FSA sites protected. $Z_{\text{mat}}^{\text{br}}$ is identical to the total mortality of juveniles under the status quo (Equation (3)), while $Z_{\text{mat}}^{\text{bnr}}$ is the total mortality of adults given in Equation (1). As to the adult subpopulation constituted of individuals unfaithful to spawning sites, its FSA fishing mortality is simply reduced by a factor $(1 - C_r)$, such that

$$Z_{\text{mat}}^{\text{nb}} = M + (1 - C_s)q_{\text{ns}}E + (1 - C_r)C_sq_sE. \quad (6)$$

When pre-reserve fishing effort is redistributed, fishing mortality at non-protected FSA sites is increased by a factor of $1/(1 - C_r)$. Therefore, the total mortality of the fraction of the faithful adult population spawning at protected FSA sites ($Z_{\text{mat}}^{\text{br}}$ for gonochoristic populations) remains the total mortality of juveniles under the status quo, whereas the total mortality of the fraction of the faithful adult population spawning at fished FSA sites ($Z_{\text{mat}}^{\text{bnr}}$ for gonochoristic populations) is equal to the total mortality of adults under the status quo increased by a factor of $1/(1 - C_r)$. As to the adult

Table 1. Description of the marine reserve scenarios simulated in the present study.

| Reserve scenario | Description |
|------------------|---|
| Scenario #1 | A fraction of spawning sites is closed to fishing; the fishing effort previously in reserves disappears at the time of reserve creation |
| Scenario #2 | A fraction of spawning sites is closed to fishing; the fishing effort previously in reserves is fully redistributed to spawning sites remaining open to fishing |
| Scenario #3 | All spawning sites are closed to fishing; the fishing effort previously in reserves disappears at the time of reserve creation |
| Scenario #4 | All spawning sites are closed to fishing; the fishing effort previously in reserves is fully redistributed to normal residence areas |
| Scenario #5 | A fraction of normal residence areas is closed to fishing; the fishing effort previously in reserves disappears at the time of reserve creation |
| Scenario #6 | A fraction of normal residence areas is closed to fishing; the fishing effort previously in reserves is fully redistributed to normal residence areas remaining open to fishing |

subpopulation constituted of individuals unfaithful to spawning sites, FSA fishing mortality is both decreased by a factor $(1 - C_r)$ and increased by a factor of $1/(1 - C_r)$, so that its total mortality is that of adults under the status quo.

All FSA sites in reserves

If all FSA sites are protected and pre-reserve fishing effort disappears, the total mortality rate of adults becomes that of juveniles under the status quo. On the other hand, if pre-reserve fishing effort is redistributed to normal residence areas, fishing effort concentrates entirely in normal residence areas, and adults and juveniles are then subject to the same total mortality rate:

$$Z_{\text{mat}} = Z_m = Z_f = Z_j = M + q_{\text{ns}}E. \tag{7}$$

Normal residence reserves

If a fraction, C_r , of normal residence areas is protected and pre-reserve fishing effort disappears, the fishing mortality of adults and juveniles in normal residence areas $((1 - C_s)q_{\text{ns}}E)$ is simply reduced by a factor $(1 - C_r)$ compared with the status quo.

Conversely, if pre-reserve fishing effort is redistributed to non-protected normal residence areas, adult and juvenile populations must be divided into two subpopulations, one that experiences no fishing mortality in normal residence areas, and one that has the normal fishing mortality in these areas increased by a factor of $1/(1 - C_r)$.

Metrics

To investigate the long-term impacts of spawning reserves and normal residence reserves, female SSBR and YPR are evaluated under the scenarios described above. Female SSBR (hereafter simply referred to as ‘‘SSBR’’) and YPR are obtained by integrating the product of weight-at-age and survival-at-age over relevant age ranges. For protogynous populations, female : male SR in the presence of marine reserves is also evaluated. SR is a proxy for the production of fertilized eggs (Coleman *et al.*, 1996; Fitzhugh *et al.*, 2006) and is given by the ratio of integrals of survival to age over the female and male age ranges. Equations for SSBR, YPR, and SR are provided in Supplementary Appendix A1.

For the reserve scenarios where the study population decomposes into several subpopulations, given that we assume a mixed larval pool, population-wide per-recruit quantities are weighted averages of the corresponding per-recruit quantities for the different subpopulations. For example, when a fraction of FSA sites is protected and the fishing effort previously in reserves is redistributed to non-protected FSA sites, i.e. under Scenario #2, population-wide SSBR (SSBR^{POP}) is given by

$$\text{SSBR}^{\text{POP}} = C_b[C_r\text{SSBR}^{\text{br}} + (1 - C_r)\text{SSBR}^{\text{bnr}}] + (1 - C_b)\text{SSBR}^{\text{nb}}, \tag{8}$$

where C_b is the proportion of the population faithful to FSA sites, C_r is here the fraction of FSA sites in reserves, SSBR^{br} is the SSBR of the subpopulation faithful to protected FSA sites, SSBR^{bnr} is the SSBR of the subpopulation faithful to fished FSA sites, and SSBR^{nb} is the SSBR of the subpopulation unfaithful to FSA sites.

In the results and figures, SSBR is given relative to the natural (unfished) SSBR (i.e. the fraction of natural SSBR or FNSSBR), whereas YPR is given relative to the maximum YPR in the absence of marine reserves. Reduction in egg fertilization rates due to biased SR occurs

at a local level. Therefore, for protogynous populations, we report both population-wide average SR and the local SR at both protected and fished FSA sites. Local SRs are compared with a ‘‘critical SR’’, above which local production of fertilized eggs and reproduction is assumed to fail (Coleman *et al.*, 1996; Fitzhugh *et al.*, 2006).

Analyses

We evaluated the six reserve scenarios described above for the *S. sutor* population of the main granitic islands of Seychelles and the *E. fuscoguttatus* population of Farquhar Atoll, Seychelles. Both *S. sutor* and *E. fuscoguttatus* populations are assumed to grow according to a von Bertalanffy growth function, and weight is an allometric function of growth. The parameterization of our model for the two populations is detailed in Grüss *et al.* (2013) and parameter values are provided in Table 2. In addition, we made the assumption that 87% of the spawning individuals of the *S. sutor* population are faithful to FSA sites (Bijoux *et al.*, 2013b) and that the adult population of *E. fuscoguttatus* is entirely faithful to spawning sites (Bijoux *et al.*, 2013a). Finally, following Grüss *et al.* (2013), we considered a critical SR of 50 : 1 for *E. fuscoguttatus*.

Under the status quo, the default total annual fishing effort of the *S. sutor* and *E. fuscoguttatus* populations, E_{base} , is the current annual fishing effort exerted on these populations in the main granitic islands and at Farquhar Atoll, respectively (95 000 trap sets per year for *S. sutor*; Robinson *et al.*, 2011; 169 fishing days per year for *E. fuscoguttatus*; J. Robinson, personal observation). For *S. sutor*, the value of E_{base} is close to that of E_{max} , the annual fishing effort at which YPR reaches a maximum (Grüss *et al.*, 2013). In contrast, the value of E_{base} is ~13 times less than that of E_{max} for *E. fuscoguttatus* (Grüss *et al.*, 2013). All reserve scenarios were evaluated under annual fishing effort, E , levels ranging from 0 to 3 times E_{base} . For *E. fuscoguttatus*, all reserve scenarios were also evaluated under E levels ranging from 3 to 26 times E_{base} . E levels for *E. fuscoguttatus* ranging from 3 to 26 times E_{base} are less likely than E levels ranging from 0 to 3 times E_{base} (J. Robinson, personal observation), but are considered to examine changes in SSBR, YPR, and SRs under annual fishing effort levels greater than and up to twice the level of E_{max} . Moreover, for reserve scenarios where only a fraction of habitat C_r is closed to fishing (i.e. Scenarios #1 and 2, #5 and 6), we present results only for $C_r = 30$ and 60%.

Siganus sutor is a short-lived and fast-growing species (Grandcourt, 2002), whereas *E. fuscoguttatus* is long-lived and slow-growing species (Pears *et al.*, 2006). To quantify the relative impacts of spawning-site catchability (q_s) and life history traits on our results, we carried out sensitivity analyses consisting in evaluating the consequences of (i) increasing q_s by a factor of 10 for *S. sutor* (yielding a ratio of q_s to catchability in normal residence areas (q_{ns}), q_s/q_{ns} , of the same magnitude as that of *E. fuscoguttatus*); (ii) decreasing q_s by a factor of 10 for *E. fuscoguttatus* (yielding a q_s/q_{ns} of the same magnitude as that of *S. sutor*); (iii) decreasing natural mortality rate, M , or instantaneous growth rate at small size, k , by a factor of 10 for *S. sutor*; and (iv) increasing M or k by a factor of 10 for *E. fuscoguttatus*. All sensitivity analyses were conducted under E levels ranging from 0 to 3 times E_{base} .

