Gag grouper, marine reserves, and density-dependent sex change in the Gulf of Mexico

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ABSTRACT

The use of marine reserves for fishery management remains a controversial tool despite evidence of their success. In the Gulf of Mexico (GOM), two marine reserves were put in place in order to protect spawning aggregations of gag grouper, which has experienced a steep decline in the male to female sex ratio since the 1970s. Reserve success is ultimately a function of the total amount of spawning aggregations protected, and fisher response to reserve implementation may have significant influence on the ultimate effectiveness of the reserves. We modeled the GOM gag grouper population under a range of potential reserve sizes and fisher responses. In general, larger reserves resulted in higher adult populations and sex ratio. Fisher response to reserves also had a large impact on reserve success. When we included density-dependent sex change in the model, the results showed a reduction in the sex ratio under high fishing pressure when compared to model simulations when sex change was fixed. While our model suggests that the reserves currently in place should result in a small increase in adult sex ratio given the current level of fishing mortality, such benefits might not be achieved in practice given possible future changes in transition rates or fisher behavior.

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1. Introduction

Marine reserves are increasingly used as a tool for managing marine resources, protecting habitat, and conserving biodiversity (Coleman et al., 2004). Evidence from existing marine reserves indicates that reserves can produce rapid positive changes in the biomass and density of fish within them (Halpern and Warner, 2002; Russ et al., 2008) and when properly designed can be an effective tool for promoting recovery of fish stocks and protecting them from overharvest (Claudet et al., 2008; Gerber et al., 2003). These benefits are especially prevalent in older reserves (Edgar et al., 2009; Molloy et al., 2009; Stobart et al., 2009), which are expected to contain more older, larger individuals and also contribute larvae to surrounding areas (Bohnsack and Ault, 1996). Marine reserves nevertheless remain a controversial issue for marine-resource management (Hilborn et al., 2004; Norse et al., 2003), as not all of their anticipated benefits necessarily accrue (Halpern et al., 2004; Hart, 2006).

In the northeast Gulf of Mexico (GOM), the Gulf of Mexico Fishery Management Council (Gulf Council) implemented two experimental marine reserves in 1999 designed to protect offshore spawning aggregations of gag grouper (Fig. 1; GMFMC, 1999). Marine reserves were identified by the Gulf Council as beneficial to management in this case because of the particular life history and behavioral patterns of gag (GMFMC, 1999; Koenig et al., 2000). Gag grouper (*Mycteroperca microlepis*) is a large, long-lived protogynous serranid that experiences a number of ontogenetic habitat shifts during its life: larval gag settle to coastal sea-grass habitat in the spring, where they remain until fall, when they move to nearshore hard-bottom reefs (Koenig and Coleman, 1998). Juvenile gag remain on these nearshore reefs until maturity, when they begin annual spawning migrations to deepwater reefs on the West Florida Shelf (Coleman et al., 1996). Spawning occurs when adult fish create large mixed-sex aggregations on the shelf-edge from December to May, with peak activity during February and March (Domeier and Colin, 1997; Hood and Schlieder, 1992). After spawning, female gag return to the nearshore reefs, whereas males remain offshore (Coleman et al., 1996). This pattern of life-stage separation, migration, and aggregation is well known and exploited by fishers, who fish gag heavily at both nearshore and spawning sites. The most recent stock assessment, completed in 2007 and updated in 2009, determined that the gag population was overfished and undergoing overfishing (SEDAR, 2007, 2009). Perhaps more importantly, the adult gag population has undergone a shift in the adult sex ratio over the last three decades from approximately 20% male in the 1970s to less than 5% male by 2004 (SEDAR, 2006), presumably because of preferential harvest of larger individuals more likely to be male (Coleman et al., 1996; McGovern

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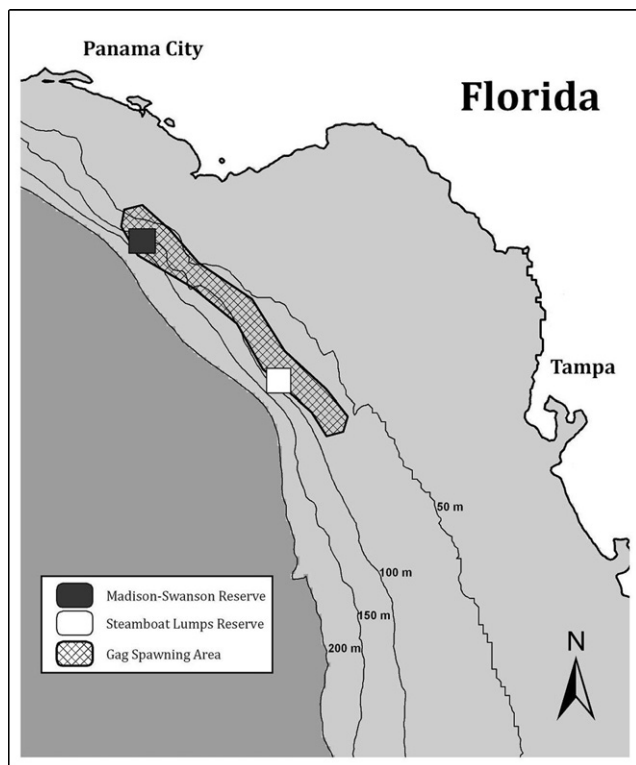E-mail address: rdellis@bio.fsu.edu (R.D. Ellis).

Fig. 1. Map of the northeastern Gulf of Mexico showing the main gag grouper spawning area (as identified by Coleman et al., 1996) and the approximate locations of the two gag-specific marine reserves.

et al., 1998). As a result of this observed decline, the gag population might experience sperm limitation and reproductive failure leading to reduced recruitment and continuing population decline (Armsworth, 2001; Bannerot et al., 1987; Beets and Friedlander, 1992; Huntsman and Schaaf, 1994). The importance of including sex change into stock assessment models has been recognized, if not implemented (Alonzo et al., 2008; Brooks et al., 2008), and the importance of sex change in gag was explicitly recognized by the Gulf Council in their decision to utilize spatial closures in the management of the fishery (GMFMC, 1999). Specifically, implementation of the reserves was done to reduce the fishing mortality of older individuals in part to stop the decline in sex ratio observed in the adult gag population and prevent future sperm limitation.

