

**MODELING GAG GROUPER (*MYCTEROPERCA MICROLEPIS*) IN THE GULF OF
MEXICO: EXPLORING THE IMPACT OF MARINE RESERVES ON THE
POPULATION DYNAMICS OF A PROTOGYNOUS GROUPER**

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Master of Science

in

The Department of Oceanography and Coastal Sciences

by
Robert D. Ellis
B.S., University of California Santa Barbara, 2004
August 2009

ACKNOWLEDGEMENTS

I would like to thank the State of Louisiana Board of Regents for funding this research with an 8G Fellowship. My research and thesis were greatly improved by the comments and assistance of many people, first among them my advisor Dr. Joseph Powers who provided valuable insight into the research process as well as general guidance and advice regarding my education. Thanks also to my committee members Dr. Dubravko Justic and Dr. Jay Geaghan whose comments throughout the process helped me to improve this thesis, and to Dr. Kenny Rose, in whose class the first version of the IBM was written, who provided not only valuable assistance with coding but also was a constant competitor on the basketball court.

Thanks go out to all the assorted graduate students from the Department of Oceanography and Coastal Sciences and the members of the Marine Environmental Researchers, especially the other members of the Powers Lab, Shane Abeare and Melissa Hedges, and my office-mate Christian Briseno. Lastly, thanks to my mom for her unflagging confidence in her son, and to my grandfather for his constant encouragement throughout my academic life.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	ii
ABSTRACT.....	v
CHAPTER 1: GENERAL INTRODUCTION.....	1
1.1 Gag Life History.....	1
1.2 Review of Protogyny.....	5
1.3 Marine Reserves.....	8
1.4 Managing Protogynous Fish Stocks.....	11
1.5 Objectives and Modeling Approaches.....	13
CHAPTER 2: AGE-STRUCTURED MODEL.....	16
2.1 Introduction.....	16
2.2 Methods.....	18
2.2.1 Model Description.....	18
2.2.2 Management Options.....	23
2.2.3 Model Simulations.....	25
2.3 Results.....	26
2.4 Discussion.....	32
CHAPTER 3: INDIVIDUAL BASED MODEL.....	37
3.1 Introduction.....	37
3.2 Methods.....	39
3.2.1 Model Description.....	39
3.2.2 Management Options.....	44
3.2.3 Model Simulations.....	47
3.3 Results.....	48
3.4 Discussion.....	56
CHAPTER 4: DENSITY-DEPENDENT SEX CHANGE.....	60
4.1 Introduction.....	60
4.2 Methods.....	64
4.2.1 Age-Structured Model.....	64
4.2.2 Individual Based Model.....	67
4.3 Results.....	69
4.3.1 Age-Structured Model.....	71
4.3.2 Individual Based Model.....	76
4.4 Discussion.....	80
4.4.1 Age-Structured Model.....	80
4.4.2 Individual Based Model.....	82
4.4.3 General Considerations.....	84
CHAPTER 5: MODEL COMPARISON AND CONCLUSION.....	86
5.1 Model Comparison.....	86
5.1.1 Fixed Sex Change.....	86

5.1.2 Density-Dependent Sex Change.....	92
5.2 Management Recommendations.....	93
5.3 Conclusion	95
REFERENCES	97
APPENDIX A: AGE-STRUCTURED MODEL CODE.....	102
APPENDIX B: INDIVIDUAL BASED MODEL CODE.....	113
VITA.....	124

ABSTRACT

The gag grouper (*Mycteroperca microlepis*) population in the Gulf of Mexico supports both a commercial and recreational fishery but has experienced a decrease in the male to female sex ratio over the past thirty years. Protogynous fish populations naturally have a smaller male to female ratio than gonochoristic fish populations; however the decline in the gag population is such that sperm limitation may be occurring. In an effort to correct the decline in sex ratio, fishery managers have recently implemented two marine reserves designed specifically to protect gag spawning aggregations.

Results from two population models (an age-structured model and an individual based model) suggest that utilizing marine reserves in the management of gag (a female-first protogynous grouper) may be an effective method to increase the male to female sex ratio in the population. Both models show that marine reserves can have a positive impact on sex ratio, but the effectiveness of marine reserves is a function of the magnitude and pattern of fishing effort. The inclusion of density-dependence to the sex change function of the models, in an effort to model socially-induced sex change, showed that the mechanism controlling sex change in the population will impact the population response to fishing. Socially-induced sex change may act as a buffer to high fishing mortality and increase the expected benefits of marine reserves. Both models successfully simulated a protogynous fish population and these methods may improve upon existing stock assessment models.

CHAPTER 1: GENERAL INTRODUCTION

Gag grouper (*Mycteroperca microlepis*) is a species of large grouper abundant in the Gulf of Mexico (GOM) and western Atlantic. Gag are long lived (up to 30 years), grow to maximum size of 145 cm, and have a protogynous life history, a type of sequential hermaphroditism where fish initially mature as females and later switch into males. As they mature, gag undergo a series of ontogenetic habitat shifts from seagrass beds to nearshore reefs and finally to offshore shelf-edge banks where they form spawning aggregations (Collins et al. 1998; McGovern et al. 1998; Coleman et al. 1996). The population of gag in the GOM supports both a commercial and recreational fishery. In the most recent stock assessment of gag in the GOM, it was estimated that the spawning stock biomass is large, so the stock is not considered overfished. However, the fishing mortality rate was estimated as above the desired threshold, so the fishery is undergoing overfishing. In addition, the ratio of male to female fish has declined from approximately 20% male in the 1970s to less than 4% male in 2004 causing some concern that the population may be experiencing sperm limitation due to a lack of males (SEDAR 2006).

1.1. Gag Life History

Like many grouper species, gag gather in large aggregations at specific sites to spawn (Coleman et al. 1996). Spawning aggregations as defined by Domeier and Colin (1997) are gatherings of conspecific fish in densities higher than those found during non-reproductive periods. This behavior is well documented in both large and small serranids such as the Nassau grouper (*Epinephelus striatus*; Colin, 1992), and the red hind (*Epinephelus guttatus*; Domeier and Colin, 1997). Most of the information regarding the location of gag spawning aggregations comes from interviews with commercial fishermen (Coleman et al., 1996). In the northeastern GOM, the main gag spawning habitat is located off the west-central coast of Florida in an area known as the Florida Middle Grounds, a bank of deep (50-120 m) reefs on the West Florida

Shelf (WFS). The WFS itself is comprised of two parallel carbonate ridges separated by a valley and makes up the most extensive area of high relief in the northeastern GOM (Nipper et al., 2007). Location of the main gag spawning area (Fig 1.1) is determined by the catch of fecund individuals. In general, gag caught in water deeper than 50m are more likely to be fecund than individuals caught in shallower water (Coleman et al. 1996). Because the bulk of the gag fishery is concentrated on the WFS it has been suggested that this is the major spawning area for gag grouper in the GOM (SEDAR 2006). However, there have also been documented spawning aggregations at the Campeche Banks on the northern edge of the Yucatan Peninsula in the southern GOM (Brule et al. 2003). Gag are also caught in south Florida and on the east coast up to North Carolina, so while the majority of spawning likely occurs on the WFS, spawning aggregations of gag probably occur elsewhere.

Gag grouper are considered to be winter-spring spawners, and time of spawning has been well documented by timing the catches of fecund individuals (McErlean, 1963; Hood and Schlieder, 1992; Coleman et al., 1996; Collins et al., 1997), and by dating the age of post-settlement larvae (Keener et al., 1988; Renan et al., 2006). The widest range of spawning time was found by Hood and Schlieder (1992) who found evidence of spawning from late December to early May. However, this may be an overestimate of the actual spawning period by including fish preparing to spawn and those that have completed spawning and moved away from aggregation sites. All cited studies agree that spawning occurs during late winter and early spring with the peak of spawning activity in February and March.

Following fertilization at shelf-edge spawning sites, gag larvae endure a 30 to 50 day planktonic stage before settling in estuaries (Fitzhugh et al. 2005). The use of estuarine habitat as nursery areas is well documented in the northeastern GOM (Fitzhugh et al., 2005), in south Florida (Casey et al., 2007), in the southern GOM (Renan et al., 2005) and in the

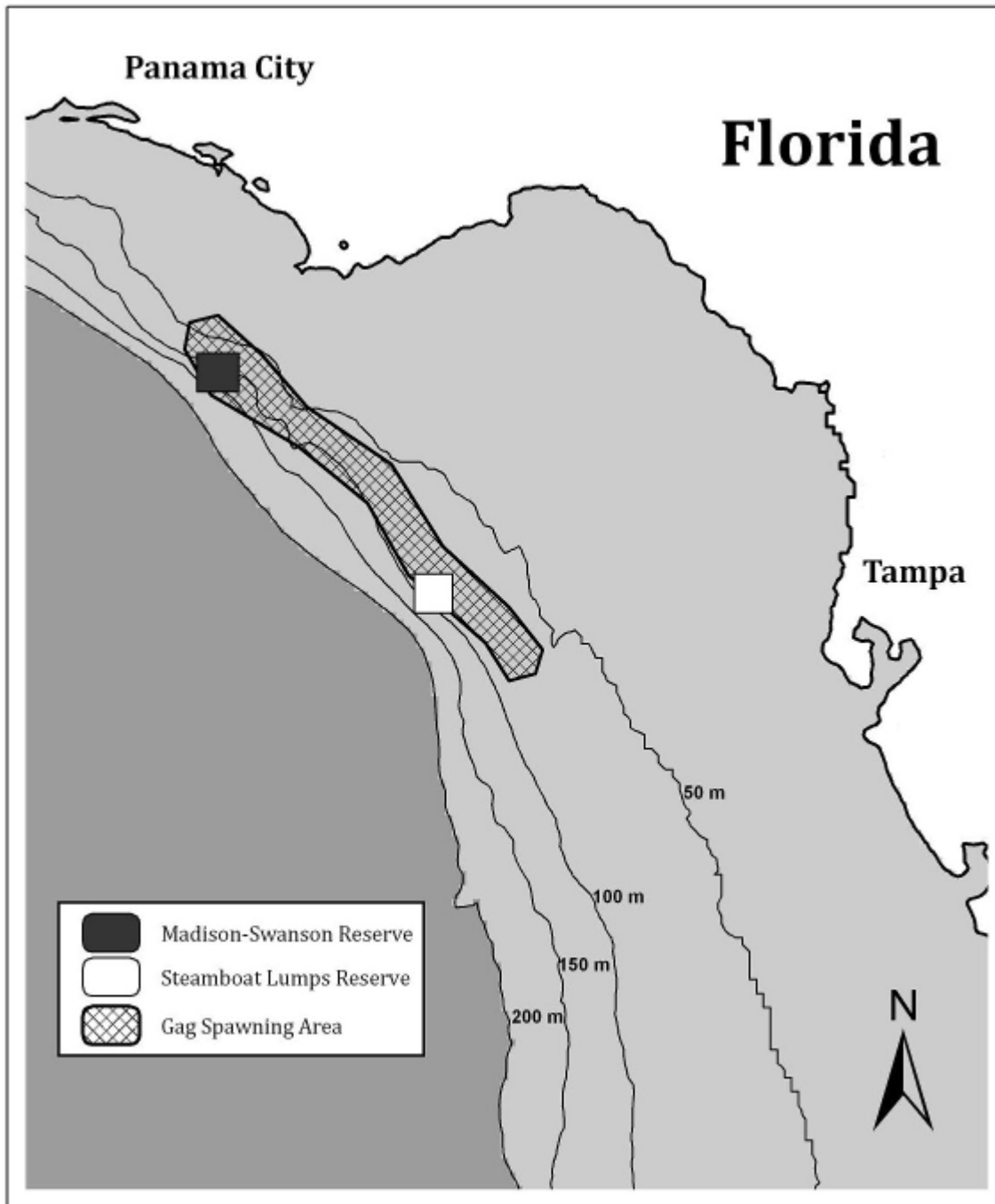


Figure 1.1. Map of the main gag grouper spawning area in the northeastern GOM showing the location and approximate size of the two gag-specific marine reserves.

Atlantic (Keener et al., 1998; Ross and Moser, 1995). Settlement begins in early April and usually concludes mid June. Keener et al. (1988) studied the ingress of gag larvae into estuaries in South Carolina and found that settling larvae had a mean age of 43 days and were relatively large upon entering the estuary. Estimates for larval duration in the GOM are similar. Within estuaries, a variety of substrate was found preferential to settling larvae. In the northeastern GOM, Koenig and Coleman (1998) found seagrass beds to be the preferred habitat for settling gag larvae, while Keener et al. (1988) found Atlantic gag settle on estuarine oyster reefs. Keener et al. (1988) also found that gag larvae were abundant in surface waters during flood tide and absent during ebb tide, behavior consistent with a vertical migration mechanism for larval ingress to an estuary.