Results

Conservation and fisheries effects of spawning reserves vs. normal residence reserves for *S. sutor*

For *S. sutor*, conservation benefits in the form of increases in SSBR occur under all reserve scenarios, though these benefits are relatively

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

| Parameter | Definition | <i>Siganus sutor</i> | <i>Epinephelus fuscoguttatus</i> |
|------------|--|---|--|
| M | Natural mortality rate | 0.63 year ⁻¹ (Grandcourt, 2002) | 0.1 year ⁻¹ (Hoenig, 1983) |
| E | Total annual fishing effort | 95 × 10 ³ trap sets per year (Robinson et al., 2011) | 169 fishing days per year (J. Robinson personal observation) |
| C_s | Fraction of annual fishing effort directed towards spawning aggregations | 0.0822 (Robinson et al., 2011) | 0.0329 (J. Robinson personal observation) |
| C_f | Fraction of the spawning period that females spend at spawning sites | – | 0.45 (Seychelles Fishing Authority, unpublished data) |
| C_b | Fraction of the adults that is faithful to spawning sites | 0.87 (Bijoux et al., 2013b) | 1 ^g (Bijoux et al., 2013a) |
| q_s | Spawning-site catchability | 1.0758 × 10 ⁻⁴ | 6.5447 × 10 ⁻³ |
| q_{ns} | Catchability in normal residence areas | $q_s/10$ (Seychelles Fishing Authority, unpublished data) | $q_s/140$ (Seychelles Fishing Authority, unpublished data) |
| a_F | Age of recruitment into the fishery | 0.34 year (Robinson et al., 2011) | 9.2 year (Seychelles Fishing Authority, unpublished data) |
| a_{50} | Age of sexual maturity | 0.79 year (J. Robinson personal observation) | 9.2 year (Pears et al., 2006) |
| a_{sx} | Age of sex change | – | 25.5 year (Pears et al., 2006) |
| K | Instantaneous growth rate at small size | 0.65 year ⁻¹ (Grandcourt, 2002) | 0.16 year ⁻¹ (Pears et al., 2006) |
| L_∞ | Maximum size | 43.3 cm (Grandcourt, 2002) | 80.7 cm (Pears et al., 2006) |
| a_0 | Theoretical age at zero length | –0.379 year (Grandcourt, 2002) | –0.2 year (Pears et al., 2006) |
| A | Constant of proportionality of the allometric length–weight relationship | 5.9 × 10 ⁻³ (Samboo and Mauree, 1988) | 6 × 10 ⁻⁶ (Grandcourt, 2005) |
| β | Exponent of the allometric length–weight relationship | 2.75 (Samboo and Mauree, 1988) | 3.28 (Grandcourt, 2005) |
| SR | Female : male SR | 1 : 1 (Robinson et al., 2011) | Varies |

minor when a fraction of FSA sites is protected and pre-reserve fishing effort is redistributed (Scenario #2) (Figure 1a and b). Enhancement of SSBR is greater when normal residence areas are protected (Scenarios #5 and 6) than when a fraction of FSA sites is placed in reserves (Scenarios #1 and 2) under a wide range of fishing effort levels, even when pre-reserve fishing effort is redistributed (full and dashed violet vs. full and dashed black curves in Figure 1a and b).

Increases in SSBR are greater when all FSA sites are protected (Scenarios #3 and 4) than when a moderate fraction of normal residence areas (30%) is set aside in reserves, except at high fishing effort levels (greater than ~1.75 times E_{base} ; full and dashed green vs. full and dashed violet curves in Figure 1a). At high fishing effort levels, enhancement of SSBR is similar when all FSA sites or a moderate fraction of normal residence areas is in reserves. In contrast, protecting a large fraction of normal residence areas (60%) yields greater conservation benefits than protecting all FSA sites at fishing effort levels greater than E_{base} , even when pre-reserve fishing effort is redistributed (full and dashed violet vs. full and dashed green curves in Figure 1b).

Fisheries benefits for *S. sutor* are primarily limited to protection of normal residence areas, while protecting FSA sites generally incurs costs for the trap fishery (Figure 2a and b). Protecting FSA sites has a negative effect on YPR at fishing effort levels lower than ~1.5 times E_{base} , whereas, at fishing effort levels greater than ~1.5 times E_{base} , spawning reserves have zero or negligible effect on YPR (full and dashed black and full and dashed green curves in Figure 2a and b). In contrast, when pre-reserve fishing effort disappears, at fishing effort levels greater than E_{base} , normal residence reserves have a positive effect on YPR, which increases with both fishing effort and the fraction of normal residence areas in reserves (Scenario #5; full violet curve in Figure 2a and b). Fishing effort redistribution reduces the fisheries benefits of normal residence

reserves (Scenario #6; dashed violet curve in Figure 2a and b). When a moderate fraction of normal residence areas ($C_r = 30\%$) is set aside as reserves, YPR increases only slightly with fishing effort at fishing effort levels greater than ~1.75 times E_{base} (dashed violet curve in Figure 2a). With the protection of a large fraction of normal residence areas ($C_r = 60\%$), YPR increases with fishing effort at fishing effort levels greater than ~1.5 times E_{base} , and fisheries benefits are also greater than when a moderate fraction ($C_r = 30\%$) is protected (dashed violet curve in Figure 2b).

Conservation and fisheries effects of spawning reserves vs. normal residence reserves for *E. fuscoguttatus*

For *E. fuscoguttatus*, conservation benefits in the form of increases in SSBR occur under all reserve scenarios, though are limited when a fraction of normal residence areas is set aside as reserves and pre-reserve fishing effort is redistributed (Scenario #6) (Figure 1c and d; Supplementary Figure SA2). Increases in SSBR are greater when spawning reserves are implemented than when a fraction of normal residence areas is protected. An exception to this general pattern occurs under fishing effort levels lower than ~2 times E_{base} , when 30% of the normal residence areas are protected and pre-reserve fishing effort disappears, which produces similar increases in SSBR to protecting 30% of FSA sites when pre-reserve fishing effort is redistributed (Figure 1c; Supplementary Figure SA2a).

Decreases in YPR occur in all reserve scenarios (Figure 2c and d; Supplementary Figure SA3). These decreases are substantial when all FSA sites are set aside as reserves (full and dashed green curves in Figure 2c and d; Supplementary Figure SA3). YPR levels for *E. fuscoguttatus* are higher with normal residence reserves than with spawning reserves (Figure 2c and d; Supplementary Figure SA3).

Reduction in population-wide average SR occurs under all reserve scenarios except when a fraction of FSA sites or of normal residence areas is in reserves while the fishing effort formerly in