Changes to population structure like the decline in adult sex ratio experienced by gag can have long-term implications for stock health and fishery production. Empirical observations (Molloy et al., 2008) and modeling analyses of harvest strategies for protogynous fishes both support the hypothesis that reducing the fishing mortality of older fish by means of spawning-area reserves can increase the adult sex ratio in a protogynous fish population (Alonzo and Mangel, 2004; Heppell et al., 2006). However, previous studies ignored two potential problems in the case of protogynous fishes: (1) the redistribution of fishing effort after an area closure and (2) possible density-dependent changes in the rate of sex change in adult females.

Following the closure of fishing grounds, changes in allocation of fishing effort and the behavior of fishers can actually lead to an increase in total fishing mortality. For example, the "spillover" effect, which occurs when the density of fish inside a reserve increases to the point where fish preferentially leave the reserve and become vulnerable to harvest, is often a promised benefit of marine reserves and has resulted in the common tactic of "fishing the line" (Kellner et al., 2008). A recent study by Smith et al. (2008) revealed that the actual fisher response to a seasonal

closure for grouper increased the total number of fishing days by 5%. Stevenson et al. (2011) found that established fishers increased effort following implementation of marine reserves on the west coast of Hawaii. These results suggest that the assumption that fishing mortality will decline following spatial closures is not necessarily borne out. Even if total fishing effort remains constant, the reallocation of effort may effectively nullify any benefits from the spatial closure if fishers shift their effort to target more vulnerable individuals. Models evaluating management options should consider multiple scenarios for fishing effort changes after management action to account for a range of possible responses to spatial closures.

In gag, the specific mechanism that controls sex change in gag is as yet unidentified. The two main hypotheses for the controlling mechanism of sex change in gag are social cues and size-related cues. Previous analyses have suggested that heavy fishing on spawning aggregations could result in high size-selective mortality and the disruption of social structure, both of which would decrease the proportion of males in a population of protogynous fish (Shapiro, 1987). For gag, the Gulf Council concluded that marine reserves were the preferred management strategy for addressing both issues (GMFMC, 1999), but previous analyses have not considered how density-dependent social processes might affect the rate of sex change in the gag population. The model for socially induced sex change is essentially a density-dependent process: females change sex on the basis of the rate at which they encounter males, which is a function of the adult sex ratio (Ross, 1990). As the number of males in the population declines, the number of males a given female encounters goes down and so the rate at which females change sex should increase. Because the management actions put in place by the Gulf Council are intended to increase the proportion of males in the population, success would result in more males and a corresponding shift in the rate of sex change. Models evaluating management actions that may increase the male proportion of the population should take into account possible changes in the rate of sex change.

In order to evaluate the marine reserves put in place by the Gulf Council in light of effort redistribution and density-dependent sex change, we developed an age- and stage-structured model of the gag grouper population to test a range of marine-reserve options. We were primarily motivated by the question: if a stated goal of a marine reserve is to have a population level effect on adult sex ratio, how much spawning area must be protected in order to observe a population level response? Our model allows for changes in fishing effort after reserve implementation, both in terms of total effort and redistribution following area closures. We also include a density-dependent sex-change process to account for possible changes in the rate of sex-change on population size and sex ratio resulting from management actions. Although a system of marine reserves that provides full protection for gag grouper spawning aggregation sites is unlikely to be implemented and fishers' behavioral responses to closures are uncertain, our model permits comparison of population level responses to different management actions.

Throughout the paper, we use the term "sex ratio" to mean the ratio in numbers of adult males to adult females (expressed as a percentage for discussion in the text), and "marine reserves" to refer specifically to year-round spawning-area closures as a percentage of the total known spawning area.

2. Methods

2.1. Model description

We developed our model on the basis of the age-structured population model described by Heppell et al. (2006), which predicts the sex ratio, adult population size, and fishery yield as

Table 1
Parameters used in the model.

Parameter	Description	Source	Value
Linf	von Bertalanffy growth curve asymptote	SEDAR (2006)	1310 mm
k	von Bertalanffy growth curve slope	SEDAR (2006)	−0.14
t_0	von Bertalanffy growth curve x-intercept	SEDAR (2006)	−0.37
wa	Length–weight conversion intercept	SEDAR (2006)	1×10^{-8}
wb	Length–weight conversion slope	SEDAR (2006)	2.99
Θ	Fertilization parameter	SEDAR (2006)	50
Φ	Recruitment maximum	Heppell et al. (2006)	1×10^{7}
Rv	Recruitment variability	Fit to age 1 abundance from SEDAR (2006)	0.46
S_E	Egg survivorship	Fit to baseline stochastic growth rate	3.3×10^{-5}
S_L	Larval survivorship	Koenig and Coleman (1998)	0.3
ma	Lorenzen curve multiplier	Scaled to age	0.4298
mb	Lorenzen curve power	Scaled to age	0.488
FL	Young of the year fishing mortality	SEDAR (2006)	0.0
FJ	Juvenile fishing mortality	SEDAR (2006)	0.4
FF	Female fishing mortality	SEDAR (2006)	0.4
FM	Male fishing mortality	SEDAR (2006)	0.33
r	Slope of maturation probability	Fit to SEDAR (2006) proportions at age	8.41
q	Intercept of maturation probability	Fit to SEDAR (2006) proportions at age	2.946
y	Slope of transition probability	Fit to SEDAR (2006) proportions at age	0.0597
z	Intercept of transition probability	Fit to SEDAR (2006) proportions at age	5.745

functions of stage-specific fishing mortality. The model population follows the stage classifications described by McGovern et al. (1998), which represent the ontogenetic and seasonal habitat shifts experienced by gag. Parameters describing growth, mortality, fertilization, fecundity, and transition probabilities (maturation and sex change) were based on information available from the most recent stock assessment of gag (Table 1; SEDAR, 2007). Fitting of model parameters to stock assessment data was performed with SAS software, Version 9.1.3.

The stages followed by the model population are age 1 or young-of-the-year (YOY), juvenile (age 2 to sexual maturity), female (post-maturity to sex change), and male (post-sex change). The YOY stage represents the number of recruits from the previous year that survived to settlement. All surviving YOY fish transition to the juvenile stage after one time step. Juveniles and females follow stage-specific transition probabilities to determine the number of individuals that mature or change sex to the next stage each time step. Age ranges for the juvenile, female, and male stages are left flexible, except for a minimum age bound (2 years) for the juvenile stage and a minimum age bound (6 years) for the male stage.

