

MODELS TO COMPARE MANAGEMENT OPTIONS FOR A PROTOGYNOUS FISH

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Abstract. Populations of gag (*Mycteroperca microlepis*), a hermaphroditic grouper, have experienced a dramatic shift in sex ratio over the past 25 years due to a decline in older age classes. The highly female-skewed sex ratio can be predicted as a consequence of increased fishing mortality that truncates the age distribution, and raises some concern about the overall fitness of the population. Management efforts may need to be directed toward maintenance of sex ratio as well as stock size, with evaluations of recruitment based on sex ratio or male stock size in addition to the traditional female-based stock–recruitment relationship. We used two stochastic, age-structured models to heuristically compare the effects of reducing fishing mortality on different life history stages and the relative impact of reductions in fertilization rates that may occur with highly skewed sex ratios. Our response variables included population size, sex ratio, lost egg fertility, and female spawning stock biomass. Population growth rates were highest for scenarios that reduced mortality for female gag (nearshore closure), while improved sex ratios were obtained most quickly with spawning reserves. The effect of reduced fertility through sex ratio bias was generally low but depended on the management scenario employed. Our results demonstrate the utility of evaluation of fishery management scenarios through model analysis and simulation, the synergistic interaction of life history and response to changes in mortality rates, and the importance of defining management goals.

Key words: grouper; hermaphrodite; management strategies; marine reserves; *Mycteroperca microlepis*; population model.

INTRODUCTION

Most fishery models and stock assessments—and therefore the management strategies based upon them—ignore the effects of fishing on reproductive patterns, sex-specific survival, and subsequent recruitment (Bannerot et al. 1987, Coleman et al. 2000, Alonzo and Mangel 2004). Further, they ignore the size-specific contribution of females and all contributions of males to reproductive success. Recently, the disproportionate contribution to recruitment made by older, larger females has been brought to light (Berkeley et al. 2004). Ignoring males, however, continues primarily because (1) females represent the sex that produces eggs; (2) females are usually more limiting than males because males can mate or spawn with multiple females; and (3) because the standard practice for many reef fish is to use female biomass as a benchmark indicating population health (i.e., whether or not a stock is overfished). While these may be reasonable assumptions most of the time, they may not be valid when considering sequential hermaphrodites (Bannerot et al. 1987, Huntsman and Schaaf 1994, Armsworth 2001). In protogynous hermaphrodites (animals that reproduce first as females and then change sex to become male), there

is a naturally occurring female bias in the sex ratio (Allsop and West 2004). Unless there is a compensatory shift in age or size at sex change, fishing pressure enhances this bias by preferentially removing males (the larger individuals) or simply by reducing the mean lifespan of the population, thereby reducing the probability that females will survive long enough to become males (Armsworth 2001). The result is a shift in spawning stock biomass that affects calculation of yield per recruit and other standard fisheries assessment endpoints (Punt et al. 1993, Shepard and Idoine 1993, Alonzo and Mangel 2004), and a potential loss of productivity due to sperm limitation (Bannerot et al. 1987). Despite strong theoretical support for consideration of models that consider both sexes and the effect of sex ratio on reproductive success, few assessment models for grouper or other hermaphroditic fishes in the United States have been modified explicitly to include both sexes and the effects of fishing on sex ratio.

The sex ratio of gag (*Mycteroperca microlepis*, Family Serranidae) has shifted dramatically over the last two decades, from an approximately 6:1 female to male ratio under relatively light fishing pressure in the late 1970s to as much as a 30:1 female to male ratio in the 1990s (Coleman et al. 1996, McGovern et al. 1998). This shift in sex ratio occurs for other fished species of grouper as well (Beets and Friedlander 1992, Coleman et al. 2000, Armsworth 2001). While the short-

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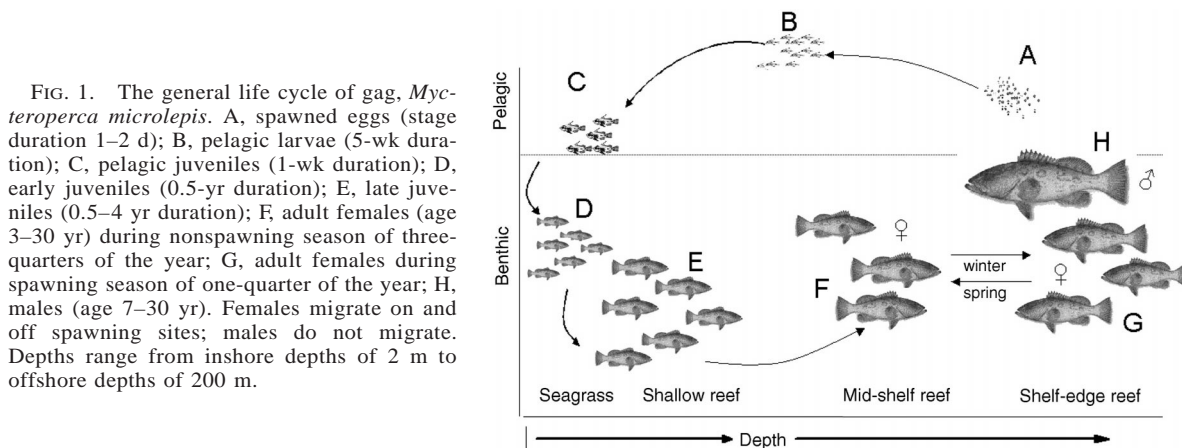


FIG. 1. The general life cycle of gag, *Mycteroperca microlepis*. A, spawned eggs (stage duration 1–2 d); B, pelagic larvae (5-wk duration); C, pelagic juveniles (1-wk duration); D, early juveniles (0.5-yr duration); E, late juveniles (0.5–4 yr duration); F, adult females (age 3–30 yr) during nonspawning season of three-quarters of the year; G, adult females during spawning season of one-quarter of the year; H, males (age 7–30 yr). Females migrate on and off spawning sites; males do not migrate. Depths range from inshore depths of 2 m to offshore depths of 200 m.

term ramifications are unknown, the long-term outlook is clear. As males become rare, the population has the potential to experience reproductive failure (Bannerot et al. 1987, Huntsman and Schaaf 1994). Sex ratio bias occurs even when fishing mortality rates are constant across age classes, simply because of the reduced probability of survival to an age or size class capable of sex change. Gag are relatively inflexible in size or age at sex change (McGovern et al. 1998), in comparison to a variety of other hermaphroditic fishes that change sex based on social status and exhibit strong plasticity in size or age at transition (Ross 1990). Therefore, reproductive failure is more likely to occur at a lower fishing mortality rate in sequential hermaphrodites such as gag than it is in gonochoristic species, as was demonstrated with a constant recruitment model simulation for graysby (*Epinephelus cruentatus*) (Huntsman and Schaaf 1994).