Newly settled gag remain in estuarine nursery areas until the arrival of the first winter cold front, at which point they resettle on nearshore reefs (Ross and Moser 1995; McGovern et al. 1998). Juvenile gag inhabit nearshore reefs until reaching sexual maturity, when they start yearly migrations out to the shelf-edge spawning sites to mate. Evidence from both fishery dependent data (Hood and Schlieder 1992) and from tagging studies (Moe 1966; Van Sant et al. 1994; McGovern et al. 2005) reveal a positive trend between depth and size: as depth increases so does the mean size of gag. This data supports the hypothesis of juvenile resettlement and also suggests that gag continue to move offshore as they grow. Females spend the majority of the year at depths of less than 30 m and migrate offshore only to mate (McGovern et al. 1998). Following sex change, male gag stay offshore at the spawning sites year round (depth 50 to 80 m; Coleman et al. 1996). High site fidelity by males is common for species that form spawning aggregations (Gilmore and Jones 1992). Site associated males which exhibit little movement is a key factor in determining the potential efficacy of marine reserves for use in managing the gag fishery.

1.2. Review of Protogyny

In addition to a life history featuring a series of ontogenetic habitat changes, gag also experience a complex pattern of sexual maturity. Protogyny, or female-first sequential hermaphroditism, has been identified as a life history strategy in many fish families, and is commonly found in members of the Serranidae (groupers), Sparidae (porgies), and Labridae (wrasses) (Sadovy de Mitcheson and Liu 2008). Of many hypotheses offered to explain the adaptive significance of sex change, the one commonly accepted is known as the size-advantage model (Ghiselin 1969). The size-advantage model states that sequential hermaphroditism arises when there is a size advantage for a specific sex. This is the accepted explanation for protandry (male-first sequential hermaphroditism) due to the fact that eggs are more energetically expensive to produce than sperm: by delaying the female stage until an individual has obtained a larger size, that individual will be better suited to producing eggs. Warner (1974) expands on this hypothesis stating that selection pressure will favor sequential hermaphroditism as long as an individual will have a higher lifetime reproductive output as a hermaphrodite than not. However, some other mechanism, such as complex sexual behavior, male care for young or intense sexual selection is often cited to more fully explain sequential hermaphroditism (Ghiselin 1969). Gag form harem spawning aggregations, a complex behavior that implies larger males will have a reproductive advantage over smaller ones if they are able to better compete for females. Thus, sex change in gag is delayed until individuals are large enough to compete for harems.

While the evolutionary advantage of protogyny may be theoretically apparent, the mechanism for triggering sex change in individual fish is less clear. Two common hypotheses used to explain the initiation of sex change in individual fish are size-mediated control and socially-mediated control. The size-mediated control hypothesis states that sex change only occurs once an individual has reached a fixed size threshold. The specific size threshold is likely

controlled by physiological factors. 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. These cues can take the form of the sex ratio of other fish encountered (Shapiro and Lubbock 1980) or the size ratio of fish encountered (Ross et al. 1983). Both the sex-ratio hypothesis and size-ratio hypothesis imply that group composition cues initiate sex change in individuals. The size-ratio hypothesis relies on group composition cues but implies that sex change occurs when group composition reaches a threshold level of size differences (Lutnesky 1994). The sex-ratio hypothesis assumes that individuals are able to distinguish the sex of other group members (Ross, 1990). In general, both social-control hypotheses further assume that sex change is elastic with respect to individual size.

For gag there is confounding evidence over which mechanism controls sex change (size or social cues). From 1976 to 1995 the sex ratio of gag in the South Atlantic region decreased from 19.6% male to 5.5% male during which time the average size of transitioning females increased from 995 to 1025 mm and the average age at transition decreased from 11.7 years to 10.5 years (SEDAR 2006). In the GOM the sex ratio declined from 17% male in 1977 to less than 4% male in 2004, but with no corresponding decrease in the average size of transitioning females (size at 50% transition = 1100 mm; SEDAR 2006). While the Atlantic data suggests that gag are able to alter the age of transition towards younger fish, the GOM data suggests that transition may be fixed. As the sex ratio in a population declines, individual females will receive both sex and size-ratio cues as males are removed from the population. One possible explanation is that the two mechanisms work together on the population: above some minimum size threshold the average size of transitioning females changes via social cues, but once the size threshold is reached then sex change is fixed. 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) that often occur with large changes in population age structure. Despite a lack of conclusive data, it is generally assumed that sex change in gag is at least partially mediated by social control (SEDAR 2006).

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 corresponding drop in sex ratio has been observed in a number of heavily fished protogynous fish populations (Buxton 1993; Hawkins and Roberts 2003). High fishing mortality can also drive down sex ratio through the removal of large females, 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 been modeled in a number of species including graysby (*Epinephelus cruentatus*; Hunstman and Schaaf 1994), and gag (Alonzo and Mangel 2004; Heppell et al. 2006). Alonzo and Mangel (2005) 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.

The specific management actions used to manage a protogynous fish population should differ depending on the mechanism controlling sex change. If sex change is controlled by the size of the individual, it is most beneficial to reduce fishing mortality on all age classes. If sex change is socially controlled, the population may be able to adjust the rate of sex change to buffer the loss of males. In this case, necessary social cues are transmitted during spawning aggregations so it is important to reduce interruptions of social contact between fish by

protecting entire aggregations from fishing pressure. Koenig et al. (2000) argued that protection of spawning aggregations is the best way to reduce the impact of fishing pressure on the sex ratio of gag. One way to protect spawning aggregations from fishing pressure is to use marine reserves.

1.3. Marine Reserves

Marine reserves (also called marine protected areas, MPAs, or no-take zones) are areas in the ocean that where some activities, most often consumptive harvest, are restricted. Reasons for the use of marine reserves include protection of habitat and biodiversity, preservation of harvestable biomass and others. In the GOM marine reserves are used in the protection of critical habitat, to solve allocation issues, and increase yield or reduce fishing effort. In their review of GOM protected areas Coleman et al. (2004) found that marine reserves intended to resolve allocation issues were the most successful, and that failure was due to a lack of a priori planning, post-implementation monitoring and compliance, and because of mismatch between action and objective. So although marine reserves have been shown to positively impact fishery yield and abundance, problems in implementation and enforcement can reduce their utility as a management tool.

Many studies have shown the positive effects of marine reserves on marine communities and fisheries. Haplern and Warner (2002) reviewed 80 different reserves worldwide and found that the implementation of reserves resulted in a rapid increase in average density, biomass and diversity of animals in reserves. Perhaps more significantly, not only did the increases happen quickly, but they also were sustained through time. In an analysis of 58 European reserves, Claudet et al. (2008) found that size and age of reserves were positively correlated to density and species richness of fish within reserves. Larger reserves contained higher densities of commercially important fish, and older reserves had higher densities than younger ones.

Another analysis of marine reserves by Molloy et al. (2008) found that protogynous species benefited from marine reserve protection more than protandrous or gonochoristic species, but only in reserves that were more than a decade old. Because of the long time scales involved, marine reserves are often popular subjects for modeling efforts. After reviewing marine reserve models, Gerber et al. (2003) concluded that dispersal is an important factor influencing reserve efficacy. If marine reserves are well designed with respect to recruitment patterns of marine populations, then they can positively impact communities.

In terms of fisheries impacts, Roberts et al. (2001) found that marine reserves has a positive impact on the catch rates of artisanal fishers in South Africa. Fishers who targeted areas adjacent to the reserves had a higher catch per unit effort than fishers elsewhere. It is common for fishers to target areas immediately adjacent to reserves in order to exploit the higher density of fish within reserves. This is known as spillover, when a successful reserve can drive up the density of fish within its boundaries to the point where fish are forced out. Fisher behavior known as “fishing the line” has been shown to positively impact catch per unit effort (CPUE) in areas adjacent to reserves (McClanahan and Mangi 2000) and to impact fish density within reserves (Kellner et al. 2007). Fisher response to two reserves implemented in the GOM in 2000 followed this pattern as fishing effort increased along the edges of the reserves (GMFMC 2003).

The GOM reserves were created specifically to protect gag spawning aggregations in response to the observed decline in the sex ratio. They were created in 1999 when the Gulf of Mexico Fishery Management Council (Gulf Council) authorized the creation of the Madison-Swanson and Steamboat Lumps Fishery Reserves effective June 2000. The stated objectives for the reserves were to provide protection to spawning aggregations of gag, and also to a portion of the male gag population (GMFM 1999). The Madison-Swanson reserve is approximately 394 square kilometers in total area, and the Steamboat Lumps reserve is approximately 357 square

kilometers. Together they offer year-round protection to 751 square kilometers of gag spawning habitat which represents roughly 18 percent of known spawning area identified in 1996 by Koenig et al, although trolling is allowed during non-spawning months. The reserves were initially created with a four year sunset clause which was extended for six more years in 2004 and then indefinitely in 2008 (GMFMC 2003; GMFMC 2008). In 2008 the GMFMC also implemented a seasonal area closure known as The Edges that protects an additional 1338 square kilometers of gag spawning habitat from January to May each year. All together, the three reserves should protect about half of known spawning habitat during the time of spawning (GMFMC 2008).

Successful reserves not only require cooperation from fishers to not fish within their boundaries, but also that reserves are adequately sized so they can actually contain fish long enough to experience a reduction in fishing mortality and that they are properly located to ensure continuous recruitment of new individuals. Recruitment to marine reserves, and dispersal out of them, is an important issue in reserve efficacy. Modeling work by Gerber et al. showed that dispersal negatively impacted the benefits of marine reserves, but as long as there was a net positive movement into reserves, then they were more effective at increasing population growth rate than catch reduction (2005). One mechanism for ensuring adequate recruitment to reserves is to create a system of reserves over a large spatial area. Results from a network of marine reserves established on the Great Barrier Reef in Australia found the density of coral trout, a major target of local fisheries, was significantly higher within reserves across the entire network, an area over 1000 km across (Russ et al. 2008). For gag, there are identified mechanisms to account for both recruitment and dispersal. Female migration to spawning sites ensures that, as long as reserves are located to contain aggregation sites, there will be a supply of fish to reserves.

High site fidelity by males to aggregation sites year round potentially offers near total protection of older fish once they recruit to reserves.

Beyond supporting local fisheries through spillover effects there is the expectation that over time reserves will protect older and larger fish which will in turn have a larger reproductive contribution to the population. These older individuals supply eggs and larvae that are dispersed by ocean currents and recruit to other areas within the population, producing a reproductive reserve (Bohnsack and Ault, 1996). In a 2004 study, Domeier identified such a recruitment pathway from a marine reserve in south Florida to inshore grass beds by tracking drifter vials released at spawning aggregations of mutton snapper (*Lutjanus analis*). While such a pathway has not yet been empirically identified for gag,

Results from the two GOM gag reserves show some short-term localized success: the sex-ratio of gag within the reserves rose as compared to the population wide-estimate, and the National Marine Fisheries Service (NMFS) found gag spawning aggregations in both reserves along with an increase in the abundance and diversity of fishes inside the reserves (GMFMC, 2003; Smith et al., 2007). However, while there were significantly larger and more abundant fish within the reserves than outside, these results did not apply for gag but only other reef fish. Testimony from fishers indicates evidence of a spillover effect from the reserves (GMFMC, 2003). Based on the preliminary results, the gag spawning reserves appear to work insofar as they protect spawning aggregations.

1.4. Managing Protogynous Fish Stocks

Protogynous fish offer a unique challenge for fishery managers. Not only does it appear that size-selective harvest may have excessive impacts on sex changing fish (due to changes in the sex ratio discussed earlier), but also traditional measures of stock health may be inappropriate for use in describing protogynous fish stocks. The difficulties of managing protogynous fish

stocks using traditional management techniques and benchmarks have long been recognized. Bannerot et al. (1987) found that use of Yield Per Recruit (YPR; the expected lifetime yield per fish recruited to the stock) and stock production models (used to determine fishing mortality thresholds) may overestimate thresholds for protogynous species. By modeling gag, they were able to show that although protogyny should yield reproductive benefits over gonochorism, it also increased the likelihood of reproductive disruption at high mortality rates. The inherent complexity of the reproductive and life history of protogynous species narrows the range of assumptions under which traditional management techniques can work. Brooks et al. (2008) evaluated the performance of Maximum Sustainable Yield (MSY) based reference points such as F_{MSY} (fishing mortality at MSY), and S_{MSY} (spawning stock biomass at MSY) in a model assessment and found that including a measure of male biomass resulted in more accurate estimates of reference points. When only females were used to calculate the biomass of the spawning stock, the model assessment underestimated the S_{MSY} and overestimated the F_{MSY} which could lead to overfishing. Alonzo and Mangel (2005) evaluated Spawner Per Recruit (SPR; the reproductive production (usually in eggs produced) of fish recruited to the stock) measures using a model population and found that measuring egg production alone failed to account for fishing induced changes to the population. Buxton (1992) and Punt et al. (1993) both found that traditional YPR models of protogynous fish stocks failed to account for sex ratio effects that could lead to sperm limitation. In one case, when sex ratio was considered, the new model predicted recruitment failure where the YPR model encouraged increasing fishing mortality (Buxton 1992). In both cases, predicted recruitment failure was mitigated by upstream recruitment sources, presumably from unexploited stocks protected within marine reserves. In all the cited studies, the authors recommend the use of alternate measures of stock health when managing protogynous species.