Each stage was assigned a different mortality rate, which represents changes in habitat use, behavioral characteristics, and fishing selectivity. Natural mortality was age specific and followed the Lorenzen curve used by the most recent gag stock assessment, where the natural mortality rate declined with age (Lorenzen, 1996; SEDAR, 2006). Natural mortality M was calculated for each stage j and age i with Eq. (1), where ma and mb are scaling and exponent parameters, respectively (see Table 1 for parameter values):

$$M_{j,i} = (ma)(i^{mb}) \tag{1}$$

Weighted averages of the observed proportions at age from catch data were used to convert age-specific natural and fishing mortality rates to stage-specific values. Stage-specific fishing mortality was reported as an instantaneous rate (Table 1: FL, FJ, FF and FM). Fishing mortality was later altered by the variable *fmult* to represent changes in fishing-effort regime that changed the total fishing mortality for the population. Total mortality was calculated by age as the sum of the age-specific natural and stage-specific fishing mortality rates. Mortality was assumed to be equally distributed over time and was calculated once per time step. Age-specific annual survival A for stage j and age i was calculated with Eq. (2):

$$A_{j,i} = \exp(-M_{j,i} - F_{j,i} fmult) \tag{2}$$

Because the real gag population is heavily fished, we were interested in the impacts of different options on fishery yield Y, calculated by weight (Eq. (3)), where $N_{j,i}$ is the number at stage j, age i, and $W_{j,i}$ is the weight at age i, stage j, determined by a von Bertalanffy growth equation (Eq. (4)) and the length–weight relationship used in the stock assessment (Eq. (5); SEDAR, 2006):

$$Y = \sum_{j,i} W_{j,i} \left\{ (F_{j,i})(fmult) \left[\frac{N_{j,i}(1 - A_{j,i})}{(M_{j,i} + (F_{j,i})(fmult))} \right] \right\} \tag{3}$$

$$L_i = L_{\text{inf}}(1 - \exp^{(-k(i + t_0))}) \tag{4}$$

$$W_{j,i} = (wa)(Li^{wb}) \tag{5}$$

The probabilities of maturation, P(mat), and sex change, P(sex), were modeled as functions of age i. Maturation (the transition from the juvenile stage to the mature female stage) was restricted to ages 2 through 5; all fish age 6 and older were assumed to be sexually mature. Age 6 was also the minimum age for sex change; all mature fish age 6 and younger were female. The parameter values for the maturation (Eq. (6)) and sex change (Eq. (7)) probability functions were estimated by fitting of the observed proportions at age from the stock assessment according to the method described by Heppell et al. (2006). This method derives a stable age distribution on the assumption of constant recruitment and then calculates the transition rates to fit the model distribution using least-squares analysis of the model proportions for each age class (Excel Solver, Microsoft Office 2007, Microsoft, Richmond, Washington, USA).

$$P(\text{mat})_i = \frac{1}{1 + \exp(-r - q * i)} \tag{6}$$

$$P(\text{sex})_i = 1 - \exp[-y(i - z)] \tag{7}$$

Maturation and transition probabilities were held constant for the duration of model simulations, except for simulations that included density-dependent sex change. For those simulations, the sex-change-transition probability function was modified to be a function of the sex ratio from the previous time step ($t - 1$). If the real gag population experiences density-dependent sex change, we assumed that both parameters would change: the magnitude of the probability of sex change for a given age would change according to y, and the age when fish start to change sex would change according to z. For the parameter y, we assumed a negative relationship with respect to male density: as the proportion of males in the population increases, the probability that an individual of a given age will change sex decreases. This assumption is executed by making

y inversely proportional to male density (Eq. (8)). It also means that the density effect is greatest when the percentage of males is small. Male density is represented in Eq. (8) by the variable p, a measure of the percentage of males in the population calculated at the end of each time step ($t − 1$). We calculated the value of the constant c by multiplying the fixed value of y by the value p_0, male density calculated by the status quo simulation.

$$y = \frac{c}{p_{t-1}} \tag{8}$$

To calculate the z parameter (x-intercept of the sex-change-transition probability function), we assumed that the age at first sex change increased with increasing male density. We assumed a positive nonlinear relationship with a minimum boundary representing a theorized physiological limit for successful sex change (Eq. (9); where z_{min} and d are constants derived from Eq. (8) with p_0 and the fixed value z). This minimum size threshold is reflected in the population data; no males less than 800 mm (or about 6 years of age) are found in the catch (SEDAR, 2006):

$$z = z_{min} + d(p_{t-1}^{0.5}) \tag{9}$$

Combining the transformations of y and z gives the full function used to calculate the density-dependent probability of sex change for age i:

$$P(\text{sex})_i = 1 - \exp\left[-\left(\frac{c}{p_{t-1}}\right)(i - (z_{min} + d(p_{t-1}^{0.5})))\right] \tag{10}$$

Fertilization success was defined as the proportion of eggs successfully fertilized and was modeled as a function of the fertilization parameter (Θ) and the proportion of males in the population (p). Data reported by Fitzhugh et al. (2006) show that approximately 10% of females fail to spawn when the sex ratio falls below 5% male. Therefore, we fixed the parameter value for Θ so that the fertilization success function (Eq. (11)) followed this pattern. In effect, we assumed that a male-limited population would result in reduced reproductive success in some portion of the female population and that the percentage of females that failed to spawn would increase as the proportion of males in the population declined. This function returns a smooth function of the percent of females that successfully spawn given the sex ratio for a given time step. Whereas Heppell et al. (2006) arbitrarily tested different levels of Θ, we chose to fix this parameter based on the data reported by Fitzhugh et al. Our parameterization of this variable is relatively robust to declines in sex ratio, as befitting a haremic spawner (Brooks et al., 2008). Fertilization success, $P(fert)$, was calculated for the entire population once per time step (t) as a function of Θ and the population sex ratio (p) for that model year:

$$P(fert)_t = 1 - \exp[-\Theta(p_t)] \tag{11}$$

Fitzhugh et al. (2006) also found that per capita egg production increased linearly with age. Egg production by age was calculated with equation 12, where E_i is the per capita egg production of a female age i:

$$E_i = 2 \times 10^6(i) - 4 \times 10^6 \tag{12}$$

Total egg production (E_{TOT}) for each year t was the sum of E_i times the number of females age i in year t.