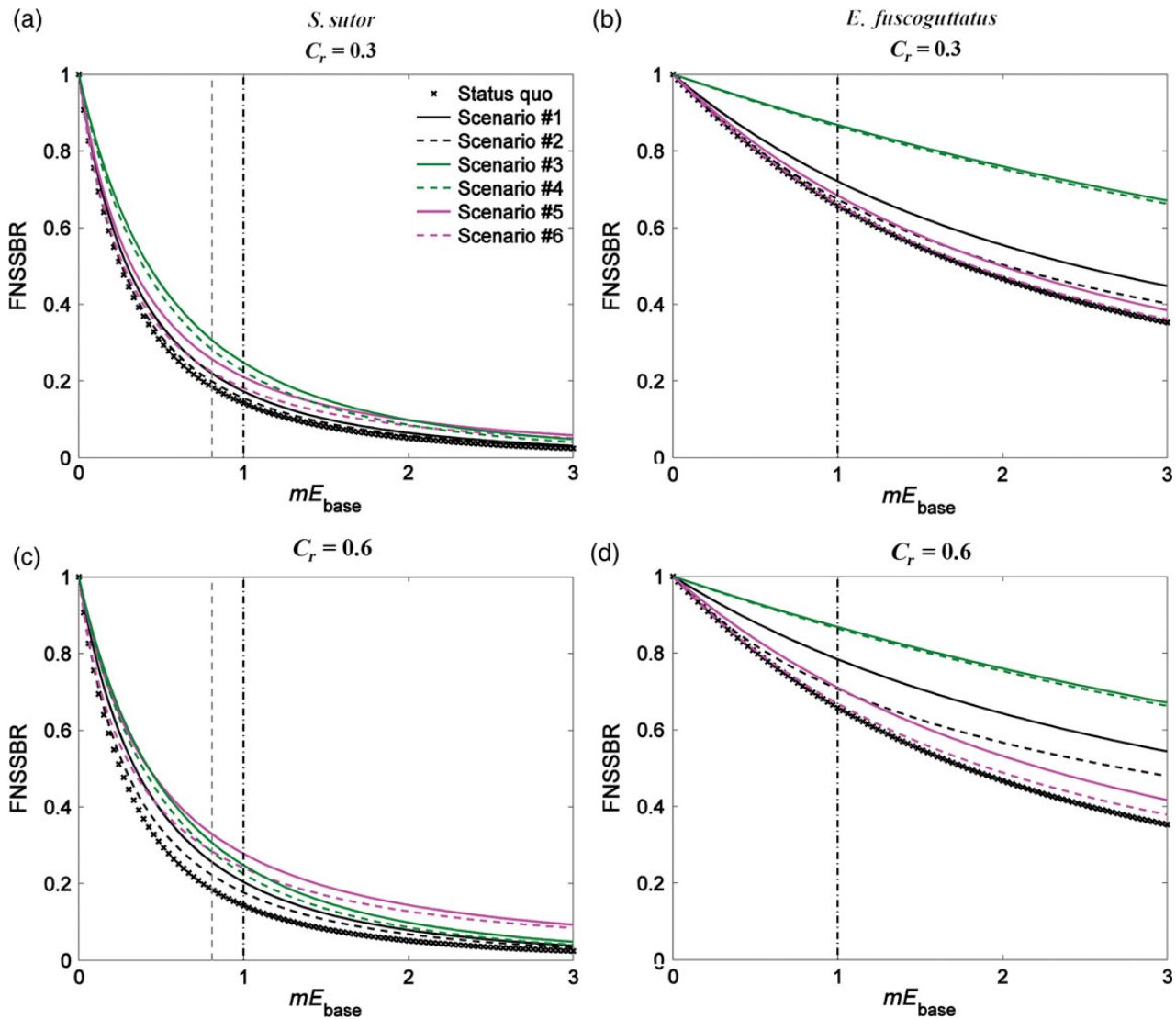


Figure 1. Fraction of natural SSBR (FNSSBR, i.e. SSBR over natural SSBR) as a function of multiplier of fishing effort (mE_{base}), for the status quo and the six reserve scenarios (Table 1). (a) and (b) are for *S. sutor*, whereas (c) and (d) are for *E. fuscoguttatus*. For Scenarios #1 and 2, the fraction of spawning sites in reserves, C_r , is 30 and 60% for (a) and (c) and (b) and (d), respectively. All spawning sites are set aside as reserves for Scenarios #3 and 4. For Scenarios #5 and 6, the fraction of normal residence areas in reserves, C_r , is 30 and 60% for (a) and (c) and (b) and (d), respectively. For all panels, the vertical dashed-dotted black line indicates the default value of annual fishing effort exerted on the population, E_{base} . For *S. sutor*, the vertical dashed grey line indicates the value of annual fishing effort at which YPR reaches a maximum for the population, E_{max} .

reserves is redistributed (Scenarios #2 and 6) (Figure 3a and b; Supplementary Figure SA4a and b). When all FSA sites are set aside as reserves (Scenarios #3 and 4), decreases in population-wide average SR and in the SR of the fished subpopulation are substantial (full and dashed green curves in Figure 3 and Supplementary Figure SA4). Under these reserve scenarios, the SR of the fished subpopulation remains below the critical SR (i.e. 50 females for 1 male) under a very wide range of fishing effort levels (under fishing effort levels up to ~ 6.5 times E_{base} ; full and dashed green curves in Supplementary Figure SA4c and d). In contrast, when a fraction of spawning sites or of normal residence areas is protected while pre-reserve fishing effort disappears (Scenarios #1 and 5), reduction in population-wide average SR is more limited and reduction in the SR of the fished subpopulation does not occur (full black and full violet curves in Figure 3 and Supplementary Figure SA4). In these two

reserve scenarios, like in the status quo, the SR of the fished subpopulation remains below the critical SR under fishing effort levels up to ~ 1.8 times E_{base} (full black and full violet curves in Figure 3c and d). Moreover, the SR of protected subpopulation is significantly reduced with spawning reserves, while it remains close to the SR under the status quo with normal residence reserves (Supplementary Figure SA5a). Therefore, it comes that closing a fraction of FSA sites or normal residence areas while pre-reserve fishing effort disappears has, respectively, virtually no impact and limited positive impact on the overall production of fertilized eggs.

When a fraction of FSA sites or of normal residence areas is protected while the fishing effort previously in reserves is redistributed (Scenarios #2 and 6), population-wide SR increases with marine reserves (dashed black and dashed violet curves in Figure 3a and b and Supplementary Figure SA4a and b), due to increases in the SR

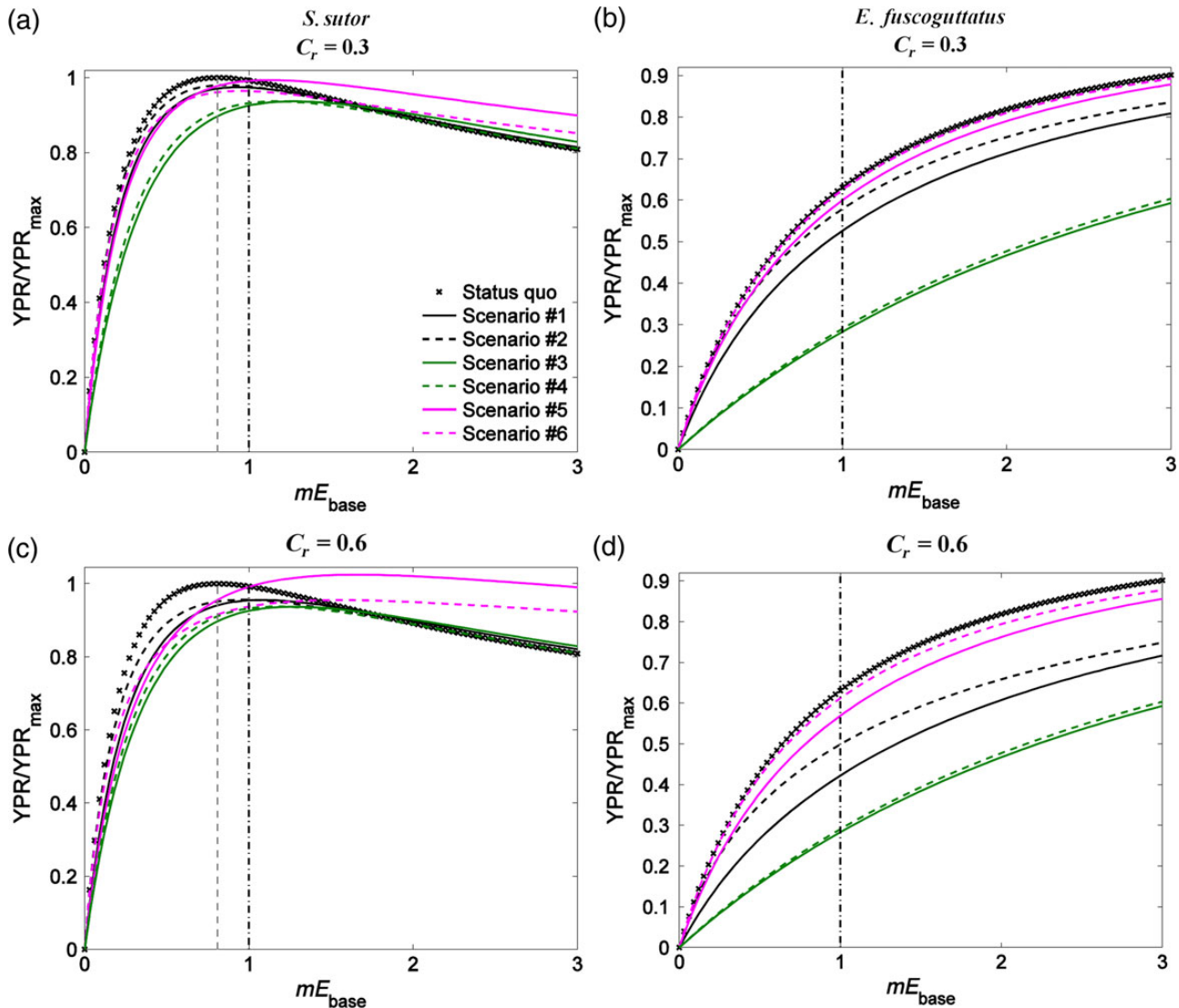


Figure 2. YPR normalized by maximum YPR in the absence of reserves (YPR/YPPr_{max}) as a function of multiplier of fishing effort (mE_{base}) for the status quo and the six reserve scenarios (Table 1). (a) and (b) are for *S. sutor*, whereas (c) and (d) are for *E. fuscoguttatus*. For Scenarios #1 and 2, the fraction of spawning sites in reserves, C_r , is 30 and 60% for (a) and (c) and (b) and (d), respectively. All spawning sites are set aside as reserves for Scenarios #3 and 4. For Scenarios #5 and 6, the fraction of normal residence areas in reserves, C_r , is 30 and 60% for (a) and (c) and (b) and (d), respectively. For all panels, E_{base} is indicated by a vertical dashed-dotted black line. For *S. sutor*, E_{max} is indicated by a vertical dashed grey line.

of the fished subpopulation (dashed black and dashed violet curves in Figure 3c and d and Supplementary Figure SA4c and d). Increases in the SR of the fished subpopulation are greater with spawning reserves than with normal residence reserves (dashed black vs. dashed violet curve in Figure 3c and d and Supplementary Figure SA4c and d). On the other hand, as mentioned earlier, increases in the SR of the protected subpopulation with spawning reserves are substantial, whereas increases in the SR of the protected subpopulation with normal residence reserves are small (Supplementary Figure SA5). Therefore, it comes that closing a fraction of normal residence areas while pre-reserve fishing effort is redistributed has a strong negative impact on the overall production of fertilized eggs, while the overall production of fertilized eggs may not be compromised with spawning reserves when pre-reserve fishing effort is redistributed if enough FSA sites are protected.