Gag experience several ontogenetic habitat shifts during their lifetime (Fig. 1). Adults spawn offshore, releasing eggs that hatch within days into planktonic larvae (Collins et al. 1987, Collins et al. 1998). Larvae remain in the plankton for 30–40 d, during which time they are transported to their estuarine nursery habitat where they settle in suitable areas, primarily seagrass beds (Keener et al. 1988, Ross and Moser 1995). Within the first year of life, most juveniles make a fall migration from the seagrass beds to nearshore reefs, perhaps under cues from cold fronts and decreasing water temperature (Ross and Moser 1995, Koenig and Coleman 1998; but see Heinisch and Fable 1999). As gag grow and mature they move progressively to deeper reefs further from shore (Bullock and Smith 1991). Adult females transition to reproductive males as early as age six or seven, but the presence of large females in the population suggests that many individuals do not change sex until later in life, or perhaps not at all (McGovern et al. 1998). Males stay on spawning sites year round while females migrate to these sites only during the winter months (January–March; C. C. Koenig and F. C. Coleman, unpublished data). This life cycle re-

sults in a dynamic process of segregation and aggregation of immature, female and male fish, both in time and space. Thus, we expect different population-level responses from management actions that focus on overall fishing mortality from those that reduce mortality only at one time or in one habitat (St. Mary et al. 2000, Gerber and Heppell 2004, Gerber et al. 2005). For hermaphrodites, an evaluation of the effects of various management actions requires more than a simple comparison of resulting biomass; sex ratio and sex-specific spawning stock biomass are also important assessment endpoints (Alonso and Mangel 2004).

The goals of this work are to evaluate the effect of different levels of fishing mortality on the sex ratio and population structure of gag, to predict population trends due to these impacts, and to evaluate the effectiveness of different management scenarios in mitigating these effects. Our specific objectives are (1) to construct a model that demonstrates the effects of fishing mortality rates on sex ratio and population age structure, (2) to explore the potential effects of decreased fertility that may occur with a highly skewed sex ratio, and (3) to evaluate the impacts of a variety of management options that affect specific life stages, including spatial and temporal closures, reduced total fishing mortality, and sex-specific fishing mortality rates. The age-structured model is relatively simple but still contains a number of unknown or uncertain parameters; therefore, the model serves as heuristic tool to assess the impacts of different management scenarios and to identify critical research needs. In spite of these limitations, the techniques developed here could be used in a qualitative manner as a rebuilding assessment tool for protogynous species.

METHODS

Model construction and parameterization

We developed an age-structured model with stage classifications (following McGovern et al. 1998) to explore the effects of various management options on

TABLE 1. Parameters for gag grouper model with high and low fishing mortality (F) levels.

Parameter	Description	Source	Low F	High F
L_{∞}	asymptote of von Bertalanffy (VB) growth curve (Eq. 3).	Schirripa and Goodyear (1994)	1435	1435
k	slope of VB equation	Schirripa and Goodyear (1994)	-0.105	-0.105
t_0	x -intercept of VB equation	Schirripa and Goodyear (1994)	1.35	1.35
θ	fertilization by sex ratio parameter (Eq. 8)	arbitrary	20 (low) 80 (high)	20 (low) 80 (high)
f_{\max}	maximum fertilization rate	arbitrary	0.8	0.8
K	recruitment maximum (seagrass capacity for YOY, Eq. 9)	arbitrary	1×10^7	1×10^7
Rv	recruitment multiplier SD (gamma distribution, mean = 1)	fit to age 1 abundance from Turner et al. (2001) VPA, based on juvenile index from Koenig and Coleman (1998)	1.5	1.5
$S(\text{egg})$	egg and larval survivorship to settlement	fit so baseline stochastic growth rate ≈ 1 w/ $\theta = 80$	6.0×10^{-7}	2.0×10^{-6}
$S(\text{YOY})$	YOY survivorship (settlement to age 1)	Koenig and Coleman (1998)	0.3	0.3
$M(\text{age1})$	age 1 natural mortality	"best guess"	0.3	0.3
$M(\text{immature})$	immature natural mortality	"best guess"	0.2	0.2
$M(\text{female})$	mature female natural mortality	arbitrary; Turner et al. (2001)	0.15	0.15
$M(\text{male})$	male natural mortality	"best guess"	0.2	0.2
$F(\text{age1})$	age 1 fishing mortality (includes discard mortality)	Turner et al. (2001)	0.1	0.1
$F(\text{immature})$	immature fishing mortality	Turner et al. (2001)	0.2	0.3
$F(\text{female})$	mature female fishing mortality	Turner et al. (2001) and fit to McGovern et al. (1998) proportions at age	0.4	0.6
$F(\text{male})$	mature male fishing mortality	Turner et al. (2001) and fit to McGovern et al. (1998) proportions at age	0.15	0.6
$r(\text{mat})$	slope of maturation probability (Eq. 5)	fit to McGovern et al. (1998) proportions and mortality rates	-6.125	-6.153
$q(\text{mat})$	intercept of maturation probability	fit to McGovern et al. (1998) proportions and mortality rates	1.955	1.972
$r(\text{trans})$	slope of transition to male probability (Eq. 6)	fit to McGovern et al. (1998) proportions and mortality rates	0.056	0.097
$q(\text{trans})$	intercept of transition to male probability	fit to McGovern et al. (1998) proportions and mortality rates	5.475	5.791

Note: YOY is young of the year.

population viability and sex ratio of gag. Populations in this model are stage based because this more realistically represents the gag life cycle, wherein different life stages occur in different habitats during much of the year (Fig. 1). We define four different stages: stage 1, larvae and young of the year, YOY (age 0); stage 2, immature (females 1 yr or older that are not mature); stage 3, females (2 yr or older that are mature but have not undergone sex change); and stage 4, males (7 yr or older that have undergone sex change).