Recruitment, R_t, was calculated as a function of total egg production, fertilization success, and the survival probability of larvae surviving to settlement, which was the combined egg survival (S_E) and larval survival (S_L). Annual variability in recruitment was introduced as a lognormal random deviate (Rv). The standard deviation of this deviate was determined by fitting of a lognormal distribution to the reported recruitment estimates from 1986 to 2004 (SEDAR, 2006). Total recruitment was limited by the parameter Φ, so that the number of recruits in year $t+1$ was calculated with Eq. (13)

when R was less than Φ and with Eq. (14) when R was more than Φ:

$$R_{t+1} = E_{TOT}P(fert)_t S_E S_L Rv \tag{13}$$

$$R_{t+1} = \Phi S_L Rv \tag{14}$$

Essentially, this recruitment function is what is termed a two-line or "hockey-stick" model in stock assessments, which approximates the behavior of the commonly used Beverton–Holt stock-recruitment model (Barrowman and Myers, 2000). The stock-recruitment parameters are therefore the egg survival S_E and the maximum recruitment, Φ. When recruitment is calculated to be above the maximum estimate, it is limited as a way to include density-dependent survival of larvae. In the model, egg survival (S_E) is implicitly a production parameter and so was set equal to the value that returned recruitment estimates equivalent to recent recruitment estimates from the stock assessment. In effect, doing so involves assuming that current population conditions are stable in terms of recruit production. Larval survival S_L was fixed for all simulations and was based on the survival estimate calculated by Koenig and Coleman (1998).

2.2. Marine reserve options and effort changes

We tested a range of spawning-area-reserve sizes to determine how the population would respond to changes in effort and the inclusion of density-dependent sex change. All scenarios were assumed to alter the vulnerability of fish to fishing effort, which was calculated as a proportional change in the fishing mortality rate. Marine-reserve scenarios were defined by the percentages of the spawning area closed to fishing. Spawning-area closure was assumed to impose stage-specific changes in fishing mortality rates, under which males within a protected aggregation were protected from fishing mortality year round, females within a protected aggregation were protected for one-quarter of the year (the amount of time females are associated with aggregations), and juvenile fishing mortality was not directly affected by spatial closures. Six marine-reserve scenarios were tested to represent a range of levels protection: 0, 18, 25, 50, 75, and 100% of total spawning area protected. These scenarios represent a range of possible options for marine reserves in the GOM; 18% represents the amount of protection afforded by the current reserves (GMFMC, 1999).

Each marine-reserve scenario was combined with one of five fishing-effort regimes (see Table 2 for the calculation of stage-specific fishing mortality change):

(1) *None*, the status quo condition, $fmult = 1.0$.
(2) *Low*, 5% increase in juvenile, female, and male fishing mortality, $fmult = 1.05$.
(3) *Mid*, 10% increase, $fmult = 1.1$.
(4) *High*, 25% increase, $fmult = 1.25$.
(5) *Prop*, proportional increase, $fmult = 1.0$.

These fishing effort regimes represent a range of possible fisher responses to reserve implementation. For the *Low*, *Mid*, and *High* regimes, we calculated the increase in fishing mortality before reducing fishing mortality by reserve area. For the *Prop* regime, we assumed that total fishing effort did not change with the implementation of reserves, but instead used a redistribution multiplier, D, to alter fishing mortality according to the reserve scenario:

$$D = \frac{1 + \text{percent spawning area protected}}{100} \tag{15}$$

The value D was then multiplied to the age and stage specific fishing mortality rate calculated in Eq. (2) to obtain the total fishing mortality rate for a given age and stage. As the amount of

Table 2
Baseline fishing mortality rate for each stage and the change in rate for the five marine-reserve scenarios and five fishing effort (F) regimes (MPA = marine reserve multiplier; D = redistribution multiplier).

Regime	Description	Stage			
		Age 1	Juvenile	Female	Male
None	No increase in F	0	0.267	$0.348 \times (1/4\ \text{MPA})$	$0.299 \times \text{MPA}$
Low	5% increase in F	0	0.28	$0.365 \times (1/4\ \text{MPA})$	$0.314 \times \text{MPA}$
Mid	10% increase in F	0	0.294	$0.383 \times (1/4\ \text{MPA})$	$0.329 \times \text{MPA}$
High	25% increase in F	0	0.334	$0.435 \times (1/4\ \text{MPA})$	$0.374 \times \text{MPA}$
Prop	Proportional increase	0	$0.267 \times D$	$0.348 \times D \times (1/4\ \text{MPA})$	$0.299 \times D \times \text{MPA}$

spawning area protected from fishing increases, we assume that fishers will shift their effort to the inshore fishery which is dominated by juvenile and female gag which will experience increasingly high fishing mortality. While this may be an extreme assumption, we included it as the upper bound of possible response scenarios.

We defined the status quo scenario to be 18% reserve area with no overall increase in fishing effort.

2.3. Model simulations

Each simulation ran for 100 model years in 1-year time steps. At each time step the age and stage distributions were updated and used to produce the number of YOY individuals for the following year. Model simulations were initialized according to estimates taken directly from the latest full stock assessment, which estimated the total gag population at 9.6 million fish (SEDAR, 2006). The initial population was distributed into observed age classes from the stock assessment; stage classifications were determined by maturation and transition probabilities fitted to these observations (SEDAR, 2006). The initialized age distribution had a starting population of approximately 4.8 million mature fish with a sex ratio of 3.46% male.

We tested model scenarios using a 6×5 factorial design, where each reserve size class ($n = 6$) was tested with each fishing-effort redistribution scenario ($n = 5$). Each scenario was then calculated with fixed sex change and with density-dependent sex change for a total of 60 scenarios. Response variables calculated were total adult population size, sex ratio, and yield by weight measured in metric tons. Yield estimates were calculated with a deterministic version of the model in which recruitment was assumed to be constant. We also calculated a "minimum effective size" for each scenario, defined as the percentage of reserve area necessary to produce and maintain a threshold percentage of males. We defined two thresholds: 5% males and 10% males, both of which represent improvement over the current estimate of 3.46% males. Each scenario was replicated 500 times, and results are reported as the mean value of the final 20 years for all replicates. Scenarios that did not reach equilibrium but instead showed a continuous increase or decrease until the end of the time series are noted in the results. Because the variance of the results is a function of the random coefficient defined in the recruitment equation, no further descriptive statistics are reported.