1.5. Objectives and Modeling Approaches

Two simulation models were used to answer the same general question: how will the GOM gag grouper population respond to the addition of marine reserves designed to protect spawning aggregations? Marine reserves may be effective when used in the management of protogynous fish if they can protect some portion of the population from fishing pressure. Reserves that protect an intact portion of the fishery may prevent collapse by providing recruits to more heavily fished areas while reserves that protect only a specific life stage may prevent collapse by maintaining social structure and reducing the potential for reproductive failure. For gag, the particular pattern of males remaining at offshore spawning sites year round means that reserves designed to specifically protect spawning aggregations can fulfill both of these functions. The success or failure of marine reserves depends on a number of factors including the population response to reserves and changes in fishing effort, but also factors like compensatory sex change. More specific questions regarding the range of possible reserve size and variability of population characteristics were also tested with the models.

In order to better understand how these marine reserves impact the gag population, numerical modeling can be an informative tool. Gag live to a maximum age of 30 and on average do not switch sex to male for 10 years so an experimental study would require both a vast area component and a long time component. Using numerical simulations to study gag populations allows for a large number of management techniques to be tested in a short amount of time without negatively impacting the population or the fishery. Two models previously developed for the study of protogynous fish populations were picked to use in my thesis research. The first is an age-structured model of gag published by Heppell et al. in 2006, and the second is an individual based model (IBM) of wrasse published by Alonzo and Mangel in 2004. Both of these models consider protogynous fish populations and report population response to

marine reserves; however the models differ in approach. The age-structured model considers both processes and effects on the population level, while the IBM considers processes on individual fish while effects are summed up to the population level. Because of this, and the fact that the available data is usually considered at the population level, the age-structured model may be better suited to considering fishery management type questions. However, the IBM may be more revealing of smaller scale patterns which may be beneficial when considering a species that has complex mating behavior or high site fidelity such as gag.

Heppell et al. (2006) used their model to investigate a range of management options (including marine reserves) on gag and found that marine reserves had the greatest impact on sex ratio while reducing fishing mortality on young fish had the greatest impact on population size. However, they considered only 100% protection of spawning aggregations: would less protection (for example 18%) have the same affect on sex ratio, or is there a minimum size under which reserves are not effective? Their model results also showed that redistributing effort (modeled by a 25% increase in fishing mortality on vulnerable fish) reduced the impacts of marine reserves on sex ratio. The IBM developed by Alonzo and Mangel (2004) considered less than 100% reserves, and the results also indicated that redistributing fishing effort reduced the benefits of reserves. Closing an area to fishing probably does little to reduce the total amount of effort expended by a fishery. Smith et al. (2008) estimated that commercial fishers increased the total number of fishing days by up to 5% in response to a seasonal closure, enough to negate any perceived benefits. The total number of fishing days by all Florida fishers increased by 6.7% from 2001 to 2006 (US DOI 2001). Thus, fishing effort should be expected to increase over time and also to show short term responses to management actions. Both changes to the total amount of fishing effort, and redistribution of effort affected by area closures were considered in my study.

The specific mechanism that controls sex change in gag has not been conclusively described. While age and growth studies suggest that sex change occurs at a fixed size, the presence of complex sexual behavior suggests some social component is involved. Which control mechanism actually works on the population will have a potential impact on the population response to fishing (Alonzo and Mangel 2005). For this reason, I added density-dependence to the sex change function in both models in order to explore how social control will alter the population response to marine reserves.

I built both models following the descriptions provided by the original authors and parameterized them using the most recent stock assessment data (SEDAR 2006, 2007). Following this introduction, Chapter 2 describes the age-structured model, its development and results, and Chapter 3 describes the same for the IBM. These two chapters were written for ultimate submission as manuscripts for publication in peer-reviewed journals and so are meant to stand alone. They include a separate Introduction, Methods, Results, and Discussion, but for the sake of repetition some extraneous material was removed. Chapter 4 describes the inclusion of density-dependent sex change to both models and a discussion of how this changed the results from the previous chapters. Chapter 4 also includes an Introduction, Methods, Results, and Discussion but was not written to stand alone due to the large amount of repetition this would have caused. Chapter 5 contains a comparison of the two modeling approaches and their results, recommendations for management, and concludes with some general concluding remarks. Because all the chapters share most of the same reference material, a full bibliography is included following chapter 5.

CHAPTER 2: AGE-STRUCTURED MODEL

2.1. Introduction

As discussed in Chapter 1, marine reserves are increasingly utilized as a tool for managing marine resources. Properly designed, marine reserves have the potential to be effective means to protect and even increase biodiversity in areas suffering from overfishing. However, the utility of marine reserves for use in managing fisheries remains controversial. While evidence from existing marine reserves indicates that reserves can yield rapid positive changes to the biomass and density of fish within reserves (Halpern and Warner 2002), other work has shown that the size and age of a reserve has a strong influence on reserve success (Claudet et al. 2008). Poorly designed or misplaced reserves may be ineffective, but in general marine reserves can be a beneficial tool to protect fish stocks from overfishing (Gerber et al. 2003). It is imperative that new reserves are effective whether their goals are increasing fishery yield, maintaining marine populations, or protecting biodiversity.

One objective in developing a reserve is to maintain appropriate age, size and sex structures within specific fishery populations. Due to its life history and behavioral patterns, gag grouper is a fish that might benefit from the use of marine reserves in the management of the fishery (Koenig et al. 2000, Heppell et al. 2006). The observed shift in sex ratio over the last three decades, from approximately 20% male in the 1970s to less than 4% male by 2004 (SEDAR 2006) has brought marine reserves into the scope of management options for the fishery. The pattern of life stage separation, migration, and aggregation that gag undergo as an artifact of their life cycle is well known and exploited by fishers who target gag both inshore and at spawning sites. However, it is precisely this differential vulnerability to fishing pressure that provides the potential for marine reserves to be an effective tool for management. An age-structured model developed by Heppell et al. (2006) showed that management options that focus

on reducing the fishing mortality rate of older fish may be effective at increasing the sex ratio in the population. Gag, once they switch sex from female to male, stay at the offshore spawning aggregation sites year round. Protecting some or all of these sites with marine reserves (specifically no-take zones) will serve to reduce the fishing mortality rate on older fish and possibly increase the population sex ratio. Ignoring significant changes to population structure, such as a shift in sex ratio, can have long term implications in terms of stock health and fishery production.

In their model, Heppell et al. (2006) explored a range of management options for gag and found that decreasing fishing mortality of male gag had the largest impact on population sex ratio. However, when considering the management option of “marine reserves” they assumed this resulted in 100% protection for all males in the population. This situation is certainly not feasible for a fishery like gag, with both a strong commercial and recreational sector, both of which target spawning areas precisely to catch large males. Assuming that the actual amount of spawning aggregation area to be protected with marine reserves is less than 100%, how much of this area requires protection in order to observe a population-level effect on the male to female sex ratio?

This chapter describes the development of an age-structured model based on the one described by Heppell et al. (2006). I chose this model to replicate because of the ability to incorporate actual population data, and the ability to test a wide range of management options and track their effects on the model population. The model evaluated the population level response to a range of marine reserve sizes, as well as changes in the amount of effort expended by the fishery. In addition, I used the model to determine the minimum amount of reserve protection that will maintain sex ratio at predetermined benchmarks as a way to better formulate the results in terms that could be useful for fishery managers. Note that throughout the thesis I

use the term “sex ratio” to mean the ratio in numbers of males to females. Also, the term marine reserves specifically refer to year-round spawning area closures, and in this chapter that is described in terms of the percentage of total spawning area closed to fishing pressure.

2.2. Methods

2.2.1. Model Description

An age- structured population model based on Heppell et al. (2006) was used to predict the population sex ratio (measured as the ratio of males to females), adult population size, and fishery yield as a function of stage-specific fishing mortality. Model functions were used as defined in Heppell et al. (2006). Parameters of the growth, mortality, fertilization, fecundity, and maturation and sex transition probability functions were based on information available from the most recent stock assessment of gag (Table 1; SEDAR 2006). Fitting of parameters to stock assessment data was performed using SAS software, Version 9.1.3. The gag population model was partitioned into four stages that represent ontogenetic and habitat shifts experienced by individual gag during their lifespan. The stages are: age 1, juvenile (age 2 to sexual maturity), female (post-maturity to sex change), and male (post-sex change). Age 1 represents the number of recruits from the previous year that survived to settlement. All age 1 fish move to the juvenile stage at the end of the first year, while juveniles, females, and males follow stage-specific probabilities for transition to the next stage. The age range for each stage is left flexible, except for males which must be at least 6 years old.

Stages were subject to differential mortality used to represent changes in habitat utilization, behavioral characteristics, and fishing selectivity. Age-specific natural mortality rates utilized in the most recent gag stock assessment (SEDAR 2006) were based on a Lorenzen curve where the natural mortality rate declines with age (Fig. 2.1; Lorenzen 1996, SEDAR

2006). Natural mortality (M) was calculated for age i with equation 1, where ma and mb are scaling constants (see Table 2.1 for parameter values):

$$(1) \quad M_i = (ma) (i^{mb})$$

Weighted averages of observed proportions at age were used to convert age-specific mortality rates to stage-specific values for both natural and fishing mortality. Age-specific fishing mortality rates estimates were also obtained from the stock assessment. Stage-specific mortality is reported as an instantaneous rate and the values are shown in Table 2.1. Fishing mortality was altered by the variable $fmult$ for all fishing effort regimes that change the total fishing mortality on the population. Total mortality was calculated for age as the sum of the stage-specific natural and 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 ages i and stages j was calculated with equation 2:

$$(2) \quad A_{j,i} = \exp(-M_j - F_j \text{ fmult})$$

Fishery yield (Y) was calculated by weight with equation 3, where $N_{j,i}$ is the number at stage j , age i and $W_{j,i}$ is the weight at age and stage determined from the von Bertalanffy growth equation (shown in equation 4), and the length-weight relationship reported in the stock assessment (equation 5; SEDAR 2006):

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

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

$$(5) \quad W_{j,i} = (wa) (L_i^{wb})$$

The probability of maturation and sex change were modeled as functions of age. Maturation (the proportion of juvenile fish that mature to female) was restricted to ages two through five. Thus, all fish older than six were assumed to be sexually mature. Age six was also assumed to be the minimum age of sex change. Maturation and transition probabilities remain

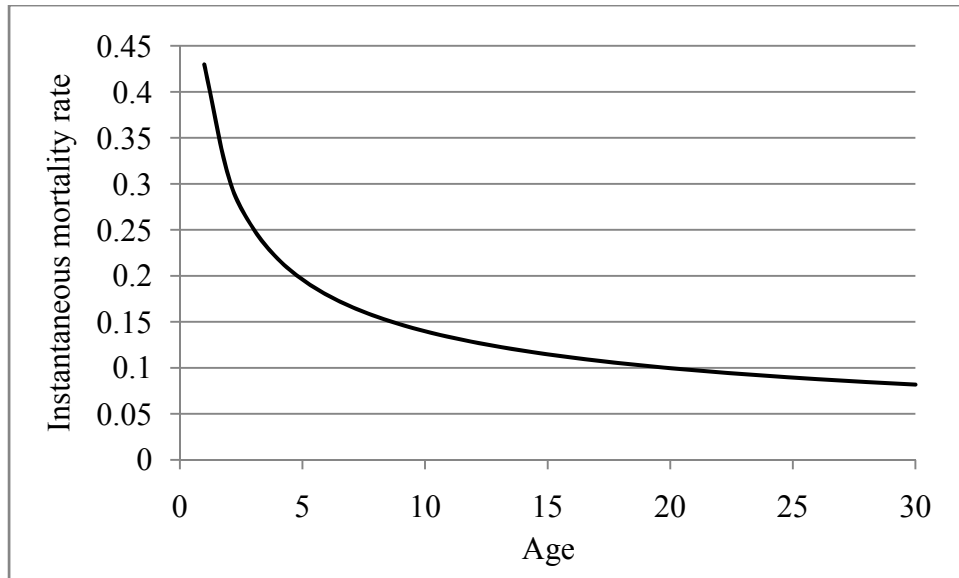


Fig 2.1. Natural mortality as a function of age for gag grouper in the GOM based on the Lorenzen curve used in the stock assessment (SEDAR 2006).

constant for the duration of all model simulations. Parameters for these probability functions were estimated using the observed proportions at age from the stock assessment (Fig. 2.2; SEDAR 2006). Following the method described in Heppell et al. (2006) a model age distribution was developed using the fishing mortality rates (Table 2.2) and assuming constant recruitment. Transition rates were fit to the model distribution using by adjusting the slope and intercept parameters (r and q in the following equations) using least-squares analysis of the model proportions for each age class (Excel Solver, Microsoft Office 2007, Microsoft, Richmond, Washington, USA). Equation 6 describes the probability of maturity for age i , and equation 7 describes the probability of sex change for age i :

$$(6) \quad P(\text{mat})_i = 1 / [1 + \exp^{-(r_{\text{mat}} - (i) (q_{\text{mat}})})]$$

$$(7) \quad P(\text{sex})_i = 1 - \exp^{[r_{\text{sex}} (i - q_{\text{sex}})]}$$

Fertilization success (the proportion of eggs successfully fertilized) was modeled as a function of the fertilization parameter (Θ) and the proportion of males in the population. Based on data reported by Fitzhugh et al. (2006), approximately 10% of females fail to spawn during