Impacts of spawning-site catchability on reserve effects

For *S. sutor*, increasing spawning-site catchability, q_s , by a factor of 10 significantly reduces the positive effects of normal residence reserves (full and dashed violet curves in Figure 4c and d vs. Figure 4a and b). In contrast, when q_s is multiplied by a factor of 10, the positive effects of spawning reserves on SSBR are dramatically increased and become much greater than those of normal residence reserves (full and dashed black and full and dashed green curves in Figure 4c and d). When q_s is multiplied by a factor of 10, spawning reserves have a positive effect on YPR only if fishing effort is much greater than E_{max} (full and dashed black and full and dashed green curves in Figure 5c and d vs. Figure 5a and b). Conversely, increasing q_s by a factor of 10 results in positive fisheries effects from protecting normal residence reserves under a wide range of fishing effort levels (full and dashed violet curves in

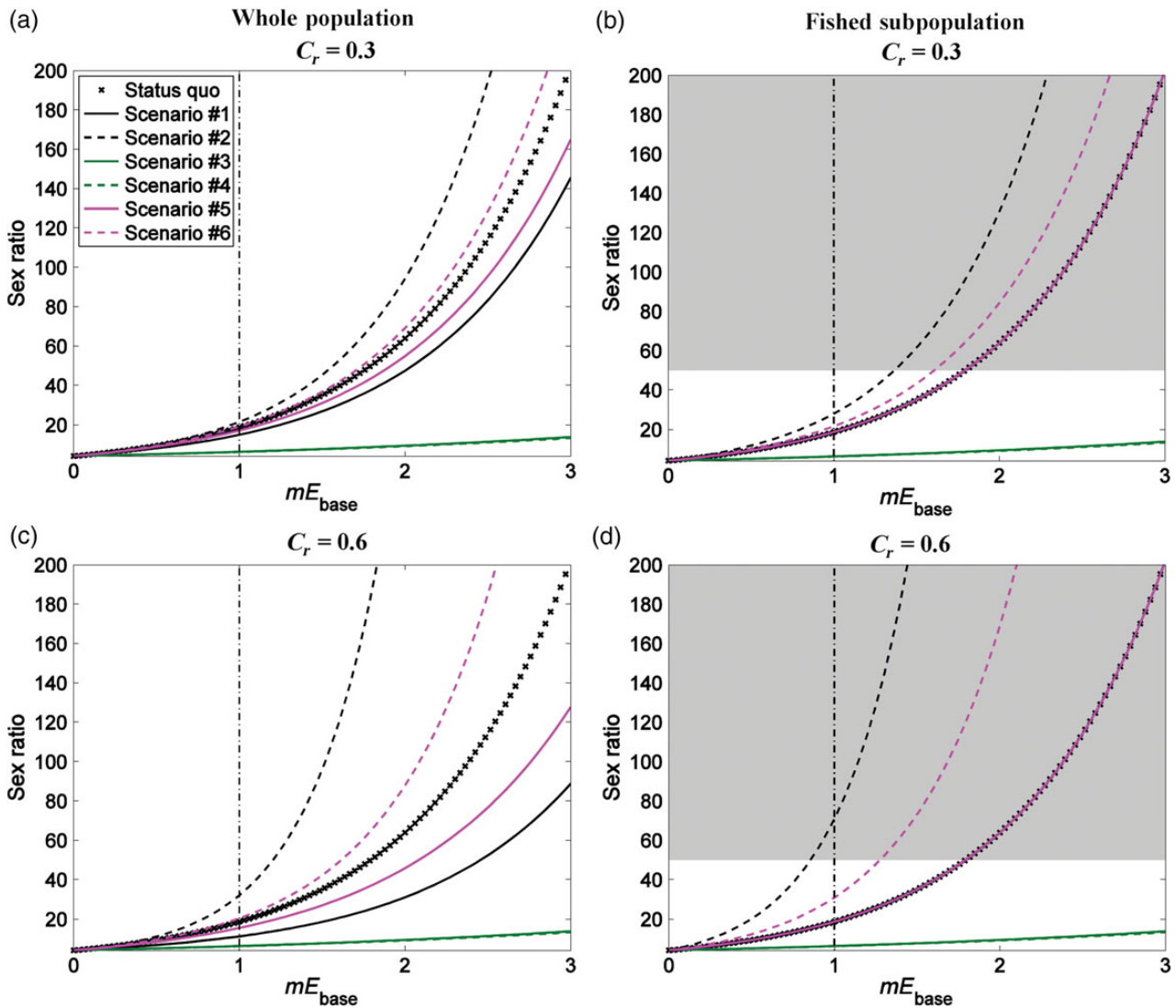


Figure 3. Female : male SR of *E. fuscoguttatus* as a function of multiplier of fishing effort (mE_{base}), for the status quo and the six reserve scenarios (Table 1). (a) and (b) give population-wide average female : male SRs, whereas (c) and (d) give female : male SRs for the fished subpopulation of *E. fuscoguttatus*. For Scenarios #1 and 2, the fraction of spawning sites in reserves, C_r , is 30 and 60% for (a) and (c) and (b) and (d), respectively. All spawning sites are set aside as reserves for Scenarios #3 and 4. For Scenarios #5 and 6, the fraction of normal residence areas in reserves, C_r , is 30 and 60% for (a) and (c) and (b) and (d), respectively. For panels (c) and (d), the light grey area indicates when the SR of the fished subpopulation is superior to the critical female : male SR (i.e. 50 : 1). For all panels, E_{base} is indicated by a vertical dashed-dotted black line. Note that the full black and full violet curves overlap in panels (c) and (d).

Figure 5c and d), though fisheries benefits are negligible or limited when pre-reserve fishing effort is redistributed (dashed violet curves in Figure 5c and d).

For *E. fuscoguttatus*, decreasing q_s by a factor of 10 dramatically reduces the positive effects of spawning reserves on SSBR, which become smaller than those of normal residence areas in the situation where pre-reserve fishing effort disappears (Scenario #5) (full and dashed black and full and dashed green curves vs. full violet curves in Figure 6c and d). The positive effects of spawning reserves on SSBR are also smaller than those of protecting a large fraction of normal residence areas (60%) in the situation where pre-reserve fishing effort is redistributed (Scenario #6) (full and dashed black and full and dashed green curves vs. dashed violet curve in Figure 6d). On the other hand, when q_s is reduced by a factor of

10, the negative effects of spawning reserves on YPR are decreased while those of normal residence reserves are increased (Figure 7c and d vs. Figure 7a and b). The negative effects of spawning reserves on YPR become smaller than those of normal residence reserves in the situation where pre-reserve fishing effort disappears (Figure 7c and d), and smaller than those of closing a large fraction of normal residence reserves in the situation where pre-reserve fishing effort is redistributed (Figure 7d).

Decreasing q_s by a factor of 10 diminishes the positive effects of protecting all FSA sites on the SR of the fished subpopulation of *E. fuscoguttatus* (Scenarios #3 and 4; full and dashed green curves in Figure 8c and d vs. Figure 8a and b). In contrast, decreasing q_s by a factor of 10 does not impact the SR of the fished subpopulation when a fraction of FSA sites or normal residence areas is