2.4. Sensitivity analysis

Given the assumptions we made in describing the density-dependent sex-change function (Eq. (9)), the uncertainty in the chosen parameter values is high. To test the model sensitivity to these parameters, we performed a proportional sensitivity analysis on the density-dependent sex-change parameters c, d, and q_{min}. For the sensitivity analysis, each parameter was allowed to vary independently of all other parameters by plus or minus 5%. Sensitivity was calculated with Eq. (16), where var_p is the response variable calculated with parameter p equal to value x:

$$\text{sensitivity} = \frac{(\text{var}_{p+5\%} - \text{var}_{p-5\%})}{0.1\,\text{var}_p} \tag{16}$$

3. Results

3.1. Effort redistribution with fixed sex change

As the amount of spawning area protected from fishing increased, so did the sex ratio (Fig. 2a), although the extent and pattern of fishing effort redistribution strongly influenced the amount of increase observed in the sex ratio. All of the simulations using alternative fishing effort scenarios achieved equilibrium. In general, as fishing effort increased, more reserve area was necessary to produce an equivalent sex-ratio response. Adult population size responded like sex ratio; increased reserve area resulted in a larger adult population (Fig. 2b). Fishery yield increased slightly as reserve area increased and then declined as the area protected grew large (Fig. 3).

With effort held constant, the largest increase in sex ratio occurred with 100% spawning area protection. The resulting equilibrium sex ratio for all reserve scenarios (including no reserves)
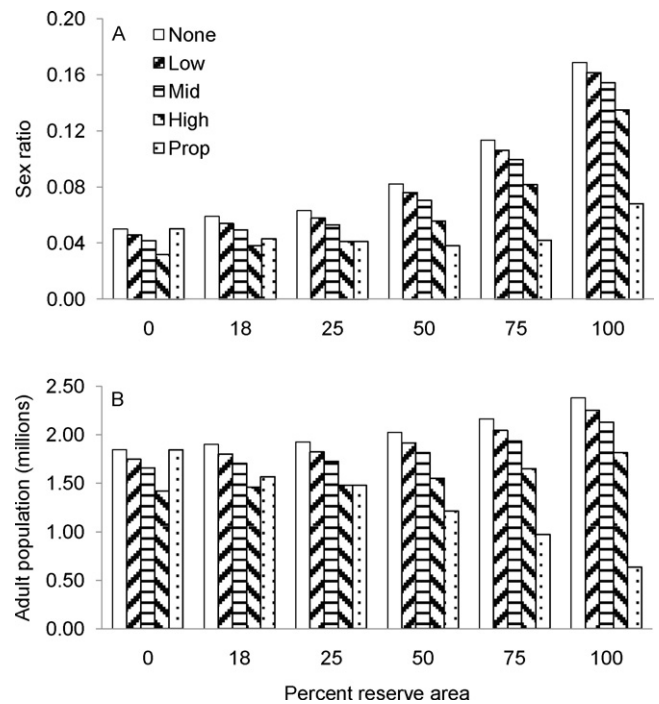

Fig. 2. Adult sex ratio (A) and adult population size (B) response to increasing reserve size and five levels of fishing effort change (initial sex ratio = 3.46% males; initial adult population = 4.8 million fish). None, the status quo condition, no change from current fishing mortality; Low, 5% increase in juvenile, female, and male fishing mortality; Mid, 10% increase; High, 25% increase; Prop, proportional increase.
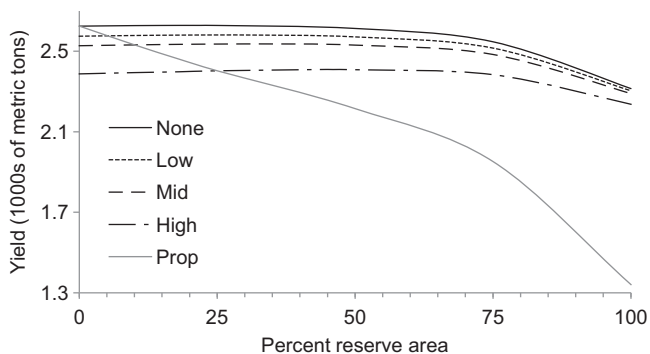
Fig. 3. Predicted fishery yield as spawning reserve size increases for the five effort-change scenarios under deterministic model conditions. The estimate of maximum sustainable yield for Gulf of Mexico gag at current fishing mortality is 3932 metric tons (SEDAR, 2006).

Fig. 4. Sex ratio response for simulations with fixed sex change (white bars) and density-dependent sex change (hatched bars) as spawning reserve area increased with no fishing effort redistribution.

was greater than the current estimate of 3.46%. The final sex-ratio value for the status quo option was 5.8% male, a 68% increase over the starting condition. The equilibrium adult population size was less than the initial condition for all simulated area scenarios, indicating that current fishing mortality will result in a smaller adult population. The average decline in adult population varied greatly and depended on the area of spawning reserves; for example, the status quo regime with no reserves resulted in a 71% decline in adult population, whereas 100% reserves resulted in only a 63% decline.

Estimates for fishery yield were all lower than the estimated maximum sustainable yield from the stock assessment (SEDAR, 2006). This is generally consistent with that assessment in that both approaches indicate that fishing mortality rates at that time were exceeding that which would produce MSY. However, our approach uses an approximation for the reproductive function, whereas the assessment uses a stock-recruitment function. Additionally, this model is inherently evaluating changes in the fishery's selectivity at age resulting from alterations in reserve size. This too changes the estimate of MSY. Minimum yield occurred in our model with 100% reserves for all fishing-effort regimes (Fig. 3). Maximum yield occurred in our model at intermediate reserve size, and the reserve size that maximized yield changed with fishing effort; as total fishing effort increased, maximum yield occurred with progressively greater reserve area. However, yield response was essentially insensitive to reserve size throughout most of the range of tested scenarios.

Sex ratio, adult population, and fishery yield all responded negatively to increased effort, but for the proportional-effort-redistribution scenarios, the results were very different from those described above. When total effort was held constant, the resulting equilibrium sex ratio declined as reserves increased in size from 0% to 50% and then increased to a maximum at 100% reserves (see Fig. 2a). The overall change in equilibrium sex ratio from the initial condition was positive for all reserve sizes: for 100% reserves, it was 6.81% male (96.8% increase over the initial value), and for 50% reserves it was 3.83% male (11.8% increase). For the proportional redistribution scenarios, both the adult population and fishery yield were maximized with no reserves and declined as reserve area increased (Figs. 2b and 3).