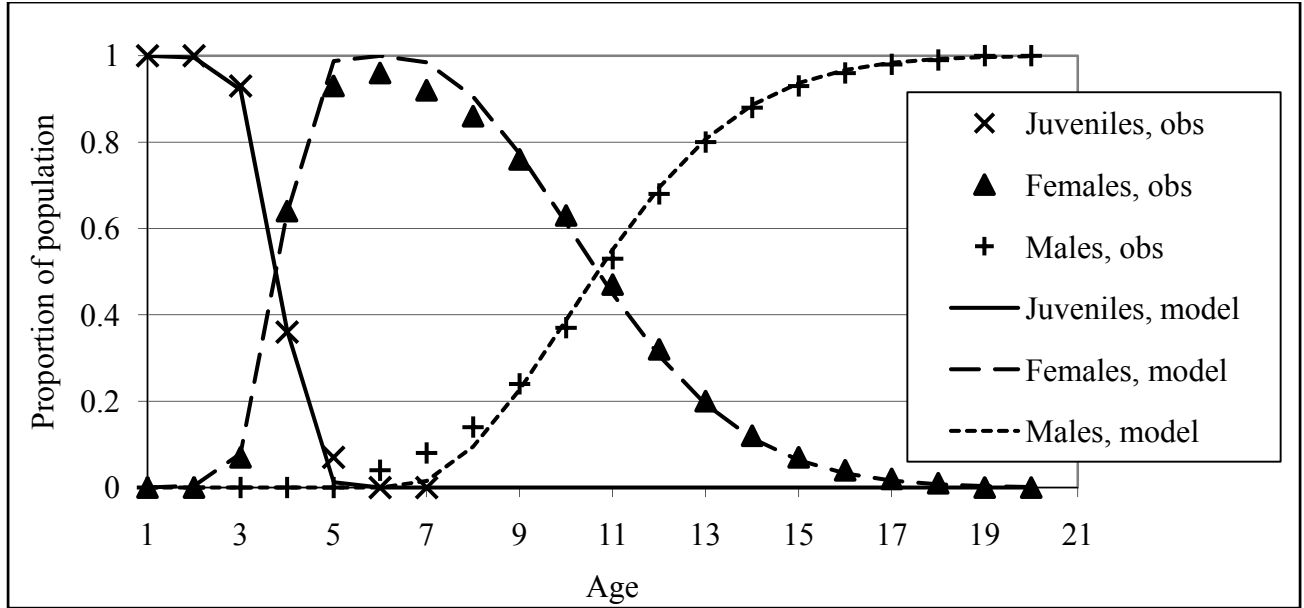


Fig. 2.2. Observed and predicted proportions by stage (juvenile, female, and male); observed values were reported in the stock assessment (SEDAR 2006) and predicted values were calculated with the transition probability functions described in the text.

years when the sex ratio fell below 5% male. Thus, Θ was defined such that fertilization success was reduced by 10% when the proportion of males was 5% (Fig. 2.3). It is assumed that a limitation of males induces reductions in reproductive success in a portion of the female population and that this pattern will become more prevalent should the proportion of males continue to decline. The parameter Θ describes the rate of that decline. Fertilization success, $P(\text{fert})$, was calculated for the entire population once per time step as a function of Θ and the population sex ratio (p_{male} , which is calculated following mortality and sex change):

$$(8) \quad P(\text{fert})_t = 1 - \exp^{-\Theta (p_{\text{malest}})}$$

Fitzhugh et al. (2006) also found that per capita egg production increases linearly with age, and was calculated using equation 9, where Eggs_i is the per capita egg production of a female of age i . Total egg production for each year t is the sum of Eggs_i times the number of females age i in year t , shown in equation 10:

$$(9) \quad \text{Eggs}_i = 2 \times 10^6 (i) - 4 \times 10^6$$

$$(10) \quad Etot_t = \sum_i Eggs_i N_{i,t}$$

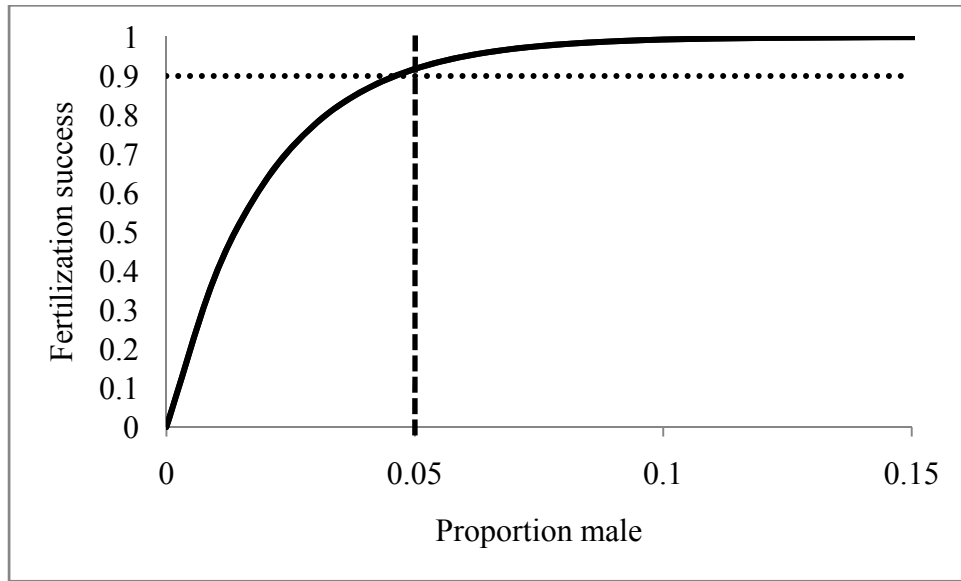


Figure 2.3. Relationship between fertilization success and proportion of males present in the population, showing 10% loss of fertilization success at 5% males.

Recruitment, R_t , (the number of age 1 individuals entering the population in year t) is a function of total egg production ($Etot$), fertilization success ($P(fert)$), and the survival probability of larvae surviving to settlement, which is a function of egg survival (S_E) and larval survival (S_L). Additionally, annual variability in recruitment was introduced into the recruitment function as a lognormal random deviate, Rv . The standard deviation of this deviate was determined by fitting a lognormal distribution to the reported recruitment estimates from 1986-2004 (SEDAR 2006). Recruitment was assumed to be limited to be below a maximum defined by the parameter Φ , so the number of recruits in year $t+1$ was calculated with equation 11 when R was less than Φ and with equation 12 when R was more than Φ :

$$(11) \quad R_{t+1} = Etot_t P(fert)_t S_E S_L Rv$$

$$(12) \quad R_{t+1} = \Phi S_L Rv$$

Essentially, this recruitment function is termed a two-line model in stock assessments, which approximates the behavior of the commonly used Beverton-Holt stock-recruitment model (Barrowman and Myers 2000). Thus, the stock-recruitment parameters are the egg survival S_E and the maximum recruitment, Φ . Egg survival implicitly is a production parameter and was set equal to the value which returned recruitment estimates equal to recent recruitment estimates from the stock assessment. In effect this assumes that current population conditions are stable.

2.2.2. Management Options

Alternative management options relating to spatial closures that protect spawning aggregation sites were examined. Management options were assumed to alter the vulnerability of fish to fishing effort which is reflected as a proportional change in the fishing mortality rate experienced by each stage. The management option scenarios were defined as the percent of the spawning area closed to fishing. The impact of percent closure on stage-specific fishing mortality rates were based upon the following. It is assumed that males identified with a protected site are protected from fishing mortality for the entire year, while females associated with protected sites are protected from fishing mortality for the amount of time they are associated with aggregation sites, or one-quarter of the year. Juvenile fishing mortality is not directly affected by spatial closures.

Six reserve scenarios, representing different amounts of reserve protection, were tested: 0%, 10%, 18%, 25%, 50%, and 100%. These scenarios represent a range of options for marine reserves in the GOM. These spawning reserve scenarios were then subject to 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 in juvenile, female, and male fishing mortality, $fmult = 1.1$;

- 4) “High” - 25% increase in juvenile, female, and male fishing mortality, $f_{mult} = 1.25$;
- 5) “Prop” – proportional increase in fishing mortality, $f_{mult} = 1.0$.

Table 2.1. Parameters used in the model, their description, source and value.

Parameter	Description	Source	Value
L_{inf}	von Bertalanffy growth curve asymptote	SEDAR (2006)	1310
k	vB growth curve slope	SEDAR (2006)	-0.14
t_0	vB growth curve x-intercept	SEDAR (2006)	-0.37
wa	Length-weight conversion intercept	SEDAR (2006)	1×10^{-8}
wb	L-W 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
F_L	Age-1 fishing mortality	SEDAR (2006)	0.0
F_J	Juvenile fishing mortality	SEDAR (2006)	0.4
F_F	Female fishing mortality	SEDAR (2006)	0.4
F_M	Male fishing mortality	SEDAR (2006)	0.33
r_{mat}	Slope of maturation probability	fit to SEDAR (2006) proportions at age	8.41
q_{mat}	Intercept of maturation probability	fit to SEDAR (2006) proportions at age	2.946
r_{sex}	slope of transition probability	fit to SEDAR (2006) proportions at age	0.0597
q_{sex}	intercept of transition probability	fit to SEDAR (2006) proportions at age	5.745

These fishing effort regimes represent a range of fisher responses to reserve implementation, as well as accounting for an overall increase in effort over time. For the Low, Mid, and High regimes, the increase in fishing mortality is calculated before the reduction for reserve area. The proportional increase regime assumes that total fishing effort does not decline with the addition

of reserves, so the redistribution multiplier D is used to alter fishing mortality according to the reserve scenario considered, where $D = 1 + \text{percent spawning area protected} / 100$.

Table 2.2 Baseline fishing mortality rate for each stage and the change in rate for the five marine reserve scenarios and five fishing effort regimes (MPA = marine reserve multiplier, and D = redistribution multiplier).

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

While it is unlikely that a system of marine reserves that entirely protect gag spawning sites can or will be implemented and fisher’s behavioral response to closures is uncertain, the model design allows for relative comparison of effects between treatments by comparing population response. Additionally, it is important to minimize the size of reserves while maintaining their effectiveness. To address this, “minimum effective size” was defined as the amount of protection necessary to reach and maintain a threshold proportion of males. Two threshold levels were examined: 5% and 10% both of which represent improvement over the current estimate of 3.46% male (SEDAR 2006). Finally, because the gag fishery supports a fishery, tradeoffs between fishery yield and the amount of closure were examined.

2.2.3. Model Simulations

Each simulation was run for 100 years with time steps of one year and then replicated 500 times. At each time step the age and stage distribution was updated for mortality, maturation, and sex change, and reproductive parameters were calculated to obtain the number of recruits for the Age 1 stage for the following year (see Fig. 2.5 for the model schematic). Model

simulations were initialized with a population of 9.6 million fish distributed into age classes estimated by the 2006 stock assessment (SEDAR 2006). Stage classifications were determined by maturation and transition probabilities fitted to these observations. Based on the initial age distribution, the starting adult population was 4.8 million fish with a sex ratio of 3.46%. Each marine reserve scenario was tested with each fishing effort regime for a total of 30 simulations. In addition, a range of fishing mortality rates was tested without any marine reserves. Response variables followed were total adult population in number, the male to female sex ratio, and the yield in biomass. Yield was only calculated for deterministic simulations. The mean value of the 500 replicates for each model year was computed. All simulations were run to equilibrium, defined as the condition where the response variable was flat with respect to time. For simulations that reached equilibrium, the value of each response variable is reported as the mean of the final 20 years of the replicate mean. Simulations that did not reach equilibrium were those in continuous increase or decline at the end of the time series, and are noted in the results. Because the variance of the results is a function of the predefined random coefficient in the recruitment equation, no further descriptive statistics are reported.

2.3. Results

Increasing the amount of spawning area protected resulted in an increase in the male to female sex ratio (Fig. 2.6), although the amount and pattern of effort redistribution had a large influence on the overall effectiveness of reserves. The model reached equilibrium within 30 years in every simulation. Increased fishing effort resulted in reduced effectiveness of reserves so larger reserves are needed in order to attain equal amount of sex ratio response. Adult population size responded like sex ratio (Fig. 2.7): increasing the amount of spawning area protected increased the equilibrium population. Fishery yield increased slightly with increasing reserves, but then declined when the area protected was large (Fig. 2.8).