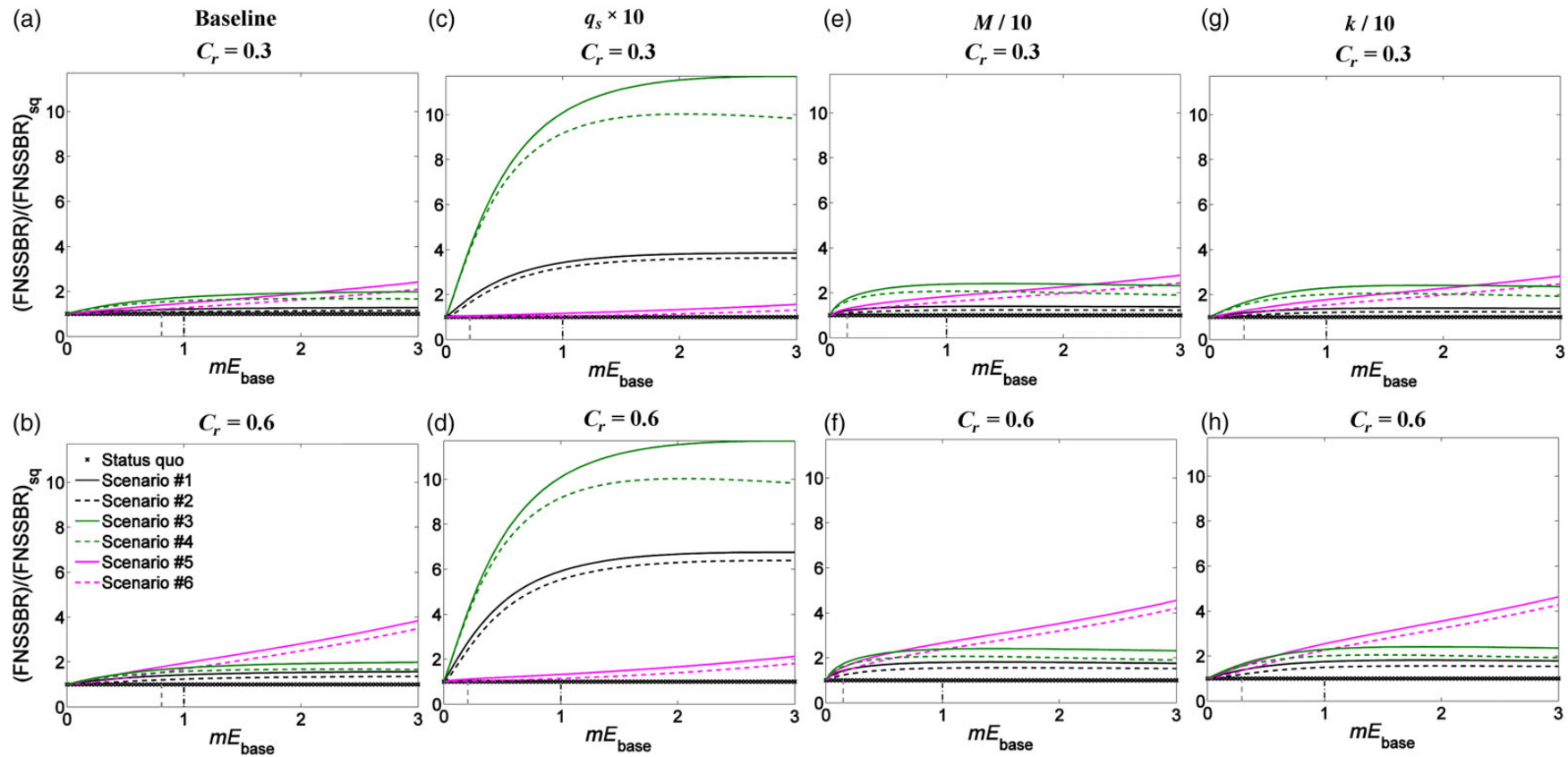


Figure 4. Marine reserve effects on the fraction of natural SSBR (FNSsBR, i.e. SSBR over natural SSBR) of *S. sutor* for the status quo and the six reserve scenarios (Table 1) under alternate assumptions. Ratio of FNSsBR to FNSsBR in the status quo situation ($(\text{FNSsBR})/(\text{FNSsBR})_{\text{sq}}$) for *S. sutor* as a function of multiplier of fishing effort (mE_{base}) for the status quo and the six reserve scenarios, in the baseline situation (a and b); when spawning-site catchability (q_s) is increased by a factor of 10 (c and d); when natural mortality, M , is decreased by a factor of 10 (e and f); and when instantaneous growth rate at small size, k , is decreased by a factor of 10 (g and h). For Scenarios #1 and 2, the fraction of spawning sites in reserves, C_r , is 30 and 60% for (a, c, e, g) and (b, d, f, h), respectively. All spawning sites are set aside as reserves for Scenarios #3 and 4. For Scenarios #5 and 6, the fraction of normal residence areas in reserves, C_r , is 30 and 60% for (a, c, e, g) and (b, d, f, h), respectively. For all panels, E_{base} is indicated by a vertical dashed-dotted black line, while E_{max} is indicated by a vertical dashed grey line.

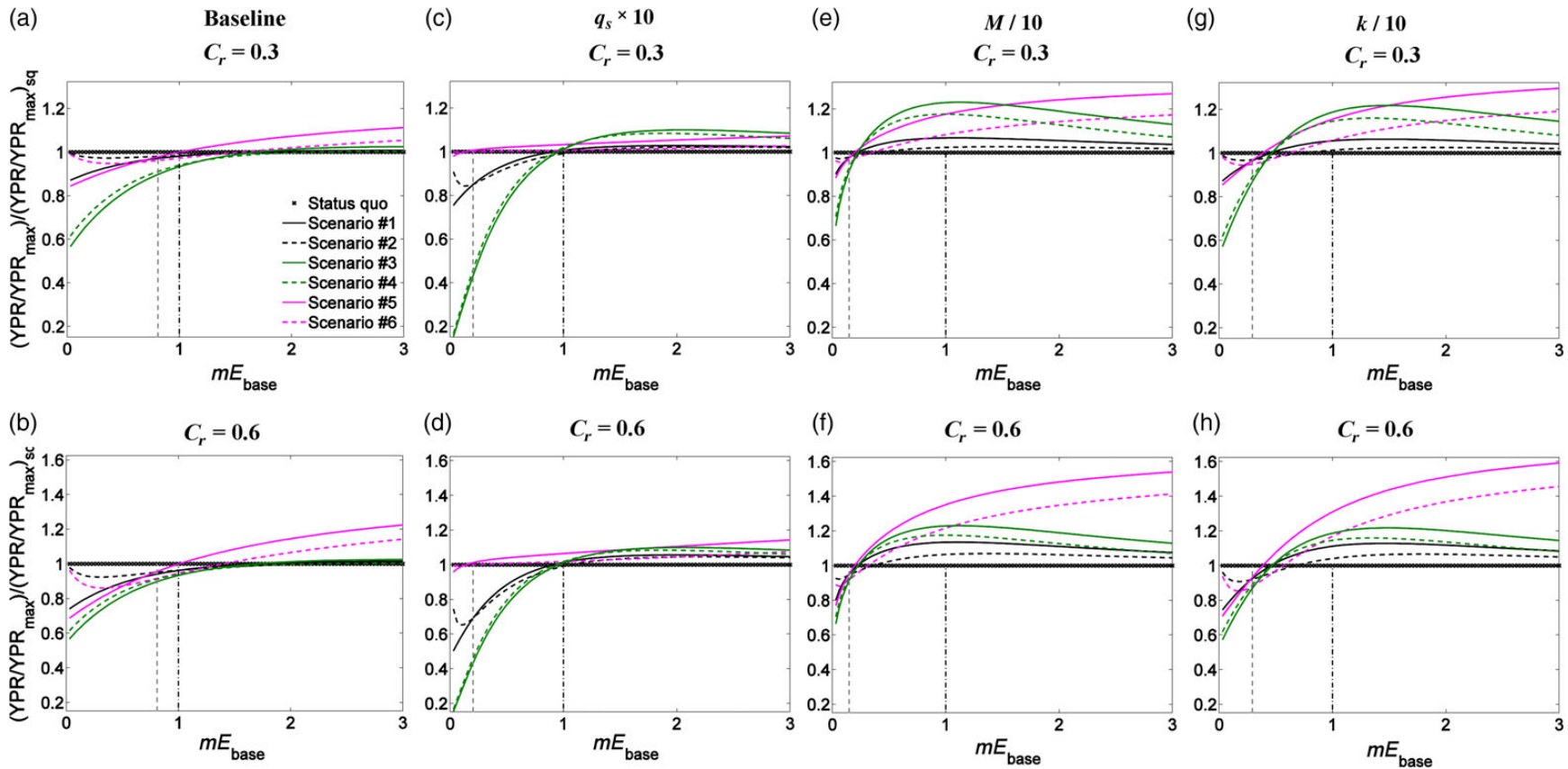


Figure 5. Marine reserve effects on the YPR normalized by maximum YPR in the absence of reserves (YPR/YPR_{\max}) of *S. sutor* for the status quo and the six reserve scenarios (Table 1), under alternate assumptions. Ratio of normalized YPR to normalized YPR in the status quo situation ($(YPR/YPR_{\max})/(YPR/YPR_{\max})_{sq}$) for *S. sutor* as a function of multiplier of fishing effort (mE_{base}) for the status quo and the six reserve scenarios, in the baseline situation (a and b); when spawning-site catchability (q_s) is increased by a factor of 10 (c and d); when natural mortality, M , is decreased by a factor of 10 (e and f); and when instantaneous growth rate at small size, k , is decreased by a factor of 10 (g and h). For Scenarios #1 and 2, the fraction of spawning sites in reserves, C_r , is 30 and 60% for (a, c, e, g) and (b, d, f, h), respectively. All spawning sites are set aside as reserves for Scenarios #3 and 4. For Scenarios #5 and 6, the fraction of normal residence areas in reserves, C_r , is 30 and 60% for (a, c, e, g) and (b, d, f, h), respectively. For all panels, E_{base} is indicated by a vertical dashed-dotted black line, while E_{\max} is indicated by a vertical dashed grey line.