3.2. Effort redistribution with density-dependent sex change

When the probability of sex change was allowed to vary with male density (Eq. (9)) the pattern of response for equilibrium sex ratio, adult population size, and fishery yield to increasing reserve area were similar to results with fixed sex change (Eq. (8)), but the magnitude of the response was notably different for sex ratio. Protecting a small reserve area resulted in higher equilibrium sex ratio
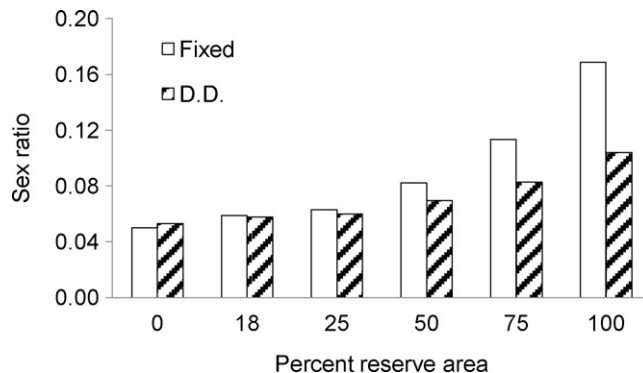
when compared to the fixed sex change model, while protecting a large reserve area resulted in lower equilibrium sex ratios than with fixed sex change (see Fig. 4).

Changes in fishing effort tended to amplify the effects of density dependence for the small-reserve scenarios. As shown in Fig. 4, when fishing mortality was held constant the equilibrium sex ratio with no reserves was 16% greater with density-dependent sex change (3.91% vs. 3.36% males), but with full spawning area protection (100% reserves) it was 59% greater with fixed sex change (9.93% vs. 6.23% males). This pattern was repeated for all fishing-effort scenarios: when total reserve area was small the density-dependent sex change model produced a higher equilibrium sex ratio; when total reserve area was large the fixed sex change model resulted in a higher equilibrium sex ratio. Equilibrium sex ratio response curves for fixed and density-dependent sex change crossed at approximately 5.67% males for all fishing-effort scenarios. The reserve size needed to produce 5.67% males increased with increasing fishing effort, as shown by the dotted line in Fig. 5.

Under the proportional effort redistribution scenario including density-dependent sex change resulted in a higher equilibrium sex ratio up to 75% reserve area. However, when all spawning area was protected with reserves the equilibrium sex ratio with fixed sex change was 7% higher than that with density-dependent sex change (4.01% vs. 3.74% males). Under this scenario, only full spawning area protection (100% reserve area) resulted in a higher equilibrium sex ratio than the initial condition, for both fixed and density-dependent sex change functions.
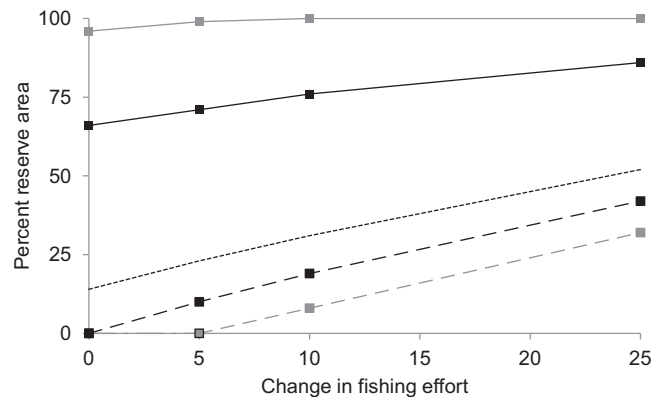

Fig. 5. Minimum spawning reserve size (as percentage of total spawning area) required to produce sex-ratio benchmarks of 5% males (dashed lines) and 10% males (solid lines); black lines indicate fixed sex change, and gray lines indicate density-dependent sex change. The dotted line indicates the reserve size necessary to produce 5.67% males, the ratio at which the density-dependent and fixed sex change functions converged.
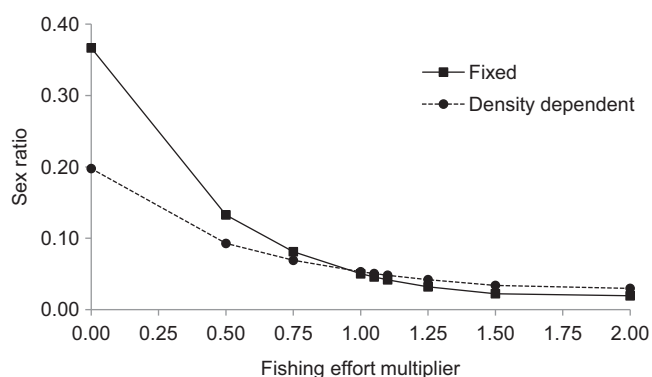
Fig. 6. Comparison of the change in equilibrium sex ratio for increasing fishing mortality rate (relative to current effort = 1) between fixed and density-dependent sex change in the absence of reserves.

3.3. Minimum effective reserve size

The calculations of minimum effective reserve size (Fig. 5) show that, for a given fishing effort regime, smaller total reserve area could yield a sex ratio of at least 5% males when sex change was density-dependent compared to when it was fixed. When density-dependent sex change was included in the model and fishing effort increased by more than 5% or was proportionally redistributed, the 10% male threshold was never reached. When the model included fixed sex change, no reserves were necessary to yield a sex ratio of at least 5% males, as long as total fishing effort increased by less than 10%. Under the proportional redistribution of effort regime, neither the 5% nor 10% threshold was ever attained under either the fixed or density-dependent sex change.

3.4. Model sensitivity

The equilibrium sex ratio for changing fishing effort with no reserves is shown in Fig. 6. Equilibrium sex ratio for an unfished population (fishing effort = 0) with fixed sex change was 36.7% males and with density-dependent sex change was 19.8% males. The two curves cross at $fmult = 1.0$, which represents the current, or status quo, fishing mortality rate. Including density-dependent sex change in the model resulted in a higher equilibrium sex ratio than did fixed sex change when the total fishing mortality was higher than the initial condition and a lower one when it was lower. Including density-dependent sex change also made the population less likely to "crash," defined here as an equilibrium population size less than 10% of the initial adult population. With density-dependent sex change included in the model, the population crashed when the total fishing morality rate was increased by 60%, or 1.6 times the initial condition. With fixed sex change included in the model, the population crashed when the total fishing mortality rate was 46%, or 1.46 times greater than status quo.

A sensitivity analysis was performed on the density-dependent sex-change parameters c, d, and q_{min}. The results of this analysis showed that only the minimum size at first transition (q_{min}) had a value other than 1, indicating that a 10% change in the parameter value resulted in a change in the equilibrium sex ratio of more than 10% (sensitivity value = -1.45). None of the density-dependent sex-change parameters had a significant impact on adult population or yield (all sensitivity values less than ± 0.01, indicating less than <1% change in the response variable for a 10% change in the parameter value).