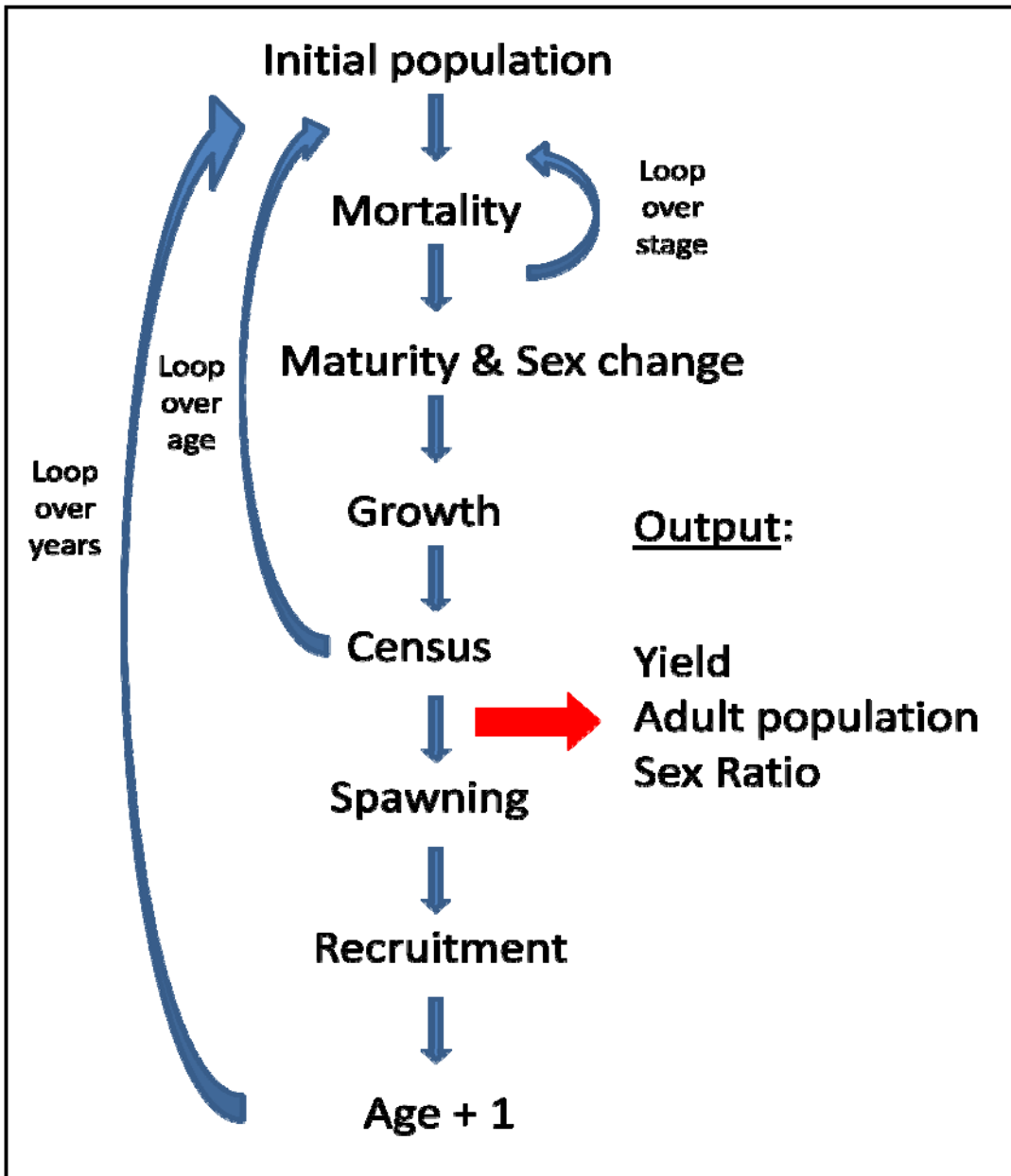


Figure 2.5. Model schematic showing the order that model functions are calculated for each time step, the output, and the nested loops within the model.

For all effort regimes, except proportional redistribution, reserve scenarios that protect adult fish result in a positive response in population sex ratio. Within effort regimes, the largest increase in sex ratio occurred with 100% spawning area protection. The equilibrium sex ratio for all reserve scenarios (including no reserves) was greater than the current estimate. For the status quo regime, defined as no increase in fishing effort and 18% of spawning area protected, the equilibrium sex ratio was 5.8% male, a 68% increase over the starting condition. The equilibrium adult population was less than the starting condition for every simulation. The average decline in the adult population within fishing regimes varied greatly and was dependent on the amount of spawning reserves; for example, the status quo regime with no reserves resulted in a 71% decline in adult population and with 100% reserves adult population declined by 63%. The High regime caused the adult population to decline by more than 90% when less than 25% of spawning area was protected. Equilibrium fishery yield was also less than the estimates of Maximum Sustainable Yield (MSY) for current fishing effort for every simulation (SEDAR 2006). For all effort regimes, yield increased to some point and then declined with the minimum yield occurring with 100% reserves (Fig. 2.8). As fishing effort increased, the point of inflection (or the maximum yield response) occurred with progressively larger reserves, with an average decline of 46% from current yield (Table 2.3).

All three metrics (sex ratio, adult population, and yield) showed a negative relationship to increased effort. However, when effort increased proportional to the amount of area closed the results were quite different. Sex ratio declined from 0% reserves to 52% reserves before increasing with reserve size (see Fig 2.6). The overall change in sex ratio from the initial value was positive for all reserve sizes, but reached a maximum with 100% reserves (97% increase from initial sex ratio) and a minimum with 52% reserves (10% increase). Adult population and fishery yield were largest with no reserves and decline as reserve size increased (see Fig. 2.7 and

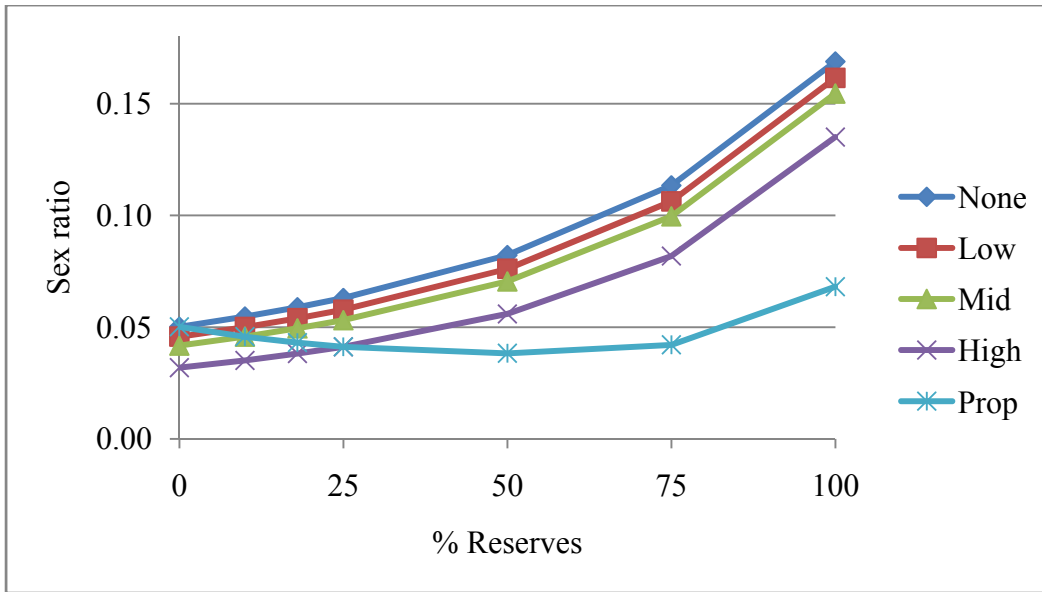


Figure 2.6. Sex ratio response to increasing reserve size and five levels of fishing effort change defined in the text, initial sex ratio was 3.46%.

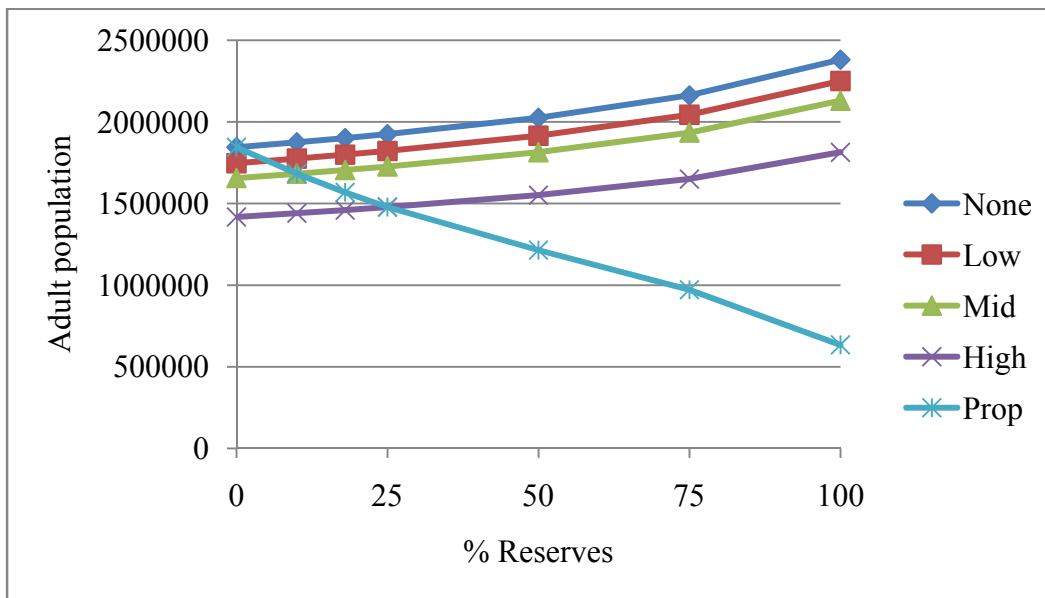


Figure 2.7. Adult population size response to increasing reserve size and five levels of fishing effort change as defined in the text, initial population was 4.8 million adults.

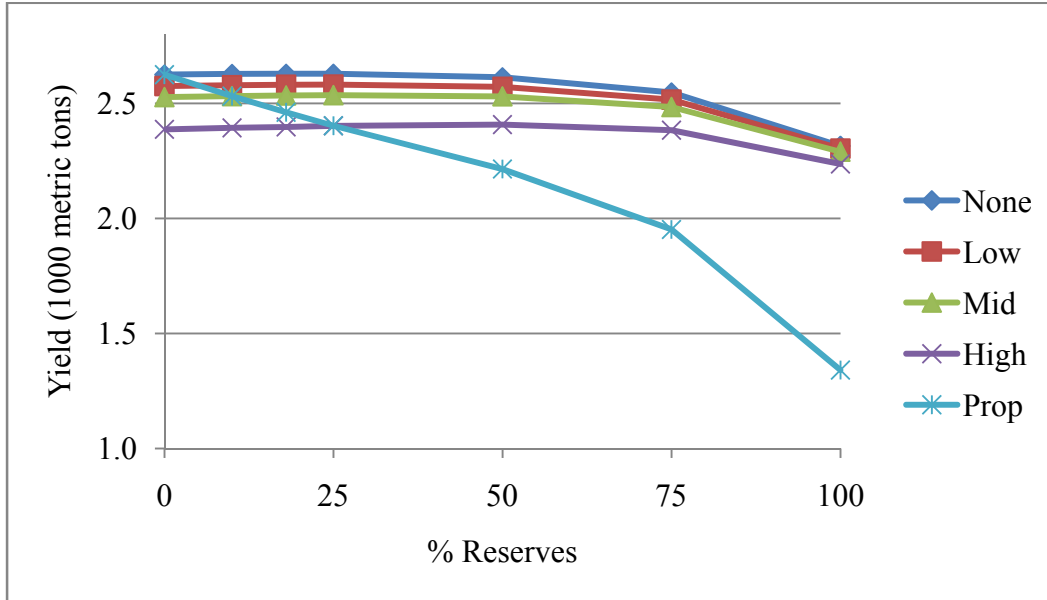


Figure 2.8. Yield response curves for increasing reserve size and five effort change scenarios under deterministic model conditions. The estimate of maximum sustainable yield for GOM gag at current fishing mortality is 3932 metric tons (SEDAR 2006).

Table 2.3. Change in yield with and without reserves.

Effort increase	% Reserves	% Decline w/ reserves	% Decline w/o	% Change
0	20	44.4	44.5	0.1
5	26	45.4	45.6	0.2
10	32	46.3	46.6	0.3
25	45	49	49.5	0.5

2.8). As reserve size increased, the fishing mortality rate experienced by fish not protected by reserves increased to the largest value under the proportional redistribution regime, which is reflected by the values for adult population and fishery yield at high reserve size.

The minimum reserve size necessary to maintain male sex ratio at the 5% and 10% benchmarks increased as fishing effort increased (Fig 2.9). With no increase in fishing effort, no reserves were needed for the population to stabilize with more than 5% males. Minimum reserve size increased linearly with increased effort for both benchmarks although the two lines had significantly different slopes ($p < 0.01$). The results for the proportional redistribution regime are not included in this analysis because there are multiple minimum reserve sizes that attained the 5% male benchmark (0% and 88% reserves), but no reserve scenario attained 10%.