We apply separate mortality rates to each stage. Stage-specific annual survival probabilities for age 1+ fish were based on instantaneous natural and fishing mortality rates:

$$S = e^{-(M+F)} \quad (1)$$

where S = survival, F = fishing mortality, and M = natural mortality. No empirical information on natural

mortality rates for adult gag is available, so these parameter values are based generally on size (Table 1). We use rates for juveniles determined by Koenig and Coleman (1998).

Fishing mortality was broken down into three-month intervals (quarters), with annual survival based on the instantaneous mortality rates for each quarter:

$$S = e^{-(M+F_1+F_{2-4})} \quad (2)$$

where F_1 is fishing mortality during the first quarter (spawning season, January through March) and F_{2-4} is fishing mortality for the rest of the year. Due to a lack of more specific information, sex-specific fishing mortality is evenly distributed throughout the year.

We produce four permutations of the model by crossing two levels of fishing mortality (F ; low and high) with two levels of fertility (θ) (low and high). We drew fishing mortality rates from those presented in the stock

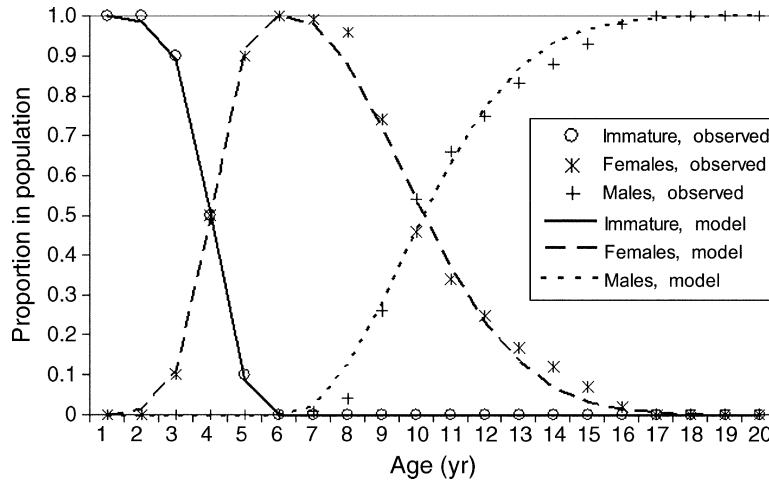


FIG. 2. Predicted and observed proportions for sex and maturational status (juvenile, female, male) by age in gag. Observed proportions are based on McGovern et al. (1998) (size converted to age using Eq. 3).

assessment by Turner et al. (2001): low $F = 0.1$ for immature fish that are one year old, 0.2 for immature fish ages 2–4, 0.4 for females, and 0.15 for males; and high $F = 0.1$ for immature fish that are one year old, 0.3 for immature fish ages 2–4, and 0.6 for all adult fish (Table 1).

All parameters for the models are given in Table 1 and defined below. Outputs include population size by life stages, female spawning stock biomass, sex ratio, eggs produced, and eggs fertilized. We used these response variables to explore how different management options might affect the population as a whole when other variables, such as growth rate and fecundity, were held constant.

We used a von Bertalanffy growth equation to relate age (x) and length (L , in mm), following Schirripa and Goodyear (1994),

$$L_x = 1435[1 - e^{-0.1051(x+1.3503)}] \quad (3)$$

and we related weight (g) to length (cm) following Collins et al. (1998),

$$W_x = 0.0309L^{2.778}. \quad (4)$$

Fitted exponential functions were used to calculate annual probabilities that a female at age x will mature [$\gamma(\text{mat})_x$] or change sex from female to male [$\gamma(\text{male})_x$] (McGovern et al. 1998) (Fig. 2):

$$\gamma(\text{mat})_x = 1/[1 + e^{-r(\text{mat})-q(\text{mat})x}] \quad (5)$$

$$\gamma(\text{male})_x = 1 - e^{-r(\text{trans})[x-q(\text{trans})]}. \quad (6)$$

(The above equation is for $\gamma(\text{male})_x \geq 0$; the expression is set at zero if negative.) The functions were fitted to observed proportions at age (McGovern et al. 1998, converted from size-based proportions by the age-length relationship, Eq. 3) by adjusting the slope parameter (r) and intercept parameter (q) in Eqs. 5 and

6 to the age distributions defined by the fishing mortality rates (Fig. 2). Fitting was by least squares for $(\text{observed} - \text{model})^2$ proportions of immature, female and male fish in each age class (Excel Solver, Microsoft Office XP, Microsoft, Redmond, Washington, USA). Maturation was restricted to age two through age five (all females age six and older are mature) and the minimum age for males was set at seven years. Maximum age for both sexes was 30 years. The high and low fishing mortality levels resulted in nearly identical fits to the data (sum-of-squares differences = 0.0505 and 0.051, respectively). Because the age-specific transition rates were fit to observed proportions within age classes, rather than proportions among age-classes, variable cohort size was not a factor. However, we do assume that maturation and transition rates are constant from year to year.

Egg production (E) for individuals in each age class (x) is based on Collins et al. (1998), where

$$E_x = 9280x^{3.94}. \quad (7)$$

We assume that fertilization success (ψ , the proportion of eggs fertilized) declines with the proportion of males (p_{male}) in the population. Although the actual relationship is unknown, we developed a simple asymptotic function with two parameters to examine this problem heuristically:

$$\psi = f_{\text{max}}(1 - e^{-\theta p_{\text{male}}}) \quad (8)$$

where f_{max} is the maximum fertilization rate and θ is a fertility parameter that determines the steepness of the curve. We arbitrarily set $f_{\text{max}} = 0.8$ and chose two levels of θ to investigate the interaction of fertility and sex ratio: $\theta = 80$ as a “high fertility” function, $\theta = 20$ as a “low fertility” function (Fig. 3).