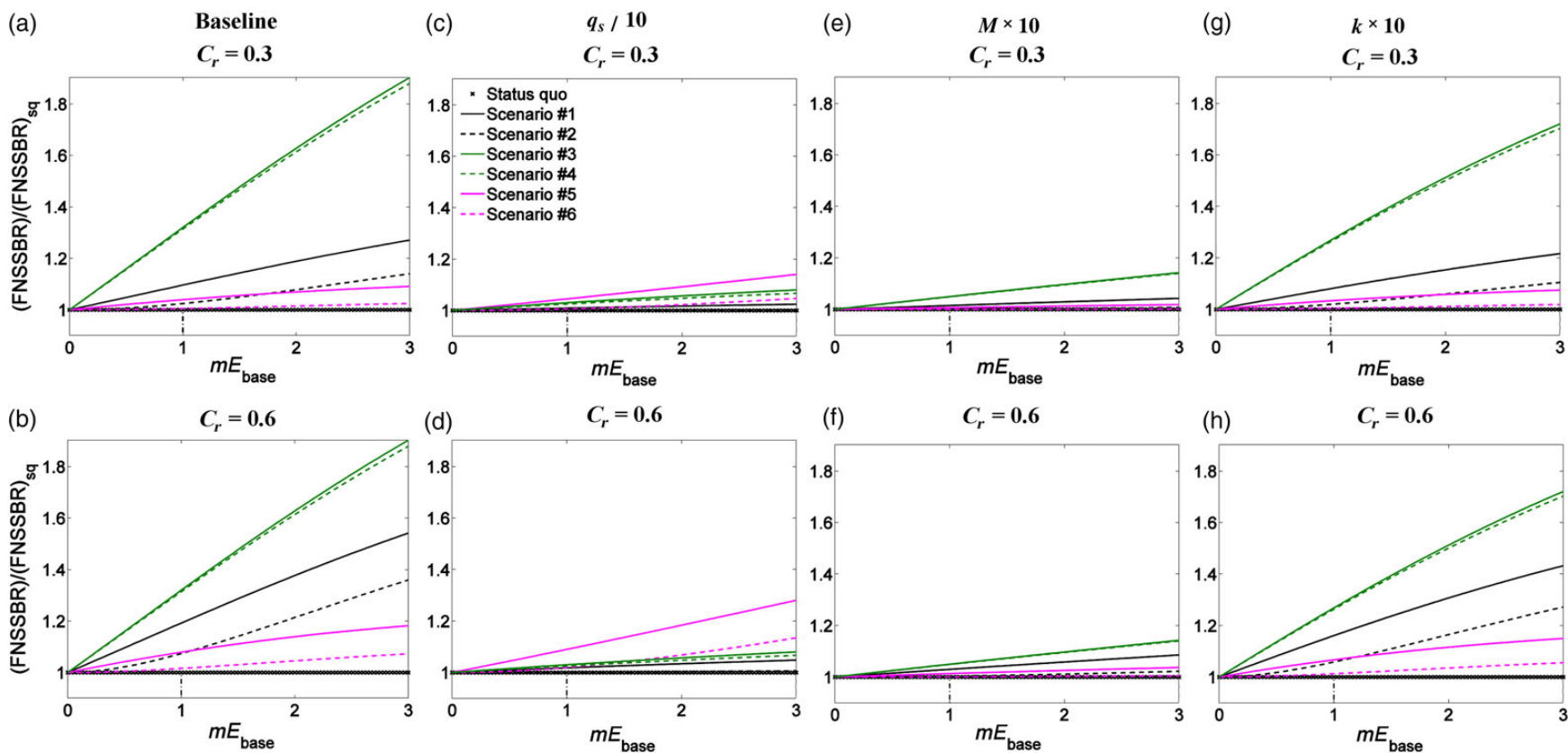


Figure 6. Marine reserve effects on the fraction of natural SSBR (FNSsBR, i.e. SSBR over natural SSBR) of *E. fuscoguttatus* for the status quo and the six reserve scenarios (Table 1) under alternate assumptions. Ratio of FNSsBR to FNSsBR in the status quo situation ($(\text{FNSsBR})/(\text{FNSsBR})_{\text{sq}}$) for *E. fuscoguttatus* for as a function of multiplier of fishing effort (mE_{base}) for the status quo and the six reserve scenarios, in the baseline situation (a and b); when spawning-site catchability (q_s) is decreased by a factor of 10 (c and d); when natural mortality, M , is increased by a factor of 10 (e and f); and when instantaneous growth rate at small size, k , is increased by a factor of 10 (g and h). For Scenarios #1 and 2, the fraction of spawning sites in reserves, C_r , is 30 and 60% for (a, c, e, g) and (b, d, f, h), respectively. All spawning sites are set aside as reserves for Scenarios #3 and 4. For Scenarios #5 and 6, the fraction of normal residence areas in reserves, C_r , is 30 and 60% for (a, c, e, g) and (b, d, f, h), respectively. For all panels, E_{base} is indicated by a vertical dashed-dotted black line.

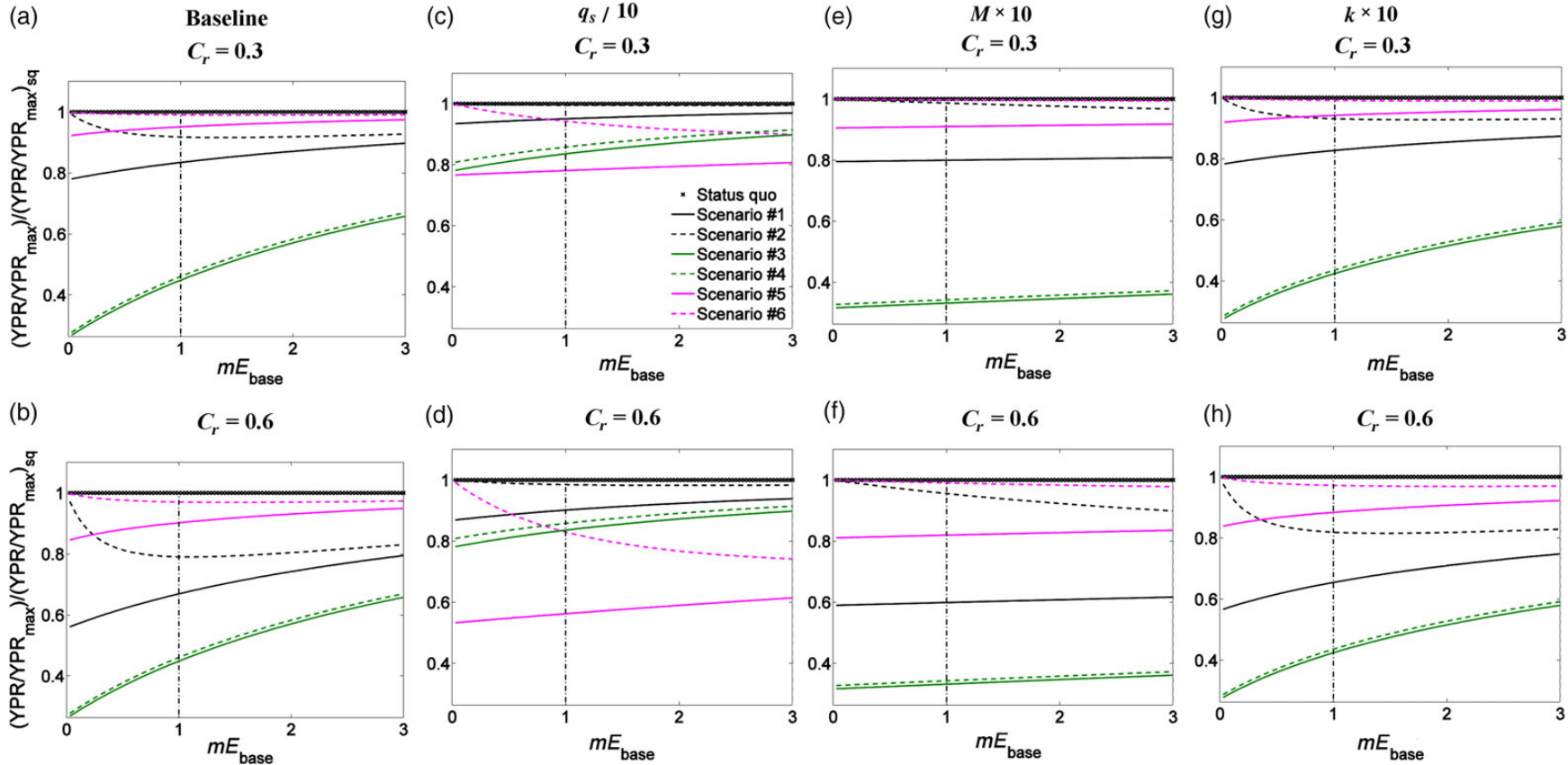


Figure 7. Marine reserve effects on the YPR normalized by maximum YPR in the absence of reserves (YPR/YPR_{max}) of *E. fuscoguttatus* for the status quo and the six reserve scenarios (Table 1), under alternate assumptions. Ratio of normalized YPR to normalized YPR in the status quo situation ($(YPR/YPR_{max})/(YPR/YPR_{max})_{sq}$) for *E. fuscoguttatus* as a function of multiplier of fishing effort (mE_{base}) for the status quo and the six reserve scenarios, in the baseline situation (a and b); when spawning-site catchability (q_s) is decreased by a factor of 10 (c and d); when natural mortality, M , is increased by a factor of 10 (e and f); and when instantaneous growth rate at small size, k , is increased by a factor of 10 (g and h). For Scenarios #1 and 2, the fraction of spawning sites in reserves, C_r , is 30 and 60% for (a, c, e, g) and (b, d, f, h), respectively. All spawning sites are set aside as reserves for Scenarios #3 and 4. For Scenarios #5 and 6, the fraction of normal residence areas in reserves, C_r , is 30 and 60% for (a, c, e, g) and (b, d, f, h), respectively. For all panels, E_{base} is indicated by a vertical dashed-dotted black line, whereas E_{max} is indicated by a vertical dashed grey line.