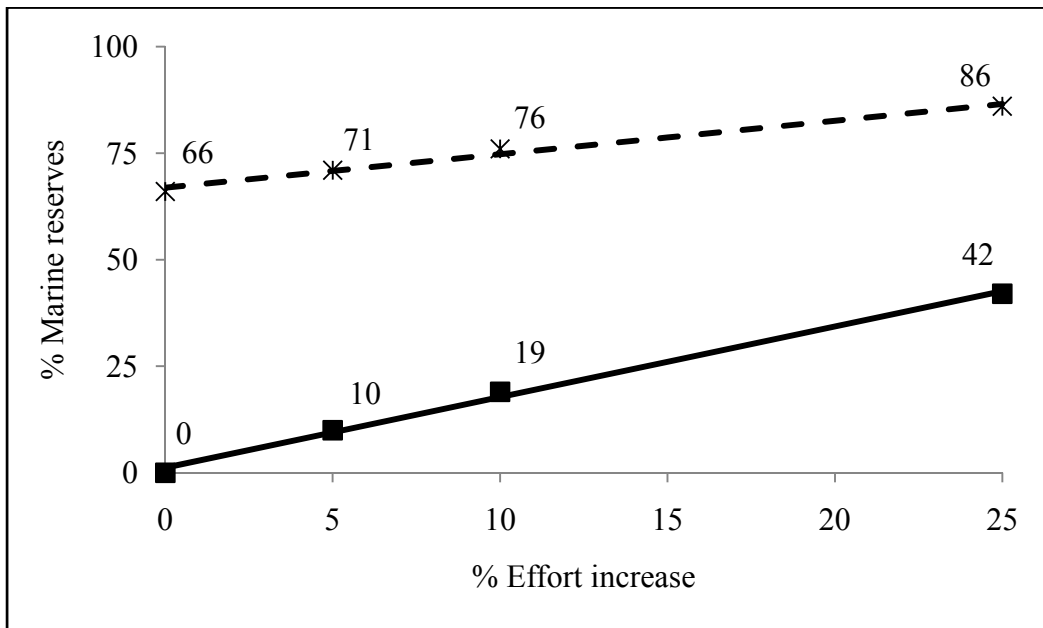


Figure 2.9. Minimum size reserves necessary to attain sex ratio of 5% (solid line) and 10% (dashed line) as fishing effort increases. The points represent the specific reserve size as a percentage of the total spawning area at which the desired sex ratio was attained.

Change in fishing mortality rate without marine reserves showed the same pattern for both adult population size (Fig. 2.10) and sex ratio. The maximum value occurred with no

fishing mortality, and as fishing mortality increased, both the adult population and sex ratio decreased. The population crashed, defined as when the equilibrium population was less than 10% of the initial value, when the fishing mortality was 1.46 times the current estimate. The yield curve (Fig. 2.11) for changing fishing mortality with no marine reserves appeared to approximate a surplus production curve, where yield increases with fishing mortality up to a point after which it begins to decrease. For this simulation the fishing mortality rate at MSY was 44% of the stock assessment estimate of MSY, for an MSY of 3085 metric tons. The MSY estimated by the stock assessment was 3932 metric tons and the fishing mortality rate at MSY was 0.201, or approximately 51% of the current estimate (SEDAR 2007).

2.4. Discussion

Heppell et al. (2006) found that marine reserves may be an effective tool to increase population sex ratio for a protogynous fish. The objective of my study was to more thoroughly explore the influence of marine reserves on the sex ratio, adult biomass, and fishery yield for a specific protogynous fish population. Due to the often contentious nature of the marine reserve implementation process, specific information about the impacts of reserves on fish populations and related fisheries are in high demand. To this end a simulation model was used to determine the minimum effective size of marine reserves for managing gag grouper sex ratio. Heppell et al. (2006) also found that the redistribution of effort following an area closure had a significant impact on the effectiveness of reserves. A recent study by Smith et al. (2007) found that fisher response to a seasonal closure actually increased fishing effort by 5%. This information suggests that effort changes following spatial or seasonal closures are highly variable. Due to the potential impacts of fishing effort on protogynous populations and marine reserve effectiveness, the model was also used to test the impact of a range of effort changes on a hypothetical population.

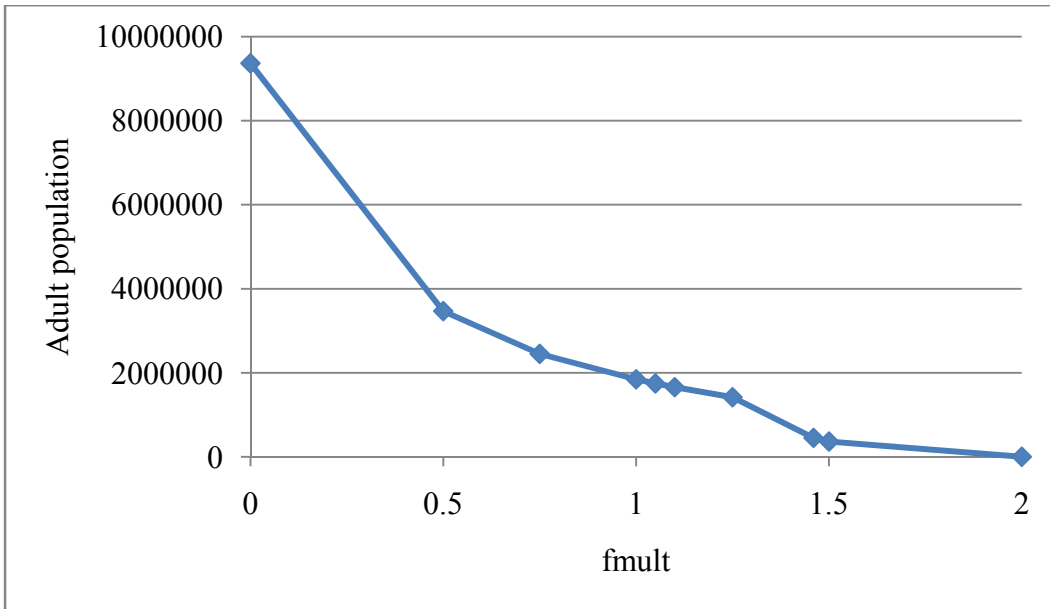


Figure 2.10. Equilibrium adult population size for fishing mortality rates from zero to double the current estimate with no marine reserves. The points represent population values for $fmult$ in increments of 0.25 plus additional points near the current effort ($fmult = 1$) and the population crash (at $fmult = 1.46$) that were included to fill out the curve.

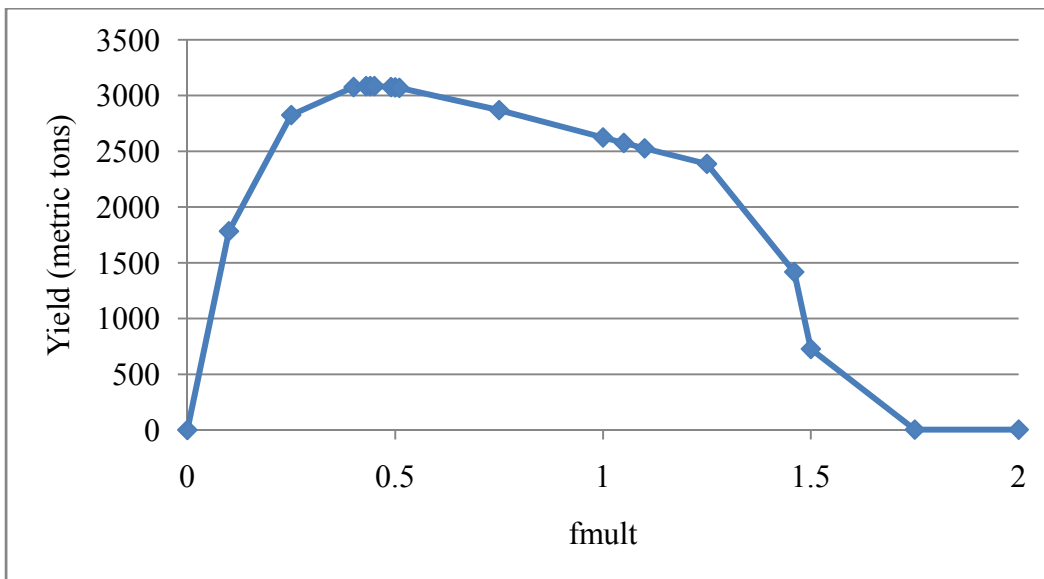


Figure 2.11. Equilibrium yield curve for fishing mortality rates from zero to double the current estimate with no marine reserves. The point represent yield estimates for $fmult$ in increments of 0.25 plus additional points at the maximum and near the population crash (at $fmult = 1.46$) that were included to fill out the curve.

In general, the results suggest that marine reserves used to protect spawning aggregation area can positively impact population sex ratio. This in turn supports the hypothesis that marine reserves may be appropriate for use in managing gag. The main benefit of marine reserves in this case is the reduction in fishing vulnerability of male fish. Even small reserves result in a positive sex ratio response. However, increases in fishing effort reduced the effectiveness of marine reserves. Marine reserves are currently being utilized in the management of gag specifically to increase the sex ratio above the current estimate of 3.46% male. While an exact estimate of the proper sex ratio has not been defined, the estimate of unfished sex ratio is about 1/5 male to female, and as such the population will likely suffer some reproductive loss when the sex ratio declines to a single male per 25 females. For gag, it appears that protecting spawning areas with marine reserves can maintain and even increase sex ratio in the population, and maintaining sex ratio is important to protect the population from reductions in fertility caused by sperm limitation.

The model results suggest long term yield in the fishery could decline by more than 45% to around 3000 metric tons if current conditions persist and recruitment does not vary. The total harvest (including discards) in 2004 was estimated at approximately 4600 metric tons, while the MSY estimated by the stock assessment was only 3932 metric tons. While the model was not designed to calculate exact changes in yield over time, all model simulations resulted in yield estimates that were smaller than current harvest. The MSY calculated for the fishery without any reserves was similar to the MSY calculated in the stock assessment. Both results suggest that the maximum long term yield from the fishery will be obtained when the fishing mortality rate is about half its current level. Likewise, all estimates of the adult population size were smaller than the current estimate of population size. These results are consistent with the conclusion of the 2006 stock assessment that the fishery is undergoing overfishing (SEDAR 2006). If the

population continues to experience fishing mortality at or above the current level and recruitment does not vary significantly, the adult population and fishery yield will decline.

The impact of fishing effort on the population is most evident when considering the proportional redistribution regime. This regime assumes that overall fishing effort does not decline as the area protected with reserves increases. This is probably the most realistic case: reducing fishable area does not in itself reduce the impetus to fish. In some cases the addition of larger closures may actually increase total effort. Compared to the fixed effort regimes, proportional redistribution of effort returned the lowest response in terms of sex ratio for a given reserve size, while adult population and yield declined steadily with the increase in reserve size. This suggests that population size and yield are most sensitive to fishing mortality on young fish, while sex ratio is most sensitive to fishing mortality on older fish. It also suggests that the ultimate mechanism that will determine the effectiveness of marine reserves is fishing effort on unprotected fish. Marine reserves can only be effective as long as there are fish to protect. Unless effort is reduced outside reserves, then the number of fish recruiting to reserves will not be large enough for reserves to be effective.

The application of marine reserves as a yield management tool is not necessarily straightforward, and using reserves to protect spawning aggregations is a very specific example. For marine reserves in general, increasing the amount of area protected from fishing decreases the number of fish available for harvest. If reserves are too large, harvest suffers because too many fish are protected; if reserves are too small, insufficient protection of spawning aggregations ultimately contributes to population and yield declines. For each scenario tested there was a specific reserve size that maximized yield: below this size too many fish were vulnerable to harvest, while above it too few fish were vulnerable to harvest. As fishing effort increased, the reserve size that maximized yield also increased, suggesting that reserves protect a

reproductive stock of adult fish which becomes increasingly important as fishing effort increases. This is evident when considering the difference between yield with and without reserves, which increases along with effort (see Table 2.3). Should fishing effort on gag substantially increase, marine reserves will not only protect the social structure of the population, but may also help maintain fishery yield.

In simulations with no fishing, sex ratio stabilizes at 35%, which is significantly higher than estimates of sex ratio in a lightly fished population (17%, McGovern et al. 1998) and model estimates of the unfished population (22%, SEDAR 2006). This result is possibly reflective of a compensatory shift in transition in response to size-selective fishing pressure. The model assumes that the rate of sex change is fixed in the population. However, it is likely that the rate of sex change varies through time in response to fishing pressure, and even small changes in the rate of sex change could have significant impacts on the population. Additional modeling of variability in the rate of sex change may indicate the conditions in that cause a change in transition rates, or more importantly, how such a shift may affect the population, the sex ratio, and the efficacy of marine reserves.

The results offer more evidence that marine reserves that protect spawning aggregations of a protogynous fish can maintain and even increase population sex ratio. The results also lend support to the assessment that the fishery is undergoing overfishing. Lacking any management actions that will decrease the fishing mortality experienced by gag grouper in the GOM, it appears that the spawning stock and fishery yield will decline in the future. While these declines may be buffered with marine reserves, the response by fishers to spatial closures will have a significant impact on their ultimate effectiveness. Fishing mortality can be reduced either with spatial closures or by other means, but utilizing spatial spawning closures is appears to be an effective way to increase male proportions in the population.

CHAPTER 3: INDIVIDUAL BASED MODEL

3.1. Introduction

The age-structured model developed in Chapter 2 simulates a population of gag grouper assuming a single spatial area. Any spatial area differences are treated implicitly by altering stage-based mortality, where each stage was defined by life history characteristics based on habitat utilization and migration patterns. The model was used to explore the impact of spatial closures on population variables by altering the vulnerability to fishing mortality at the stage level. For example reserves that protected 25% of spawning aggregation sites reduced the fishing mortality of all males by 25%, and all females by 6.25% (one-quarter of all females are protected from fishing for one-quarter of the year). It is because of stage-specific fishing vulnerability that marine reserves may be useful in the management of gag. Once female gag become males, they remain offshore at spawning sites year-round, so protection with marine reserves should be relatively simple and effective. However, the real population does not exist in one large box, rather it is spread out over space and individuals aggregate and migrate at different times throughout the year. These aggregations occur at discrete spots, the most important being the deep offshore reefs that serve as spawning sites.