The mean survival rate of fertilized eggs is an unknown, and potentially unknowable, parameter. Be-

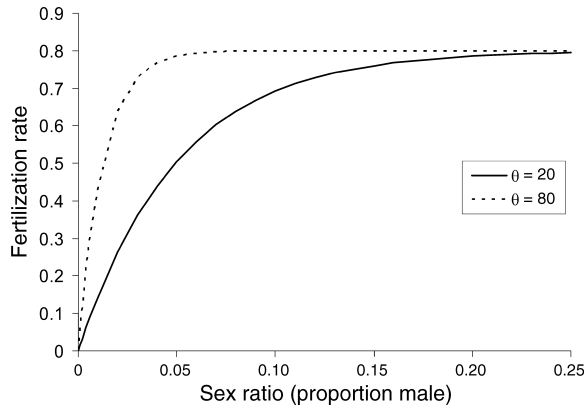


FIG. 3. Model relationship between fertilization rate and sex ratio (proportion of males), based on two different levels of fertility function, θ (Eq. 8).

cause our primary objective was to compare the relative effects of different management options on model populations, rather than to quantitatively predict current conditions or future population size, we arbitrarily chose egg survival rates that gave a relatively stable mean population for each stochastic model with $\theta = 80$. To achieve this stability, the egg survival rates ($S(\text{egg})$) varied for low and high fishing mortality rates (6×10^{-7} and 2×10^{-6} , respectively, Table 1).

To stochastically generate the number of 1-yr-old recruits each year, we used a simple, linear relationship between age-specific female egg production and young-of-the-year (YOY) abundance with an arbitrary ceiling or carrying capacity (K) of 1×10^7 YOY. Survival of fertilized eggs, $S(\text{egg})$ was multiplied by a gamma distributed random variate, rand (mean = 1, $\text{SD} = 1.5$). This variance distribution was based on a likelihood estimate for resampled age 1 abundance estimates from the virtual population analysis (VPA) presented in the stock assessment (Turner et al. 2001). This VPA included an index of juvenile abundance from seagrass

bed surveys (Koenig and Coleman 1998). The number of recruits (R , 1-yr-olds) in year $t + 1$ was equal to

$$R_{t+1} = \begin{cases} \text{egg}_t \times \psi \times S(\text{egg}) \times \text{rand} \times S(\text{YOY}) & \text{for } R \leq K \\ K \times \text{rand} \times S(\text{YOY}) & \text{for } R > K \end{cases} \quad (9)$$

where ψ was fertilization success (Eq. 8). The stock–recruit relationship was defined as the number of age 1 gag recruiting to the population relative to the number of eggs fertilized. This relationship varied as much as eightfold over a particular model run, with occasional strong year classes punctuating a lower mean level of recruitment.

Management options

The application of a management option is a two-step process that involves determining which life stages or age classes will be affected by a particular option, and then specifying the changes in survival rates or fishing mortality rates for that option. For all four model permutations of fishing mortality level and fertility level, we evaluated seven management options that reflect common management practices, including size limits and both spatial and temporal changes in fishing mortality for different life stages (Table 2):

- 1) status quo (maintaining a constant, current level of F),
- 2) increased minimum size limit (reduced F for age one and immature fish),
- 3) size limit plus spawning season closure (January through March) for all sites (zero F for all fish for one-quarter of the year),
- 4) size limit plus spawning site closure year round (zero F for males all year and for females during the spawning season [one-quarter of the year]),
- 5) spawning site closure year round with redistributed fishing effort (F increases by 25% on females

TABLE 2. Effects of management options on fishing mortality rates (F) for four different life stages of gag (*Mycteroperca microlepis*) relative to status quo levels of low $F = 0.1$ for immature 1-yr-old fish, 0.2 for immature 2–4 yr old fish, 0.4 for females, and 0.15 for males; and high $F = 0.1$ for immature 1-yr-old fish, 0.3 for immature 2–4 yr old fish, and 0.6 for all adult fish.

Management option	Immature		Adult	
	Age 1	Ages 2–4	Females	Males
Status quo
Size limit alone	0	–50%	no change	no change
Size limit + seasonal closure	0	Apr–Dec, –50% Jan–Mar, 0	Jan–Mar, 0	Jan–Mar, 0
Size limit + spawning site closure	0	–50%	Jan–Mar, 0	0
Size limit + spawning site closure with, redistributed fishing effort	0	–50%	Jan–Mar, 0	0
Nearshore closure	0	0	Apr–Dec, +25%	
Cut F by 50%	–50%	–50%	Apr–Dec, 0 –50%	no change –50%

Note: As an example, for management by size limits coupled with a spawning site closure, the effect is: $F = 0$ for age 1, $F = 0.1$ for immature fish, low $F = (0.4 \times 0.75) = 0.3$, and high $F = (0.6 \times 0.75) = 0.45$ for females, and $F = 0$ for males.

outside of the reserve during the nonspawning season [three-quarters of the year]),

6) nearshore closure (zero F on females and immature fish, no effect on males), and

7) a 50% reduction in fishing mortality from current levels year round for all life stages.

Although our model is not spatially explicit, its structure allows us to explore these types of management options in a general way. Our level of effect is intentionally extreme (e.g., elimination of fishing mortality during all or part of the year) to compare the options heuristically. In practice, the actual level of fishing mortality reduction would have to be determined through an assessment of population distribution and fisher behavior.

Sensitivity analysis

There is considerable uncertainty in a number of model parameters, although even arbitrary or “best guess” values are based on ecological principles (Table 1). To clarify which parameters had relatively large effects on primary model outputs, we conducted a simple proportional sensitivity analysis on the deterministic versions of each of the four model permutations:

$$\text{sensitivity} = \frac{\text{output}_{p \times 1.05} - \text{output}_{p \times 0.95}}{(\text{output}_p) \times 0.1} \quad (10)$$

where p is a parameter and the output is population growth rate, sex ratio, or mean spawner population size (Heppell et al. 1996). This analysis simply tests the relative effect of increasing and decreasing a parameter by 5%, independent of other parameters. Results may be positive or negative, depending on the sign of the correlation between a parameter and model output.

Model simulations

Simulations with stochastic recruitment were run for 50 years with 500 replicates. Each simulation started in model year 1995 with a population of 1×10^6 fish (1+ yr olds), distributed into age classes roughly according to observations by Fitzhugh et al. (2003). Because Fitzhugh’s samples were derived from fishery-dependent sources, we had to estimate the true distribution for ages 1–4, the immature fish that were poorly represented in the samples (Table 3). We accounted for a very strong 1993 year class (Turner et al. 2001, Fitzhugh et al. 2003).