4. Discussion

The results of our model suggest that the realized benefits of marine reserves used to manage a fishery for a protogynous fish species can vary significantly from the anticipated benefits and may ultimately depend on the response of the fishery to the area closure. How fishing effort is redistributed following an area closure will determine if the population will suffer from rather than accrue benefits expected from management actions. This result confirms previous research suggesting that the ultimate effectiveness of area closures will be compromised unless total catch by the fishery is reduced and not increased outside the closure (Coleman et al., 1999; Pascoe and Mardle, 2005). Marine reserves alone cannot solve the problems faced by a poorly managed or heavily fished population, but must be one of a set of tools used by fishery managers (Armstrong, 2007; Holland and Brazee, 1996; White et al., 2010). Our model population experienced significant reductions in all response variables when total fishing effort increased. While at some level this should be expected (increasing fishing effort in an already overfished population should lead to further population decline), the amount of spawning area requiring protection to maintain a stable population size and sex ratio even under modest (5–10%) increases in fishing effort was much larger (>50% area of total spawning area) than we anticipated and much larger than the amount of area protected by reserves currently in place (see Table 3).

When we considered the proportional effort redistribution scenario, where total effort remains constant following area closures but is shifted to other stages, the model showed that redistributing effort resulted in the smallest equilibrium sex ratio for a given reserve size. For our case, the proportional redistribution scenario represents the extreme response by fishers, but one that may be entirely plausible: reducing fishable area does not necessarily reduce the total fishing mortality experienced by a fished population. Area closures by themselves do not lessen the impetus to fish; in fact they may encourage fishers to fish more by promising more and bigger fish (Kellner et al., 2008; Stevenson et al., 2011). After an area closure, the same amount of fishing effort is concentrated on a smaller area and, in the case of gag, where different life stages inhabit different habitats; this shift of effort may result in higher fishing mortality of younger fish.

A second and more significant result from our model is that adding density-dependence to the sex-change function in the model resulted in an equilibrium population that was more resilient to high fishing pressure, at least in terms of the male to female sex ratio. This is important as it suggests that socially induced sex change can act as a buffer against high fishing mortality. As the sex ratio in a model protogynous fish population declines as a result of size-selective fishing, the probability that a given female will change sex increases, resulting in higher equilibrium sex ratio compared to a model population where such a density-dependent mechanism is not included. There are two hypotheses that describe the mechanism controlling sex change in protogynous fishes: size-mediated and socially mediated control. The size-mediated control hypothesis states that sex change will only occur once an individual has exceeded some physiologically based size threshold (Allsop and West, 2003). The socially mediated control hypothesis states that social cues received by an individual during its interaction with other individuals within a local area or aggregation control the initiation of sex change. Social cues can either take the form of the sex ratio of other fish encountered (Shapiro and Lubbock, 1990; Ross, 1990) or the size ratio of fish encountered (Ross et al., 1990; Lutnesky, 1994). Both the sex-ratio and size-ratio hypotheses imply that group composition cues initiate sex change in individuals. If the size or sex composition of spawning groups is altered by fishing, this would in turn

Table 3
Resulting adult population size and sex ratio relative to status quo conditions for increasing marine reserve size and fishing effort regimes with fixed sex change and density-dependent sex change. Values greater than 1 represent increases over the status quo and are shown in italics; those for which both values are greater than 1 are marked in addition with asterisks.

Fishing effort	Reserve area					
	0	18	25	50	75	100
Fixed sex change						
None	0.97, 0.85	*1.00, 1.00**	*1.01, 1.07**	*1.07, 1.40**	*1.14, 1.92**	*1.25, 2.87**
Low	0.92, 0.78	0.95, 0.92	0.96, 0.98	*1.01, 1.29**	*1.08, 1.80**	*1.18, 2.74**
Mid	0.87, 0.71	0.90, 0.84	0.91, 0.91	0.95, *1.19*	*1.02, 1.69**	*1.12, 2.65**
High	0.75, 0.54	0.77, 0.65	0.78, 0.70	0.82, 0.95	0.87, *1.39*	0.95, *2.29*
Prop	0.97, 0.85	0.83, 0.73	0.78, 0.70	0.64, 0.65	0.51, 0.71	0.33, *1.16*
Density-dependent sex change						
None	*1.13*, 0.92	*1.00, 1.00**	0.95, *1.04*	0.94, *1.20*	0.93, *1.43*	0.92, *1.80*
Low	*1.07*, 0.87	0.95, 0.95	0.90, 0.99	0.89, *1.15*	0.88, *1.38*	0.87, *1.75*
Mid	*1.02*, 0.83	0.90, 0.91	0.86, 0.95	0.85, *1.10*	0.84, *1.33*	0.82, *1.70*
High	0.87, 0.73	0.77, 0.80	0.73, 0.83	0.72, 0.97	0.72, *1.19*	0.70, *1.57*
Prop	0.31, 0.92	0.60, 0.85	0.73, 0.83	0.78, 0.80	0.84, 0.84	0.92, *1.08*

alter the rate at which individual fish transition from one sex to another.

For gag there is confounding evidence over which specific mechanism controls sex change (size vs. social cues). Gag possesses all the characteristics defined by Ross (1990) as required for a population to have socially mediated control of sex change: they are protogynous, they experience periodic separation of the sexes, they form large and permeable social groups, and they are socially dimorphic (gag show a coloration change following sex change where the belly appears darker, and the appearance of the "copperbelly" coloration was identified with males in 98% of fish histologically examined for the age and growth study in the 2006 stock assessment; SEDAR, 2006). In addition, the number of transitional gag (individuals that are undergoing sex change) present in the catch increases post-spawning, suggesting that social cues transmitted during aggregation may initiate sex change (Hood and Schlieder, 1992; Collins et al., 1998).

In the South Atlantic (SA) management region, the gag population showed a shift in the mean age at sex change from 1976 to 1995 as the sex ratio in the SA population decreased from 19.6% male to 5.5% male. During this period, the mean age of transitioning females decreased from 11.7 years to 10.5 years (SEDAR, 2006). However, although the GOM population experienced a similar decline in sex ratio (from 17% male in 1977 to less than 4% male in 2004), there was no corresponding decrease in the mean age of transitioning females (SEDAR, 2006). While the data from the SA population suggests that gags are able to alter the age of transition towards younger fish, the GOM data suggests that transition may be fixed. However, the ability to parse out social influence from age and growth studies is likely confounded by changes in the growth rate (evident in the South Atlantic population; SEDAR, 2006) that often occurs with large changes in population age structure. As the sex ratio in a population declines, individual females receive both sex and size-ratio cues as males are removed from the population. It may be possible that both size and social control mechanisms work to influence sex change in gag: above a minimum size threshold the average size of transitioning females can change based on social cues. Despite a lack of conclusive evidence supporting either mechanism of sex change control, it is generally assumed that sex change in gag is at least partially mediated by social cues (SEDAR, 2006), and in fact the assumption that social cues control sex change has been used as support for management action (GMFMC, 1999).