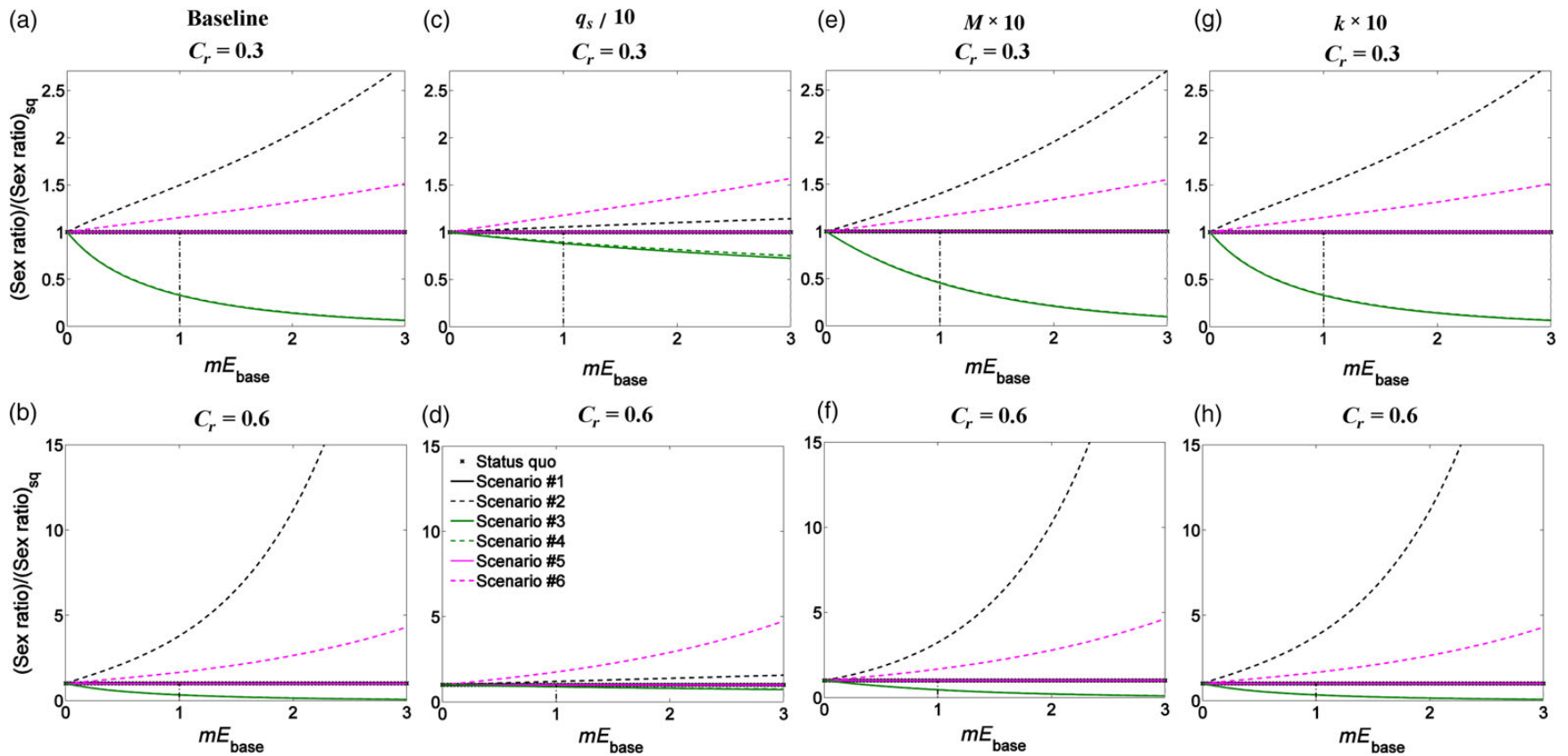


Figure 8. Ratio of female : male SR to female : male SR in the status quo situation ($\text{sex ratio}/(\text{sex ratio})_{\text{sq}}$) for the fished subpopulation of *E. fuscoguttatus* as a function of multiplier of fishing effort (mE_{base}) for the status quo and the six reserve scenarios, in the baseline situation (a and b); when spawning-site catchability (q_s) is decreased by a factor of 10 (c and d); when natural mortality, M , is increased by a factor of 10 (e and f); and when instantaneous growth rate at small size, k , is increased by a factor of 10 (g and h). For Scenarios #1 and 2, the fraction of spawning sites in reserves, C_r , is 30 and 60% for (a, c, e, g) and (b, d, f, h), respectively. All spawning sites are set aside as reserves for Scenarios #3 and 4. For Scenarios #5 and 6, the fraction of normal residence areas in reserves, C_r , is 30 and 60% for (a, c, e, g) and (b, d, f, h), respectively. For all panels, E_{base} is indicated by a vertical dashed-dotted black line. Note that curves for Scenarios #1 and #5 overlap in all panels.

protected while pre-reserve fishing effort disappears (Scenarios #1 and 5; full black and full violet curves in Figure 8c and d vs. Figure 8a and b) and reduces the negative effects of protecting a fraction of FSA sites or normal residence areas in the fishing effort redistribution situation (Scenarios #2 and 6; dashed black and dashed violet curves in Figure 8c and d vs. Figure 8a and b). Moreover, when q_s is decreased by a factor of 10, the SR of the protected subpopulation of *E. fuscoguttatus* is closer to the SR under the status quo when a fraction of FSA sites is set aside as reserves than when a fraction of normal residence areas is protected (Supplementary Figure SA5b). All these results suggest that both spawning reserves and normal residence reserves have limited effects on the overall production of fertilized eggs when q_s is reduced by a factor of 10.

Impacts of life history traits on reserve effects

For *S. sutor*, decreasing natural mortality rate, M , or instantaneous growth rate at small size, k , by a factor of 10 increases the positive effects of both spawning reserves and normal residence reserves on SSBR (Figure 4e–h vs. Figure 4a and b). Assuming a slower life history for *S. sutor* also enhances the fisheries benefits of normal residence areas and results in increases of YPR with spawning reserves at fishing effort levels much greater than E_{\max} (Figure 5e–h vs. Figure 5a and b). Both the SSBR and YPR of *S. sutor* can increase with marine reserves when M or k is decreased by a factor of 10 because *S. sutor* is severely overexploited under the status quo in this situation, while the species is fully exploited under the status quo in the baseline situation (Figure 5g and h vs. Figure 5a and b). Therefore, implementing marine reserves reduce fishing mortality rates so that annual fishing mortality is moved to the left of the YPR curve and higher YPR levels can be obtained (results not shown here).

For *E. fuscoguttatus*, increasing M or k by a factor of 10 diminishes the positive effects of both spawning reserves and normal residence reserves on SSBR (Figure 6e–h vs. Figure 6a and b). Moreover, assuming a more rapid life history for *E. fuscoguttatus* increases the negative effects of spawning reserves on YPR, but has virtually no impact on the fisheries effects of normal residence reserves (Figure 7e–h vs. Figure 7a and b). Reductions of the positive effects of spawning reserves and normal residence reserves on SSBR and enhancement of the negative effects of spawning reserves on YPR are more pronounced when M is increased than when k is increased (Figure 6e and f vs. Figure 6g and h and Figure 7e and f vs. Figure 7g and h).

Increasing M or k by a factor of 10 does not impact on the effects of marine reserves on the SR of the fished subpopulation of *E. fuscoguttatus* (Figure 8e–h vs. Figure 8a and b). The SR of the protected subpopulation of *E. fuscoguttatus* remains closer to the SR under the status quo when a fraction of normal residence areas is set aside as reserves than when a fraction of FSA sites is protected (Supplementary Figure SA5c and d).

Discussion

This study applied a simple per-recruit model to determine whether spawning reserves or normal residence reserves achieve long-term conservation benefits (i.e. improve SSBR and reduce bias in female : male SR) and fisheries benefits (i.e. enhance YPR) for two aggregation-forming populations from Seychelles. Selection of the two populations enabled contrasts of life history traits and sexual modes, as well as differing spawning-site catchability and current

exploitation levels. Our results and recommendations differ markedly for these two populations.

Effectiveness of spawning reserves vs. normal residence reserves for *S. sutor*

For the *S. sutor* population of the main granitic islands, our goal was to determine the relative benefits of spawning reserves and normal residence reserves in terms of both SSBR and YPR. Overall, our results suggest that normal residence reserves are more effective in providing both conservation and fisheries benefits for this species. In Seychelles and Kenya, many marine reserves are already established in normal residence areas of *S. sutor* (Graham *et al.*, 2007; McClanahan *et al.*, 2007), and may therefore contribute to the observed resilience of this species at high fishing effort levels (McClanahan and Hicks, 2011; Robinson *et al.*, 2011).

Nevertheless, the potential benefits of normal residence reserves for the *S. sutor* population need to be considered in light of total annual fishing effort, the potential for fishing effort displacement after reserve creation, and the fraction of habitat that can be protected without adverse socio-economic impacts. Fishing effort evolution after reserve implementation is difficult to predict (Fulton *et al.*, 2010), yet increase in total annual fishing effort is likely given the growing pressure on coral reef resources (FAO, 2012; Worm and Branch, 2012). Consequently, assessing the effectiveness of normal residence reserves for *S. sutor* under the assumption of full fishing effort redistribution and/or increase in annual fishing effort is a conservative approach. Given that normal residence areas are much larger than FSA sites, protecting a large fraction of normal residence reserves would likely impose a significant socio-economic burden (McClanahan *et al.*, 2005). Moreover, contrary to FSA sites for *S. sutor*, the normal residence areas of the species typically support multispecies fisheries. Therefore, the benefits accruing to *S. sutor* from the implementation of normal residence reserves, even if a moderate fraction of normal residence areas (e.g. 30%) was protected, would need to be weighed against socio-economic impacts resulting from loss of access to other resources in these areas.