To avoid variance in model output caused by initial conditions, we did not include the first five years of any simulation in our analysis. Our response variables were population recovery rate, mean female spawning stock biomass, adult sex ratio, and “lost productivity,” or the reduction in fertilized eggs from that expected when males are not limiting. Results were based on the means of 500 runs and, for some outputs, on a mean calculated for each run over several years. Descriptive statistics for model output were based on runs, rather than the mean of runs; for example, population growth rates were reported as the mean of the log slopes for years 2001–2015 ($n = 500$) and the standard deviations of those slopes.

TABLE 3. Age-specific initial abundance and transition rates for gag (*Mycteroperca microlepis*) models.

Age (yr)	Initial abundance (1995)	Low F		High F	
		$\gamma(\text{mat})$	$\gamma(\text{male})$	$\gamma(\text{mat})$	$\gamma(\text{male})$
1	200 000	0.015	0	0.015	0
2	400 000	0.098	0	0.099	0
3	100 000	0.435	0	0.441	0
4	200 000	0.845	0	0.850	0
5	37 762	1	0	1	0
6	36 364	1	0.029	1	0.020
7	9790	1	0.082	1	0.111
8	4196	1	0.133	1	0.193
9	2797	1	0.180	1	0.267
10	6993	1	0.225	1	0.335
11	4196	1	0.268	1	0.396
12	1399	1	0.308	1	0.452
13	839	1	0.346	1	0.503
14	699	1	0.382	1	0.548
15	314	1	0.416	1	0.590
16	189	1	0.448	1	0.628
17	113	1	0.478	1	0.662
18	68	1	0.507	1	0.694
19	41	1	0.534	1	0.722
20	24	1	0.559	1	0.747
21	15	1	0.583	1	0.771
22	9	1	0.606	1	0.792
23	5	1	0.628	1	0.811
24	3	1	0.648	1	0.829
25	2	1	0.668	1	0.844
26	1	1	0.686	1	0.859
27	1	1	0.703	1	0.872
28	0	1	0.719	1	0.884
29	0	1	0.735	1	0.894
30	0	1	0.749	1	0.904

Notes: Key to notations: $\gamma(\text{mat})_x$ is the probability of maturing, given that an immature fish of age x survives, and $\gamma(\text{male})_x$ is the probability of changing to male, given that a female fish of age x survives. These transition probabilities combine with survival probabilities to give the proportions at age shown in Fig. 2 and are not affected by recruitment variability or fertilization rate.

RESULTS

One of our primary objectives was to investigate the potential interaction of fertilization success and sex ratio on populations of gag, modeled as a smooth function with an arbitrary steepness parameter, θ (Fig. 3). Deterministic population growth rates (estimated as the slope of the population trajectory for years 2001–2015), equilibrium spawner sex ratio, and mean spawner population sizes from our four model permutations suggest that a reduction in the fertility function can have an impact on these model outputs (Table 4). Lower population fertility resulted in a dramatic reduction in population growth rate when the population experienced high fishing mortality. However, the sensitivity analysis suggests that within a model permutation, the fertility function has a lower proportional effect on model results than most other parameters. These results should be compared qualitatively, because the baseline model growth rate was set to 1.0 by adjusting the mean egg survival rate (see *Methods*).

Deterministic population growth rates and spawner abundance were most sensitive to the annual survival

TABLE 4. Sensitivity analysis for gag model with high and low fishing mortality rates and θ set at 20 (low fertility with decreasing male sex ratio) or 80 (high fertility with decreasing male sex ratio).

Parameter	Population growth rate, adults (2001–2015)				Mean spawner sex ratio (proportion of males, 2020–2047)	
	Low F		High F		Low F	
	Low θ	High θ	Low θ	High θ	Low θ	High θ
Status quo result (deterministic)	-0.020	0.003	-0.080	0.008	0.080	0.068
Proportional sensitivity						
Fertility (θ)	-0.151	0.057	-0.078	0.593	-0.021	-0.002
Egg or YOY survival	-0.417	3.527	-0.100	1.196	-0.052	-0.066
Survival (age 1)	-0.425	3.567	-0.103	1.215	-0.052	-0.066
Survival (immature)	- 1.215	9.235	-0.323	3.406	-0.105	-0.131
Survival (females)	- 1.917	12.161	-0.461	3.934	-0.023	-0.018
Survival (males)	-0.550	0.287	-0.152	1.062	0.233	0.283
Maturation slope, $r(\text{mat})$	-0.370	0.884	-0.186	1.418	0.098	0.136
Maturation intercept, $q(\text{mat})$	0.292	-0.664	0.156	- 1.154	-0.082	-0.113
Transition slope, $r(\text{trans})$	0.004	-0.783	-0.041	0.309	0.061	0.078
Transition intercept, $q(\text{trans})$	0.128	1.965	0.331	- 2.868	-0.216	-0.288

Notes: Results are for deterministic models, and represent the mean proportional change in the response variable following a 5% increase and 5% decrease in each model parameter (Eq. 10). Sensitivities >1 are in bold; these are parameters that will cause a proportional change in model output that is greater than the proportional change in the parameter.

rate of female fish (Table 4). However, the survival rate of males had the largest effect on equilibrium sex ratio. This suggests that management options that increase adult female fish survival through decreased fishing mortality will show the strongest response in population recovery rates and mean spawner population size, but sex ratio may be influenced more strongly by management options that increase male survival. The functions that determine the transition rates from female to male also have a strong proportional effect on model results, as shown by the relatively high proportional sensitivity of model results to changes in the transition intercept (minimum age of transition).

Model simulations indicate different mean recovery rates and equilibrium spawner population sizes for gag for each management option (Fig. 4). All active management options had positive effects on population growth rates relative to the status quo, with the fastest recovery rates occurring with a nearshore closure (plan 6, which reduced fishing mortality on females by 75% and eliminated fishing mortality for juveniles). A 50% reduction of fishing mortality for all life stages (plan 7) showed the second highest recovery rate and equilibrium population size. However, the equilibrium population size (number of spawning fish per year) for the nearshore closure was nearly double that of the 50% fishing mortality reduction option. Spatial closures focused on deep water habitats were most effective for model permutations with high fishing mortality; without displaced fishing mortality on females the spawning reserve was nearly equivalent to an overall 50% reduction in F (Fig. 4c and d). The efficacy of size limits and seasonal closures was low, particularly when fertility was strongly affected by sex ratio ($\theta = 20$).