If sex change in gag is socially controlled, it has been suggested that the observed sharp decline in sex ratio should not have occurred (GMFMC, 1999). Size-selective fishing causes a disproportionate loss of males from protogynous populations and

a similar drop in sex ratio has been observed in a number of other heavily fished protogynous fish populations (Buxton, 1992; Hawkins and Roberts, 2003). High fishing mortality can also drive down sex ratio through the removal of large females, exactly the individuals most likely to change into males. Protogynous fish populations may in fact be more vulnerable to fishing pressure than gonochoristic species because an extreme alteration of sex ratio can lead to sperm limitation (Armsworth, 2001), a situation which has previously been modeled in a number of species including graysby (*Epinephelus cruentatus*; Hunstman and Schaaf, 1994), and gag (Heppell et al., 2006). Alonzo and Mangel (2004) found that the specific control mechanism for sex change had a clear impact on the response of a population to fishing pressure: when sex change was variable (either based on size-ratio or sex-ratio), the model population was more resilient to fishing pressure than when sex change was fixed. However, in all cases the protogynous fish appeared to be less resilient to high fishing mortality than a gonochoristic population (Alonzo and Mangel, 2004). Our results support these findings and further reiterate the importance of including consideration of the sex-change mechanism when considering management actions.

With density-dependent sex transition rates included in our model, the realized benefits in terms of equilibrium sex ratio resulting from spawning-area protection changed (see Table 3). In general, for small reserves (less than 25% of total spawning area), estimates of equilibrium sex ratio and adult population were higher when density-dependent sex change was included. For large reserves (>50% of total spawning area) equilibrium sex ratio and adult population size were higher when sex change was fixed. The addition of density dependent sex change to the model approximated the expected effect that socially induced sex change should have on a heavily fished protogynous population: when fishing effort is high, the equilibrium sex ratio was higher with density-dependent sex change. Our model results reflect this expected outcome for sex ratio, but surprisingly the pattern was not reflected in the population size or yield estimates. Population size and fishery yield were more sensitive to fishing effort than was sex-ratio, but as high fishing pressure depletes the population, density-dependent sex change may serve to maintain enough males in the population to limit fertilization failure.

When both proportional redistribution of fishing effort and density-dependent sex change were included in the model, the equilibrium sex ratio appeared to flatten out: sex ratio was lowest at intermediate reserve sizes for both fixed and density-dependent sex change simulations, but the absolute change was less when density dependence was included. Density-dependent sex change may act to reduce fluctuations in sex ratio caused by high fishing

mortality. Conversely, density-dependent sex change may also reduce the realized benefits from management actions such as large reserves.

Sensitivity analysis revealed that the model was most sensitive to small changes in the minimum age at sex change parameter, q_{min}. We included this parameter in the model to represent an assumed physiological limit that individuals must meet before changing sex. Whether this limit is physiological or evolutionary in origin (see Allsop and West, 2003), a minimum size limit does appear to exist for gag as no males smaller than 800 mm are found in the catch (SEDAR, 2006). However, we expected that the other two parameters, c and d, which represent changes in the shape of the probability function would be more sensitive to change, given the way that socially induced sex change is thought to work. As males become rare in a protogynous population, females might either change sex at an earlier age or become more likely to change sex at a given age. We assumed that the minimum size at first transition is bounded by a physiological threshold, whereas variability in sex-change rate instead works on individuals already past this barrier. Recent research has suggested that age at sex change may be more variable, particularly at the local, within-population scale, than the invariant sex change model would suggest (Collin, 2006; Molloy et al., 2010). The available data provide little evidence to indicate whether the decline in sex ratio has resulted in a change in minimum size or "faster" change. Better resolution of data on the sex structure of the gag population would help to refine our density-dependent sex-change function by indicating how transition rates change through time and thus would improve our model predictions.

The results of our modeling efforts offer more evidence that marine reserves designed to protect spawning aggregations of a protogynous fish can maintain and may even increase the population sex ratio. However, predicted benefits were highly sensitive to changes in fishing effort that resulted in higher fishing mortality on non-protected life stages. While the predicted equilibrium sex ratio for the status quo scenario (current fishing mortality rates and 18% reserve area) was 68% higher than the initial condition, suggesting that without any future changes to management or fishing effort the sex ratio in GOM gag should increase over time, these benefits were reduced as fishing effort increased outside reserves. Furthermore, although the current reserves may be sufficient to increase the sex ratio in the population, the current fishing mortality rate is too high to sustain the population size and yield that the fishery takes. While our model does not explicitly evaluate MSY, it does allow us to make simple predictions based on total fishing mortality rate and effort redistribution.

Heppell et al. (2006) found that spawning area reserves were the most effective management action to increase the sex ratio in a model population of gag grouper, and that to increase the adult population the most effective management action was to reduce fishing mortality on female fish, perhaps through the use of nearshore area closures. Our work here builds on theirs by showing how increases in sex ratio that result from spawning reserves may be reduced by changes in fishing effort or through density-dependent mechanisms of sex change. We limited our modeling scenarios to only include spawning area closures, which primarily benefit male gag, but the results of our model show that spawning area reserves had little impact on the adult population. Our results and those of Heppell et al. underscore the importance of considering different management actions in concert to attain comprehensive goals of fishery management. Offshore spawning reserves must be part of a coordinated suite of management actions for gag. While they may eventually result in an increased adult sex ratio, they will not alone be effective at maintaining the gag population especially should overall fishing effort increase outside reserves. The finding that effort increases outside closed areas influenced overall reserve

success is supported by previous work by a number of authors (e.g. Holland and Brazee, 1996; Mangel, 1998; White et al., 2010). Likewise, including a consideration of sex change in stock assessment models has previously shown to be important (Alonzo and Mangel, 2004; Brooks et al., 2008). Our work illustrates the significance of including these concepts when evaluating harvest strategies by applying them to a specific population of protogynous fish.

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