As expected, the benefits of normal residence reserves are greater if *S. sutor* is overexploited (e.g. Polacheck, 1990; Hart, 2006; Le Quesne and Codling, 2009). Stock assessments suggest that *S. sutor* is fully exploited in the main granitic islands at present (Robinson *et al.*, 2011; Grüss *et al.*, 2013). If the current annual fishing effort of the *S. sutor* population remained unchanged, protecting 30% of normal residence areas would improve SSBR but slightly decrease YPR, assuming that the fishing effort formerly in reserves is fully redistributed to non-protected normal residence areas. In contrast, if the annual fishing effort currently exerted on *S. sutor* was doubled and the species became overexploited, protecting normal residence areas would constitute a viable management response, since both SSBR and YPR would be increased at this level of fishing effort. Under the more realistic scenario of protecting a moderate fraction (30%) of normal residence areas, increases of YPR would still occur but would be limited if the fishing effort previously in reserves is entirely redistributed to non-protected normal residence areas. If a larger fraction (60%) of normal residence areas was protected, increases of YPR would be more pronounced, though still relatively moderate, even if pre-reserve fishing effort is redistributed to non-protected normal residence areas.

Our sensitivity analyses confirmed that *S. sutor*, which is a short-lived and fast-growing species, derives fewer conservation benefits

and experiences greater decreases in YPR from spawning reserves than long-lived and slow-growing species (Gaylord *et al.*, 2005; Chan *et al.*, 2012; Grüss *et al.*, 2013). The same finding holds with normal residence reserves. However, the fact that normal residence reserves are more beneficial than spawning reserves for the conservation and exploitation of *S. sutor* essentially relates to the change in catchability occurring with FSA formation. If the change in catchability of the FSAs of *S. sutor* was much greater (e.g. 100-fold greater), spawning reserves would be more beneficial for the conservation of *S. sutor*, though still undesirable from a fisheries perspective. Given that the catchability of *S. sutor* at FSA sites is only 10 times greater than its catchability in normal residence areas, fishing mortality is higher in the latter areas in the absence of reserves (0.83 year⁻¹ vs. 0.94 year⁻¹). Therefore, implementing normal residence reserves, which target juveniles and non-spawning adults, results in a significant increase in the number of individuals surviving to sexual maturity, leading to an increase in the SSB and exploitable biomass of *S. sutor*.

Effectiveness of spawning reserves vs. normal residence reserves for *E. fuscoguttatus*

For the *E. fuscoguttatus* population of Farquhar Atoll, our primary goal was to determine the most effective spatial management strategy for normalizing female : male SR. Unsurprisingly, we found that spawning reserves are more effective than normal residence reserves in reducing bias in the female : male SR of *E. fuscoguttatus* and, potentially, improving the overall production of fertilized eggs of the species. For the same reasons as those highlighted for *S. sutor*, we argue for a conservative approach in assuming full fishing effort redistribution and/or increase in annual fishing effort in evaluating the effectiveness of spawning reserves for *E. fuscoguttatus*.

The protection of all FSA sites is the most beneficial spatial management strategy for *E. fuscoguttatus* in terms of both female : male SR and SSB, but results in substantial decreases in YPR. Protecting only a fraction of FSA sites would lead to smaller declines in YPR at the expense of reduced conservation benefits. However, if trade-offs between conservation and exploitation were considered and, therefore, only a fraction of spawning sites was set aside as reserves, this fraction would still have to be large to compensate for an increase in the SR of the fished subpopulation due to fishing effort displacement.

Epinephelus fuscoguttatus is probably underexploited at Farquhar Atoll at present (Grüss *et al.*, 2013; J. Robinson, personal observation). If the current annual fishing effort of the *E. fuscoguttatus* population remained unchanged, protecting a large fraction of FSA sites would produce limited conservation benefits but lead to an ~20% reduction in YPR over the status quo situation, assuming that the fishing effort formerly in reserves is fully redistributed to non-protected spawning sites. Protecting all FSA sites would produce significant conservation benefits at the expense of an ~55% reduction in YPR over the status quo situation, assuming that pre-reserve fishing effort is fully redistributed to normal residence areas. If spawning reserves were implemented, doubling the annual fishing effort currently exerted on *E. fuscoguttatus* would be better both for conservation and exploitation. In that case, the conservation benefits of protecting a fraction or all of FSA sites would be dramatically improved. Moreover, YPR would be reduced by, respectively, ~20 and ~43% over the status quo situation, assuming full fishing effort redistribution.

It is important to note that our per-recruit model, which was developed for the data-poor contexts of many reef fish spawning

aggregation fisheries (Johannes, 1998; Sadovy and Domeier, 2005), is likely to underestimate the benefits of spawning reserves for fisheries yields. Since a stock–recruitment relationship is absent in per-recruit models, the effects of spawning area closures on recruitment cannot be quantified (Guénette and Pitcher, 1999; Botsford *et al.*, 2009). While increases in YPR for *E. fuscoguttatus* were not achieved through spawning reserves in our model, increases in fisheries yields may occur through recruitment subsidy if the study population was recruitment limited in the absence of reserves and increases in SSB compensate for lost opportunities caused by the area closures (Guénette and Pitcher, 1999; Hart, 2006; Botsford *et al.*, 2009). Future studies could consider combining hypothetical stock–recruitment relationships with the per-recruit quantities of our model to fully assess the potential fisheries effects of spawning reserves vs. normal residence reserves for *E. fuscoguttatus* (Grüss *et al.*, 2014).

While partly explained by the slow life history of the species, the positive effects of spawning reserves on the SSB and female : male SR of *E. fuscoguttatus* and their negative fisheries effects mainly relate to the change in catchability occurring with FSA formation. If the change in catchability associated with aggregation formation in *E. fuscoguttatus* was much lower (e.g. 14-fold greater, i.e. close to that for *S. sutor*), normal residence reserves would be more effective than spawning reserves at improving SSB. Assuming a 14-fold change in catchability, the fishing mortality of non-spawning females in the absence of reserves would become much greater than that of spawning individuals. This result concurs with Heppell *et al.* (2006), who found that protecting all the FSA sites of gag grouper has a smaller effect on population growth than normal residence reserves, since the fishing mortality of gag grouper females is higher in normal residence areas than at spawning sites. A much lower catchability at FSA sites would also enhance the negative fisheries effects of normal residence reserves and diminish those of spawning reserves. Finally, if the change in catchability of *E. fuscoguttatus* occurring with FSA formation was much lower, both spawning reserves and normal residence areas would have limited effects on female : male SR and the overall production of fertilized eggs. However, in such a situation, normalizing female : male SR would be a lower priority since critical SRs are reached at much higher fishing effort levels (Supplementary Figure SA5b) due to the reduced catchability of males at FSA sites.

Our per-recruit model, like any other model, is a simplified representation of a much more complex system. Simplifications that may impact on our results for *E. fuscoguttatus* include the representation of the sex change process and the relationship between SR and egg fertilization rates. While our model assumes that sex change occurs at a fixed age, sex change may in fact be controlled exogenously and triggered by cues such as local SR, population density, and individual fish body sizes in a social group (e.g. Shapiro, 1989; Pears *et al.*, 2006; Koenig and Coleman, 2013). As discussed in Grüss *et al.* (2013), the existence of exogenous factors controlling sex change may reduce the need for spawning reserves. However, assuming that sex change is mediated by age is a conservative approach and allowed our model to predict the maximum possible increases in female : male SRs. Moreover, the lack of a functional relationship between female : male SR and egg fertilization rates in our model may have impacted on our findings. A few arbitrary relationships between SR and egg fertilization rates have been formulated in the modelling literature (e.g. Hunstman and Schaaf, 1994; Alonzo and Mangel, 2004; Heppell *et al.*, 2006). To further evaluate the effectiveness of spawning reserves for *E. fuscoguttatus*, future studies could

consider combining alternative forms of this relationship, as well as alternative relationships between the production of fertilized eggs and recruitment, with the per-recruit quantities of our model (Grüss *et al.*, 2014).

Concluding remarks

Our study confirmed that there is no “one size fits all” for managing reef fish populations forming transient spawning aggregations (Sadovy and Domeier, 2005). We demonstrated that, depending on life history, sexual mode, exploitation level and spawning-site catchability, spawning reserves may not always be the most appropriate tool for the conservation and exploitation of aggregation-forming populations, and that other management measures should be considered before deciding to implement these closures. Such measures include normal residence reserves and gear measures that increase selectivity for larger fish (Rhodes and Warren-Rhodes, 2005; Russell *et al.*, 2012). It is already established that populations possessing life history traits conferring low vulnerability to fishing, such as short life and rapid growth, are more resilient to FSA fishing and may derive few benefits from spawning reserves (Robinson *et al.*, 2011; Chan *et al.*, 2012). Our study also showed that benefits of spawning reserves essentially relate to the change in catchability occurring with aggregation formation. Moreover, our results, particularly those relating to scenarios of full fishing effort redistribution, highlight that any type of marine reserves is unlikely to be effective in isolation and must be complemented by other measures controlling fishing effort or fishing gear efficiency (Kaiser, 2005; Nemeth, 2005; Russell *et al.*, 2012; Grüss *et al.*, 2014).

Supplementary data

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

Acknowledgements

We are very grateful to David Kaplan for his significant contribution to an earlier version of the model. We wish to thank very much two anonymous reviewers for constructive comments on the manuscript, which dramatically improved its scope and quality. AG was supported by the AMPED project (www.amped.ird.fr) through a grant from the French National Research Agency (ANR), Systerra Program, Grant Number ANR-08-STRA-0. JR was supported by a grant from the Marine Science for Management (MASMA) programme of the Western Indian Ocean Marine Science Association (WIOMSA).

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Handling editor: Francis Juanes