The mean proportion of males in the adult population (sex ratio) varied through time as the age structures of

the model populations shifted (Fig. 5). There were no major differences in the projections for high and low fertility, so only two of the four model permutations are shown. All management options resulted in some improvement in sex ratio for the low fishing mortality rate permutations, but the sex ratio improvement in the nearshore reserve and 50% reduction in F management options were delayed due to the time lag for females to transform into males (Fig. 5a). However, when initial fishing mortality rates were high, the most rapid improvements in sex ratio resulted from spawning reserves, regardless of whether fishing effort was displaced as a result of the closure (Fig. 5b). Size limits and seasonal closures resulted in no improvement in sex ratio over the status quo in these simulations.

We summarized the 500 simulations for each model permutation and management option for recovery rates for the period 2001–2015, and female spawning stock biomass, sex ratio, and percent loss in potential productivity for the period 2020–2047 (Fig. 6). We based the mean population recovery rates on the slopes of the log-transformed spawner population (Fig. 6a). Note that some management options (e.g., the nearshore closure) reached equilibrium populations size prior to 2015 (Fig. 4); population growth rates for those permutations are based on slopes for the years 2001–2010.

Most management options provided some improvement in population growth rate (Fig. 6a) and in mean female spawning stock biomass (SSB; Fig. 6b), especially those involving large reductions in fishing mortality (e.g., nearshore closures and 50% reduction in F). Differences in the four model permutations were most evident in sex ratio (Fig. 6c) and lost larval production, measured as the proportion of fertilizable eggs produced that go unfertilized each year (Fig. 6d). Recall that in our model iterations, sex ratio is positively

TABLE 4. Extended.

Mean spawner sex ratio (proportion of males, 2020–2047)		Mean population size, adults (2020–2047)			
High <i>F</i>		Low <i>F</i>		High <i>F</i>	
Low θ	High θ	Low θ	High θ	Low θ	High θ
0.026	0.017	73 186	22 534	13 166	347 357
-0.031	-0.023	0.133	0.013	0.227	0.184
-0.040	-0.047	0.322	0.436	0.300	0.415
-0.039	-0.047	0.329	0.443	0.304	0.419
-0.071	-0.081	0.936	1.220	0.909	1.222
0.038	0.054	1.520	1.603	1.267	1.376
0.112	0.120	0.420	0.055	0.414	0.327
0.112	0.151	0.141	-0.041	0.388	0.308
-0.094	-0.126	-0.115	0.038	-0.323	-0.246
0.048	0.056	0.011	-0.089	0.105	0.080
-0.319	-0.408	-0.151	0.213	-0.839	-0.734

linked to fertilization rate at two fertility levels: high fertility ($\theta = 80$) and low fertility ($\theta = 20$) (shown in Fig. 3). Thus, management options that improve sex ratio (spawning reserves) show the greatest reduction in lost fertility (Fig. 6D), although the relative benefits of this enhancement for SSB and population growth rate depends on the sensitivity of the model to recruitment.

DISCUSSION

Our model projections demonstrate the relative effects of different management options on a protogynous hermaphrodite. Our approach can be generalized for other hermaphroditic species, and provides several model outputs that can be considered objectively to compare different management options.

Management options

Sustaining healthy populations of gag requires a management plan that optimizes population recovery, biomass, and sex ratio and fertility. In our four model permutations, the current level of fishing mortality experienced by gag populations has far greater influence on population trajectories than does fertilization rate. However, the fertilization rate chosen (low or high) had the largest influence on the results of those management options with the least impact on fishing mortality rates (size limits and seasonal closures, followed by spawning reserves). Because our choice of management options intentionally maximized the reductions in fishing mortality, they may have swamped the more subtle effects of fertilization success.

Our ability to detect differences among management options following model outputs and real populations depends on the amount of variance experienced by the population and the sensitivity of the model to changes in age- and sex-specific survival rates. All four of our model permutations show that size limits alone do little

to promote population recovery, and fail to recover natural sex ratios over the long term (Fig. 6), regardless of whether we assume low or high fishing mortality rates or low or high fertilization success. Increasing the size limit may actually aggravate the sex ratio skew, because more young females survive, but they do not survive long enough to change sex. A seasonal closure results in moderate population growth and increased biomass, but fails to improve sex ratio or productivity because males are not protected throughout the year.

The most rapid population recovery and highest female SSB occur when females are protected in nearshore habitats (75% reduction in female fishing mortality). However, this option has little effect on sex ratio, at least over the short term, compared with management options that also protect males and/or spawning sites. When we applied nearshore protection in the model, we did not increase the fishing mortality rate on offshore populations, although one might expect this to occur if fishermen shift their effort further offshore when restricted from fishing in nearshore sites. In fact, this is what often occurs when increased size limits are imposed, because gag tend to increase in size with depth (Coleman et al. 2000). We did, however, increase the fishing mortality rate on nearshore females when we established permanent deep water closures to simulate this effect, with the result of reduced skewing in sex ratio but very slow population recovery.

While we focus on management options that protect older and larger fish, inshore habitats critical for settlement of pelagic juvenile gag should not be neglected. Sensitivity analysis showed that population growth and size were relatively more dependent on early juvenile survival than female transition-to-male probabilities and adult male survival (Table 4). Protection of critical juvenile habitats, such as seagrass beds, also ensures a high carrying capacity for these potentially limiting habitats (Koenig and Coleman 1998).