Therefore it is instructive to model the population as populating a number of smaller spatial areas. Alonzo and Mangel (2004) described an individual based model (IBM) that was designed to explore how size-selective fishing can cause sperm limitation in protogynous wrasse. The model was designed to test changing aggregation size, both in terms of the size of aggregations (number of individuals present) and the total number of aggregations, and how different management options affected population dynamics. I used a version of this model applied to gag to replicate the simulations described in chapter 2, and to explore how modeling at the individual and spawning site level contrasts from modeling at the population level. Spatial

factors are still treated implicitly, but instead of changing vulnerability at the population level, the IBM alters vulnerability to fishing at the individual level based on the characteristics of the spawning site to which they are associated.

IBMs have long been used to test a number of different ecological systems and questions, including the impact of management options on population dynamics. In general an IBM is a model that simulates a population based on discrete agents that includes some variability in the specific traits of those agents (DeAngelis and Mooij 2005). They have been used to explore variation in early life history in fish to detect how changes in prey supply (DeAngelis et al. 1993), growth rate (Rice et al. 1993), or environmental factors (Hinckley et al. 1996) may influence population structure and stock-recruit relationships. IBMs that integrate spatially explicit habitat and movement patterns have been used to explore migration patterns of motile marine fish (Huse et al. 2002), as well as dispersal patterns of sessile invertebrates (Chave et al. 2002). However, there has been little use of IBMs to explore population impacts of marine reserves, or to test specific management options.

When modeling a population, all of the characteristics and functions have some inherent variation, whether in growth rate, mortality, or fecundity. The IBM approach is essentially a series of separate submodels of different processes whose effects are summed at the end. This chapter describes the application of an IBM approach to modeling a population of gag grouper in order to investigate the impact of marine reserves on sex ratio and population size. Will protecting gag spawning aggregation sites with marine reserves positively impact sex ratio? If so, how much area must be protected in order to observe a population level response? The results of the age-structured model described in Chapter 2 suggest that marine reserves can have a positive impact on sex ratio. In this chapter, I am interested in exploring whether different patterns emerge if fish are treated individually rather than as a population. Using a different

modeling technique to explore the same phenomena, I hope to develop a better understanding of how marine reserves can impact the population dynamics of a protogynous fish. To be able to compare the age-structured approach to the IBM approach, the two models were parameterized using the same data (from the stock assessment; SEDAR 2006). Also, the IBM does not include variability within functions in order to limit the differences between models. In order to maintain a consistent nomenclature, references to sex ratio refer to ratio in numbers of males to females, and marine reserves and spawning reserves are used interchangeably to refer to spatial area closures of gag spawning aggregation sites.

3.2. Methods

3.2.1. Model Description

I used an individual-based simulation model based on Alonzo and Mangel (2004) to explore the impact of using marine reserves to protect spawning sites on the population dynamics of gag grouper. The model predicts the population sex ratio and relative population size as a function of fishing mortality. The general model functions used were those defined in Alonzo and Mangel (2004). Parameters of the growth, mortality, fertilization functions, and the maturation and sex change probabilities were based on data available in the most recent stock assessment of gag (Table 3.1; SEDAR 2006). The model followed individual fish as they varied in size, maturity, sex, fishing vulnerability, and spawning site according to the order shown in Fig 3.1. Reproductive output was a function of individual fecundity and spawning site characteristic (protected vs. not protected), and is summed over all individuals to obtain a single population recruitment estimate from year to year. Fitting of parameters to stock assessment data was performed using SAS software, Version 9.1.3.

Survival was assumed to be based on age and was modeled to replicate changes in vulnerability caused by the ontogenetic habitat shifts experienced by individuals during their

lifespan. Both natural and fishing mortality were reported as instantaneous rates. The natural mortality schedule utilized in the most recent gag stock assessment was based on a Lorenzen curve that predicts natural mortality rate to decline with age (Fig 3.1; Lorenzen 1996; SEDAR 2006). Natural mortality (M) was calculated for age i with equation 1, where ma and mb are scaling constants (see Table 3.1 for parameter values):

$$(1) \quad M_i = ma (i)^{mb}$$

The fishing mortality schedule was based on age-specific mortality estimates reported in the stock assessment (SEDAR 2006). The means of fishing mortality estimates from 2001 to 2004 for fish aged 1 to 10 were fitted with polynomial regression to obtain the smooth fishing mortality curve shown in Fig. 3.2. After age 10 it was assumed that fish experience a constant fishing mortality rate equal to 0.3. The equation for the fishing mortality rate curve for age i is shown in equation 2, where fa , fb , and fc are constants fitted by the regression:

$$(2) \quad F_i = fa ((i)^2) + fb (i) + fc$$

The fishing mortality experienced by an individual fish is also altered by sex and mating site, which is represented by individual selectivity, S_i . The specific schedule for individual selectivity varies as a function of maturity, sex, and spawning site, as shown in Table 3.2. Total mortality is calculated once per time step. Natural mortality and fishing mortality were summed to obtain age-specific annual survival A for age i :

$$(3) \quad A_i = \exp^{-(M - (F S_i f_{mult}))}$$

The probability of maturation and sex change for individuals were modeled as functions of length. Maturation is defined as the proportion of juvenile fish maturing to female each year. Sex change is defined as the proportion of female fish switching to male each year. The probability curve for maturation (the probability that a fish length L will mature; Fig. 3.3), and the probability curve for sex change (the probability that a fish length L will change sex; Fig.

3.4) were estimated by logistic regression fitting to observed proportions at age in 2004 (SEDAR 2006). Both probability curves are fixed for the duration of each simulation. In the maturation equation (4), L_m represents the length at which 50% of individuals are mature and q is a shape parameter. In the sex change equation (5), L_c represents the length at which 50% of individuals are male and r is a shape parameter.

$$(4) \quad P(\text{mat}) = 1 / [1 + \exp^{-q(L - L_m)}]$$

$$(5) \quad P(\text{change}) = 1 / [1 + \exp^{-r(L - L_c)}]$$

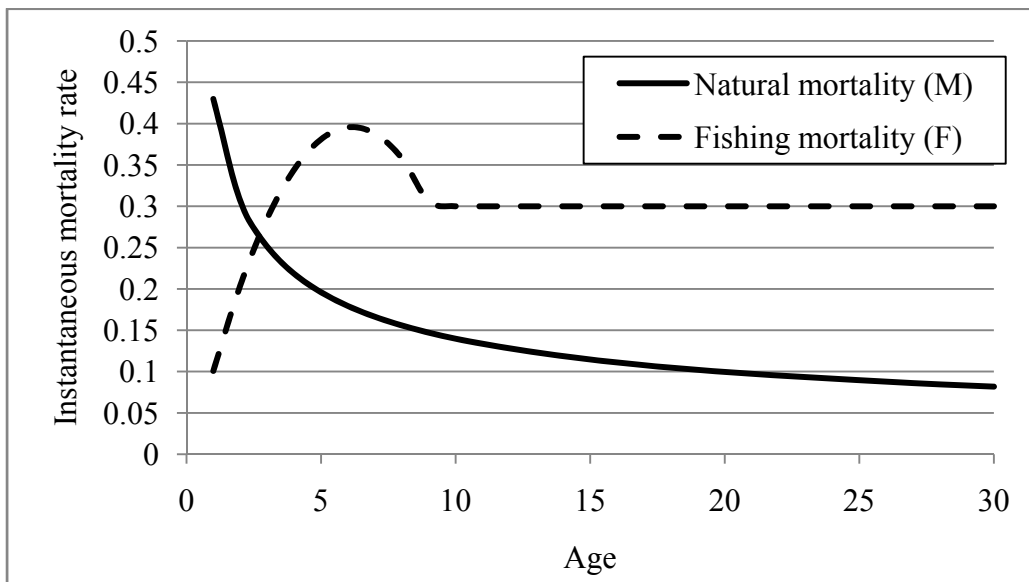


Figure 3.1. Natural mortality (based on a scaled Lorenzen curve) and fishing mortality for gag grouper in the GOM.

Fecundity was calculated for female fish and is the total eggs produced per individual as a function of length. Fitzhugh et al. (2006) found that per capita egg production increased linearly with length based on equation 6:

$$(6) \quad E = ((1.669(L)) - 1024)(25000)$$

Total egg production was calculated per spawning site as the summed egg production for all females associated with that site (E_j for all sites j). Fertilization success was defined as the

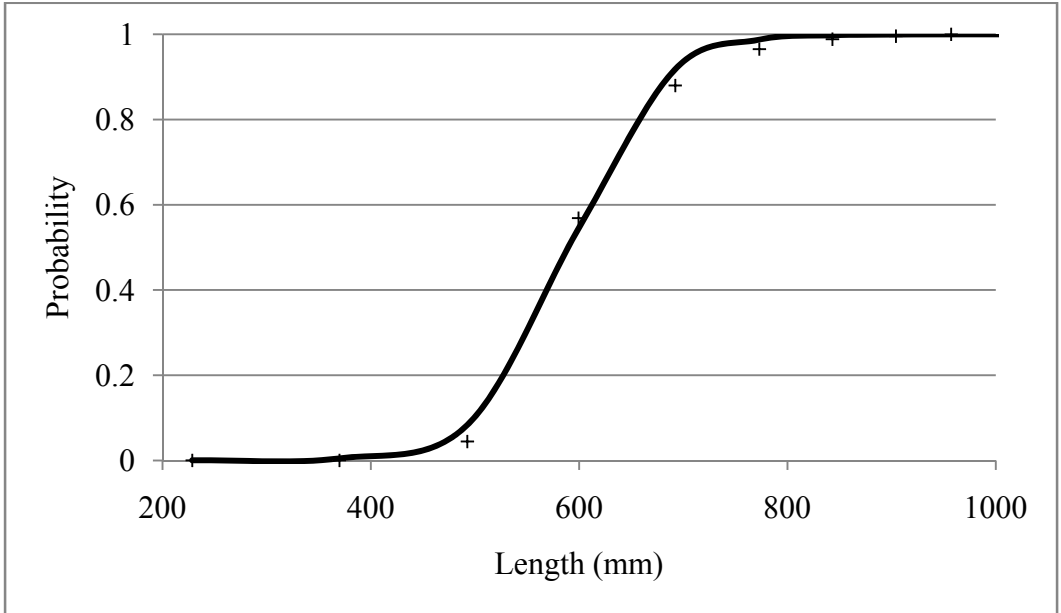


Figure 3.2. Probability curve of maturity for length from a logistic regression of the observed proportion of mature gag (crosses) in the GOM (SEDAR 2006).

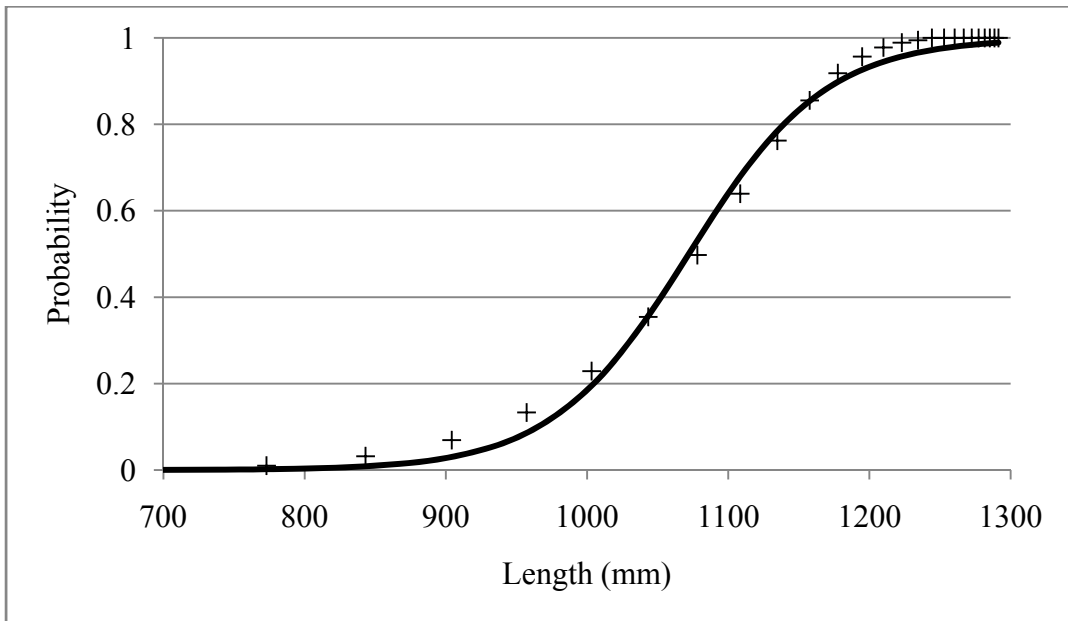


Figure 3.3. Probability curve of sex change for length from a logistic regression of the observed proportion of male gag (crosses) in the GOM (SEDAR 2006).

fraction of eggs fertilized per site and was as a function of a fertilization parameter (Θ) and the population sex ratio. Based on data from Fitzhugh et al. (2006), approximately 10% of females failed to spawn in years when the sex ratio fell below 5% male. Thus, Θ was defined such that fertilization success was reduced by at least 10% when the proportion male was 5%. The fertilization parameter assumes that fertilization failure occurs in a portion of the female population when males are limited and that fertilization failure increases as male proportion declines. Fertilization success, the percent of eggs fertilized was calculated with equation 7 for all sites j , where p_{male} is the proportion males in the population for that year:

$$(7) \quad P(f)_j = 1 - \exp^{-\Theta (p_{\text{male}})}$$

The number of fertilized eggs per site is the number of eggs per site times the percent fertilized, which is then summed over all sites to give total fertilized eggs (E_{tot}). The model assumed that all fertilized eggs contribute to a shared larval pool used to calculate recruitment. Recruitment (R_t) follows the Beverton-Holt stock-recruitment model shown in equation 8, where α and β were estimated using the steepness parameter from the stock assessment ($h=0.794$; SEDAR 2006) and the assumption that the current adult population is approximately one-quarter of the virgin (un-fished) estimate. Stock-recruitment parameters were fixed at values that returned a stable population under current conditions, in effect assuming that given no change in the population the model will return a stable result. This assumption negated the need for a limit to recruitment as all populations less than the unfished have recruitment less than the maximum.

$$(8) \quad R_t = E_{\text{tot}} / (\alpha + \beta E_{\text{tot}})$$

Recruits entered the population at the end of each time step and were assigned an initial length based on age using the von Bertalanffy growth model shown in equation 9, where asymptotic size L_{inf} , growth rate k , and t_{zero} were informed by the stock assessment. Growth of individuals

older than age 1 was calculated at the end of each time step using the discrete time version of the von Bertalanffy growth model shown in equation 10 for age i :

$$(9) \quad L(t) = L_{\infty} (1 - \exp^{-k(i+t_0)})$$

$$(10) \quad L(t+1) = L(t) + (-L_{\infty} \exp^{-k(i)}) (\exp^{-k}-1)$$

The model assumed that the population formed 100 different spawning sites. New fish (all individuals at the start of each simulation, and recruits at the start of each time step) were randomly assigned to a spawning site which was fixed for the duration of the simulation. This assumes that all individuals exhibit site fidelity, but only mature fish are affected by site specific changes. There was no limit to the number of fish assigned per spawning site.