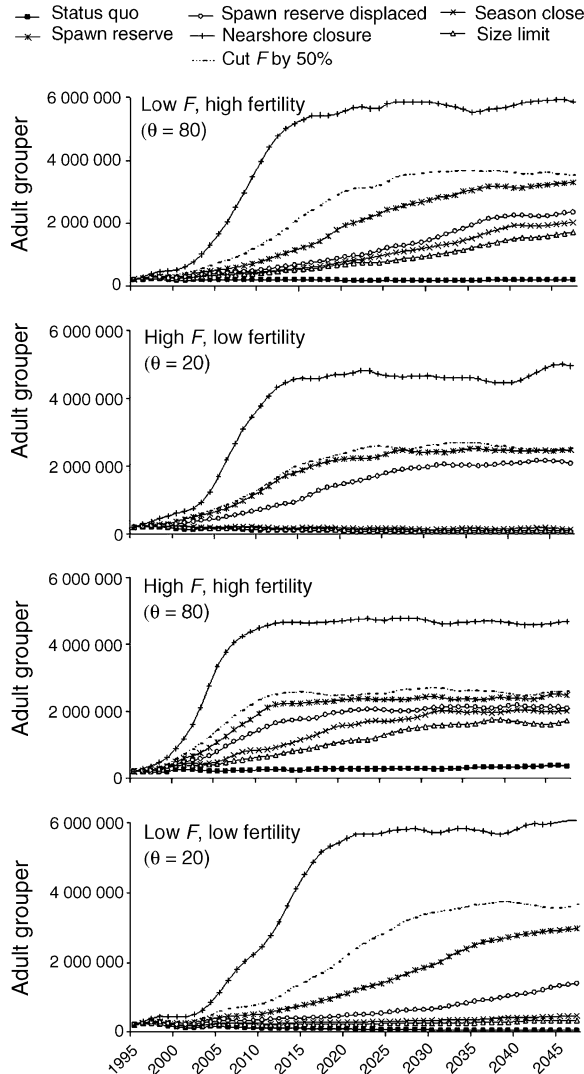


FIG. 4. Projections of spawning stock size (adult grouper) over time for model permutations with two levels of fishing mortality (see Table 1) and two fertility rates (high fertility, $\theta = 80$; low fertility, $\theta = 20$; Eq. 8). Each projection represents one of seven different management scenarios shown in Table 2, and the mean of 500 model runs with stochastic recruitment.

Model parameterization and uncertainty

This study represents a heuristic exercise demonstrating model population responses to large perturbations in fishing mortality rates for different age classes. Model results were primarily influenced by uncertainty in annual survival rates (Table 4). In the most recent gag stock assessment, fishing mortality rate estimates for fish aged nine and greater (mostly males) ranged from $F = 0.1$ to 0.6 , depending on the assessment model, with no differences in F attributed to sex and no indication of higher mortality rates on older fish for a particular model (Turner et al. 2001). There is some indication that males experience higher mortality

rates than females on spawning sites (Gilmore and Jones 1992), which could lead to significant changes in sex ratio, as well as the reduced fertilization rates and production estimates included in our models. However, we were unable to achieve a good fit to the sex ratios at age observed by McGovern et al. (1998) with a higher fishing mortality rate on males. Age and growth parameters and fecundity at age parameters were based on published literature values that likely vary from population to population, over time, and may be density dependent. This underscores the need for qualitative interpretation of our results.

Our model fitting technique to determine maturation and transition to male probabilities assumes that these rates are age specific, density independent, sex ratio independent, and deterministic. Transition probabilities for many hermaphrodites are size specific and responsive to the existing sex ratio (Ross 1990, Alonzo and Mangel 2004), so large year classes may experience very different transition rates than smaller cohorts. Further monitoring and analysis of age-specific trends in sex ratio, particularly in locations with contrasting levels of fishing mortality, are needed to improve estimates of transition probabilities.

Sex ratio considerations

Hermaphroditic species in general are unlikely to withstand the same intensity of fishing as gonochoristic species unless females compensate by changing sex at younger ages (Bannerot et al. 1987, Shepherd and Idoiné 1993, Huntsman and Schaaf 1994, Coleman et al. 2000). In our model, small changes in the age-specific likelihood of transition (sex change from female to

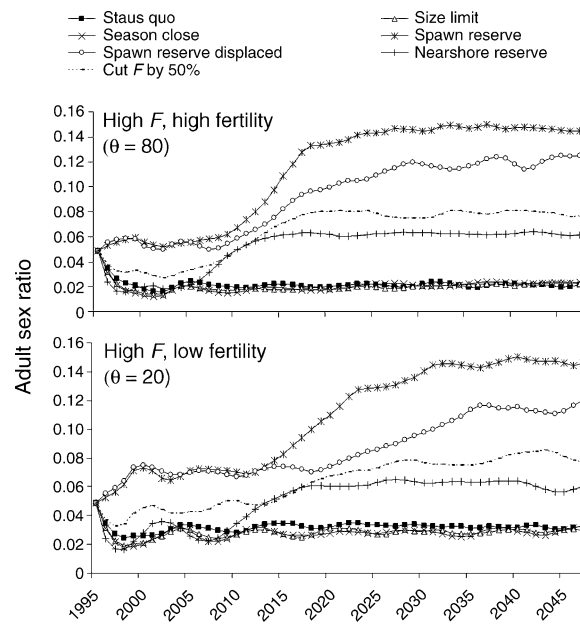


FIG. 5. Projections of adult sex ratio (proportion male) for the same models and management scenarios given in Fig. 4.

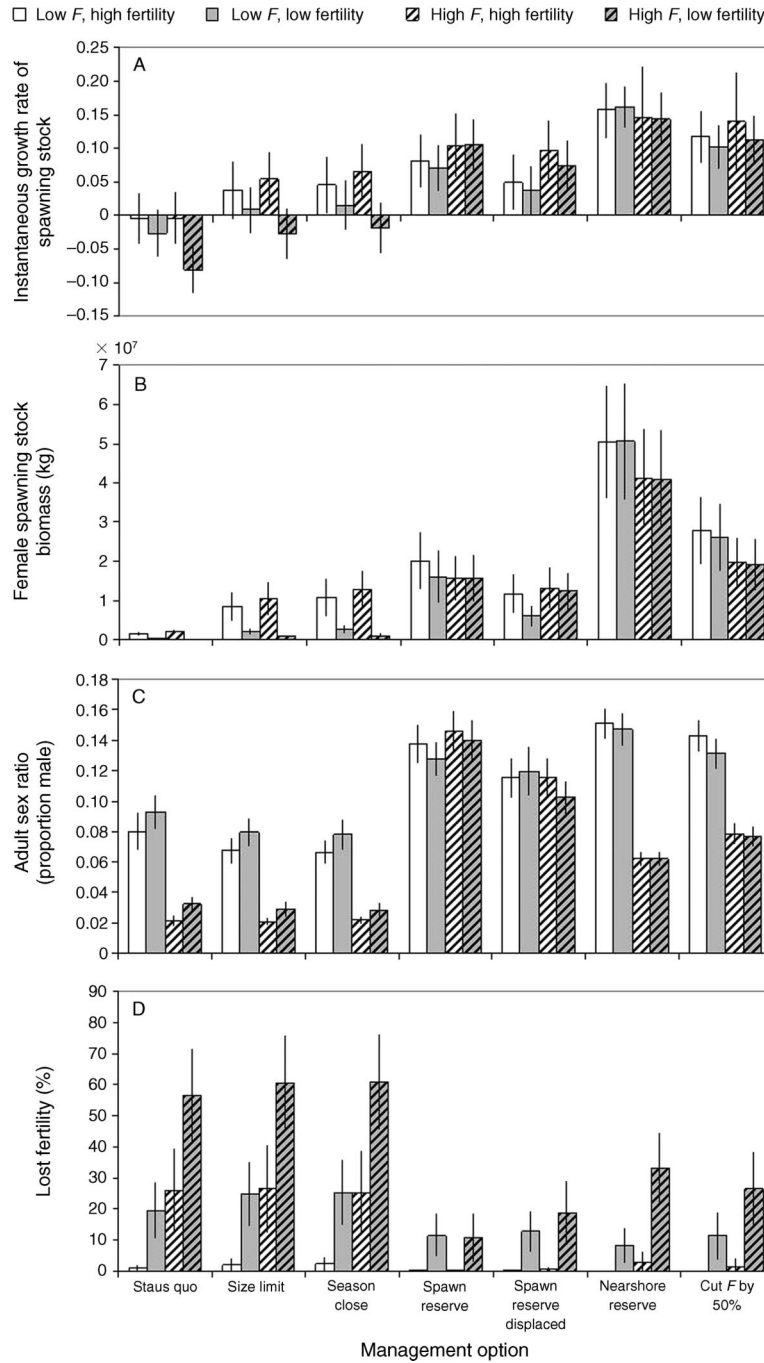


FIG. 6. Summary of results derived from the four models with seven alternative management options described in Table 2. (A) Mean \pm SD of slopes of ln-transformed adult population sizes (instantaneous population growth of spawning stock) for 500 model runs over the time period 2001–2015. Error bars represent SD of the 500 slopes. (B–D) Means \pm SD for results from 500 model runs averaged over the years 2020–2047. (B) Female spawning stock biomass, calculated by age–length (Eq. 3) and length–mass (Eq. 4) relationships. (C) Adult sex ratios. (D) Potential lost productivity, as the percentage of eggs that went unfertilized due to a lack of males in the population, determined by the fertility relationship shown in Fig. 3.

male) significantly influence sex ratio, population size and population growth (Table 4). The high sensitivity of sex ratio to transition probability is not surprising, but it is interesting because it reveals the importance of this variable in population dynamics. Current data

for gag indicate that a compensatory shift to sex change at a younger age occurs, but does not keep pace with fishing mortality (McGovern et al. 1998, Koenig et al. 2000). The reason lies in idiosyncrasies of the gag social system. Gag differ from many other hermaphro-

ditic species because males and females are separated spatially for most of the year. Any assessment of sex ratio that might influence the rate of sex change must occur during the spawning period.

In the model, when F is set to zero for all age classes, the equilibrium sex ratio is approximately 3:1 female to male, which is lower than expected for a species with this type of life history (Allsop and West 2004), and results from the relatively early age at sex change and low natural mortality among males. When intensive fishing on gag spawning aggregations started in the 1970s, sex ratios were on the order of 6:1 female to male (Hood and Schlieder 1992). We suggest that in unexploited populations, the transition-to-male probability shifts to older age classes, thereby increasing the proportion of older, larger, more fecund females. Increasing the minimum age at sex change by 3 yr and decreasing the slope parameter $r(\text{trans})$ by 50% (Table 1) under conditions of $F = 0$ for all age classes reduced the sex ratio to 5:1 female: male in both models. These changes correspond to a 1–2 yr increase in the specific age class that produces 50% males.

Currently, there are no empirical estimates of fertilization success and its relationship to sex ratio, although studies underway to investigate rates of atresia in female gag from spawning aggregations within and outside of reserves (F. C. Coleman and C. C. Koenig, unpublished data) should cast some light on this. In general, because mean fertility has relatively little impact on population growth and recruitment includes a strong stochastic component, fertilization success must be extremely low to significantly influence population dynamics in our model. However, recruitment variability may also be affected by sex ratio; the probability of strong year classes could be reduced if the population as a whole is not spawning optimally.

Future considerations

In these simple models, we have not considered the importance of social structure in gag populations. The relationship between harem size and fecundity may be an inverse one—that is, fecundity may decrease as harem size increases and females compete for fewer available mates (Greene et al. 1998). Further, if harem size is constant, then there are many females that will remain unmated as sex ratio declines.

We also do not consider the potential consequences of male absence on reproductive behavior. If sex change and spawning activity depend on males exhibiting aggressive behaviors related to territory defense or courtship, then male absence could compromise reproductive success even further. All of these behaviors appear to be androgen dependent with positive feedback loops (Kindler et al. 1989, Cardwell and Liley 1991, Hourigan et al. 1991, Oliver et al. 1995). In the absence of positive feedback (few males), reproductive capacity may be compromised.

Conclusions

Our modeling framework is flexible, robust, and can be modified as better data are collected. Because our model is not spatially explicit, the results must be compared in a qualitative manner rather than applied to specific populations. Particular research needs that would improve the model for gag and other hermaphroditic species include a reliable stock–recruit function and a function for fertility and sex ratio, as well as information on migration and habitat use that would allow parameterization of a spatially explicit model.

Coleman et al. (2000) and others have argued that marine reserves that protect spawning sites are necessary for conservation of gag and other grouper. They also acknowledge that spawning reserves do not benefit all segments of the population because of ontogenetic shifts and sex-specific variability in their spatial and temporal distribution (Gerber and Heppell 2004, Gerber et al. 2005). Our results suggest that protection of gag populations warrants a combination of reserves and other management practices such as reduced effort, although a dramatic decrease in F (50% for all age classes) alone also results in population recovery and, eventually, an increase in the proportion of males in the population. Because males represent such a small proportion of the current population, reserves that target only males and spawning females may be ineffective unless combined with lower fishing mortality rates on females, either through reduced effort or by spatial protection. We conclude that sound management of gag—and perhaps of hermaphrodites in general (Bannerot et al. 1987, Levin and Grimes 2002)—calls for a conservative management approach that integrates catch and effort controls with spatial closures.

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