3.2.2. Management Options

The main purpose of simulations was to explore population response to spatial closures that protect spawning aggregation sites from fishing pressure. Management options were assumed to alter the vulnerability of fish to fishing effort which was reflected as proportional change to the selectivity of individual fish (S_i). Simulations tested altered the fishing mortality of individuals at both the site level and at the population level. Reserve scenarios refer to the percentage of spawning sites that are closed to fishing which is reflected as a change in individual selectivity, while effort regimes refer to changes in the total fishing mortality (F).

Six reserve scenarios were tested: 0%, 10%, 18%, 25%, 50%, and 100% closures. These scenarios represent a range of options for marine reserves in the GOM, including both realized (an estimated 18% of spawning sites are currently protected with marine reserves) and potential protection. Because the total number of spawning sites is 100, the number of reserves that are closed to fishing is equal to the percentage reserves (ex. 10% reserves = 10 closed sites). It is assumed that males identified with a protected site experience zero fishing mortality for the entire year and females associated with protected sites experience zero fishing mortality for one-

quarter of the year. Juvenile fishing mortality is not affected by spawning site reserves. If an individual is a male associated with a closed spawning site, $S_i = 0$; if an individual is a female associated with a closed spawning site, $S_i = 0.75$. Note that individual site associations are fixed for life: an individual associated with a closed site would experience no change in fishing mortality as a juvenile, a one-quarter reduction in F as a female, and zero fishing mortality as a male.

Table 3.1. Parameters used in the model, their description, source and value.

Parameter	Description	Source	Value
L_{inf}	von Bertalanffy growth curve asymptote	SEDAR (2006)	1310
k	vB growth curve slope	SEDAR (2006)	-0.14
t_0	vB growth curve x-intercept	SEDAR (2006)	-0.37
ma	Lorenzen curve multiplier	Scaled to age	0.4298
mb	Lorenzen curve power	Scaled to age	0.488
fa	F-curve parameter	Fit to F-estimates from	0.01109
fb	F-curve parameter	2001 - 2004	0.1366
fc	F-curve parameter	SEDAR (2006)	0.02481
q	Maturity shape parameter	Fitted to observed proportions	0.0241
L_m	Length at 50% maturity (mm)	(SEDAR 2006)	592
r	Sex change shape parameter	Fitted to observed proportions	0.0206
L_c	Length at 50% sex change (mm)	(SEDAR 2006)	1072
Θ	Fertilization parameter	Fitzhugh et al. (2006)	50
α	Beverton-Holt recruitment A		9185
β	Beverton-Holt recruitment B		6.072×10^{-4}

In addition to the reserve scenarios, five different fishing effort regimes were tested. Effort regimes change the total fishing mortality rate by multiplying the variable $fmult$ in equation 3. The five effort regimes tested were:

1. “None” – status quo condition, $fmult = 1.0$;
2. “Low” – 5% increase in fishing mortality, $fmult = 1.05$;
3. “Mid” – 10% increase in fishing mortality, $fmult = 1.1$;
4. “High” – 25% increase in fishing mortality, $fmult = 1.25$;

5. “Prop” – increase in fishing mortality proportional to % reserves,

$$f_{mult} = [(100 + \# \text{ of sites closed}) / 100]$$

These effort regimes represent a range of possible changes to fishing effort over time, both in terms of a general increase over time, and in direct response to implementation of reserves. Each simulation tested one reserve scenario and one fishing effort regime for a total of 30 combinations.

Table 3.2. Individual selectivity (S_i) values for maturity, sex, and spawning site characteristics.

Maturity / Sex	Spawning site characteristic	Individual Selectivity (S_i)
Immature	Not protected	1.0
	Protected	1.0
Mature, Female	Not Protected	1.0
	Protected	0.75
Mature, Male	Not Protected	1.0
	Protected	0

It is unlikely that complete protection of gag spawning sites is feasible, and the range of reserve scenarios tested varies in terms of the amount of area protected. Gag probably form more than 100 spawning aggregations and these aggregations will vary in space and time and in terms of the density of fish present. In this study I was not interested in predicting actual response to management, instead the model was designed to allow for relative comparison between different management options. Likewise, fisher behavior is uncertain and accurately representing response to spatial closures is unlikely. Instead the effort regimes tested allow for a broad range of future changes in the fishery to be tested for their corresponding population effects.

I was also interested in testing for a “minimum effective size” of reserves, defined as the minimum percentage of spawning sites that must be closed in order to obtain sex ratio based

thresholds. These thresholds were defined as 5% and 10% male, both of which represent improvement over the current estimate of 3.46% male (SEDAR 2006). Finally, in order to test how the population responded to changes in fishing mortality without the presence of reserves, I tested a range of fishing mortalities outside of the range tested with the fishing effort scenarios. To do this, I changed the value of *fmult* from 0 to 2.0 (zero fishing mortality to double the current fishing mortality) by increments of 0.5. While this does not necessarily represent any real scenario likely to be faced by the fishery, it will act as a kind of sensitivity analysis to compare how the population responds to altering fishing mortality for the total population versus altering the fishing mortality for portions of the population.

3.2.3. Model Simulations

Simulations were run for 100 years and used one year time steps. Exploratory simulations showed that an equilibrium state was reached within one generation time (30 years) after which the response variables were essentially flat with respect to time. Only in rare cases did the model fail to reach equilibrium. The model follows the method described in Scheffer et al. (1995) where each age class is represented by 50 “super-individuals.” All model simulations were initialized with a population of 1500 individuals equally separated into 30 age classes so that each super-individual had an initial worth equal to 1 fish. The worth of each super-individual, in terms of the number of individuals represented, was updated each time step based on mortality. The maturity, sex, size, and reproductive output of each super-individual was initially set equal (meaning all super-individuals started as immature, female, with length according to age, and had zero reproductive output) and were then updated each time step according to the specific functions involved. The general order of model functions is shown in Fig 3.4. The model is deterministic because I was only interested in relative changes to sex ratio and population size, not in representing an actual population through time.

The response variables followed in each simulation were the population sex ratio (reported as the ratio of males to females), adult population size in number for each time step, and fertilization success output by site for each year. For simulations that reached equilibrium (the condition where the response variables are flat with respect to time), results are presented as the mean of the final 20 years of each simulation. Simulations that did not reach equilibrium were those that declined continuously until the end of the simulation and are singled out in the results. The standard deviation was calculated for sex ratio and population size for each simulation. Standard deviations were normalized by dividing by the mean to obtain the coefficient of variation. The normalization of standard deviation allows for the comparison of variability between simulations to determine how changes in fishing mortality affect the variability of response variables.

3.3. Results

Results of the simulations show that increasing the amount of spawning area closed to fishing resulted in an increase in the sex ratio (Fig. 3.5) and the adult population (Fig. 3.6). However, the effectiveness of closing spawning sites with reserves was dependent on the magnitude and pattern of fishing effort change. The response patterns for sex ratio and adult population were similar for the fixed fishing effort regimes (None, Low, Mid, and High). These regimes change fishing mortality at the population level and were not affected by the reserve scenario, unlike the proportional redistribution regime which calculated population fishing mortality as a function of reserve size. The response patterns for sex ratio and adult population for proportional redistribution differed significantly from the fixed effort regimes. In general, increasing fishing effort reduced the effectiveness of reserves so that more reserves were necessary to attain comparable response with higher effort. All reserve scenario and effort regime simulations reached an equilibrium state within 30 years, or one generation.

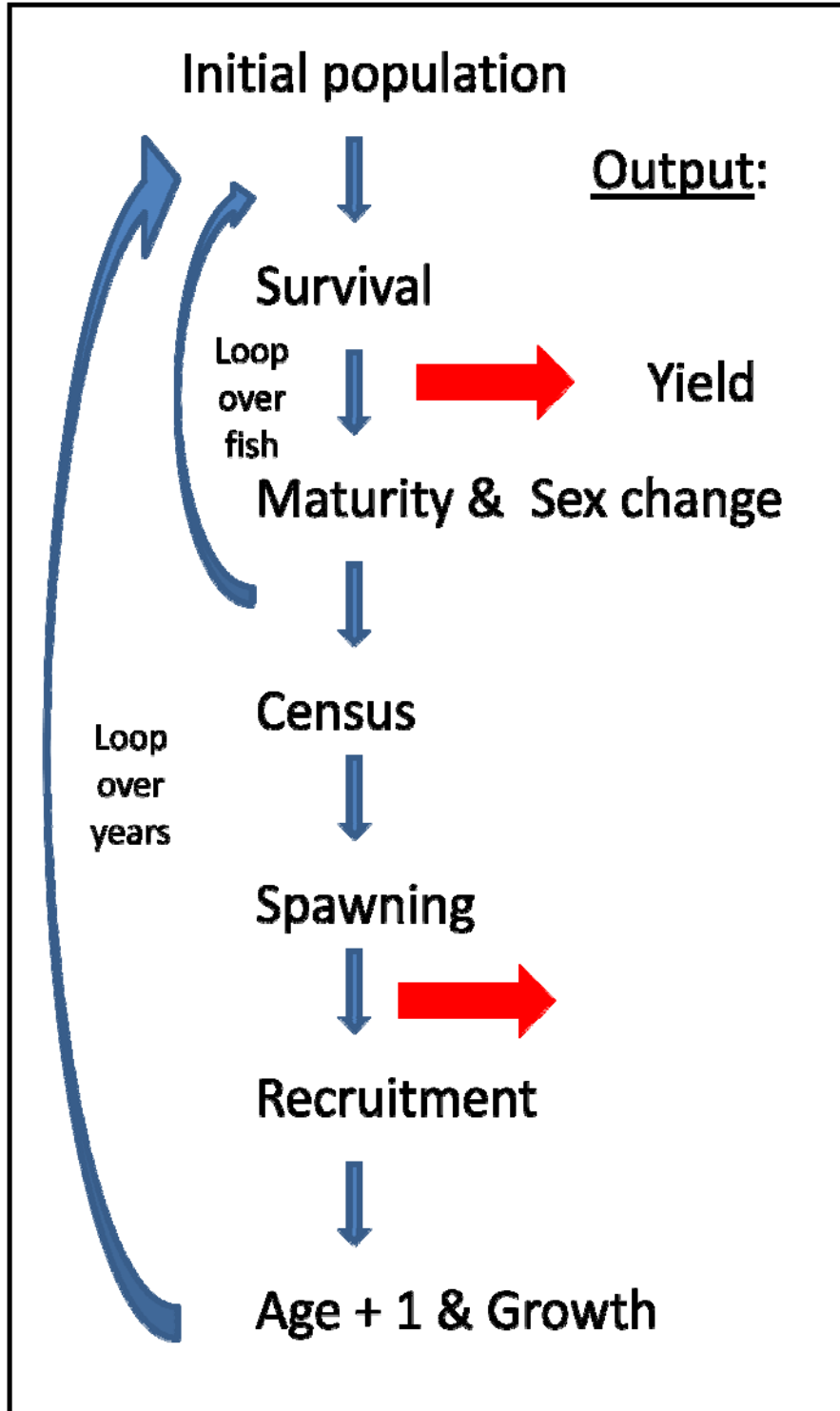


Figure 3.4. Model schematic showing the order that model functions are calculated for each time step, the output, and the nested loops within the model.

The response by sex ratio to increasing the number of reserves was consistent for the fixed effort regimes: increasing the number of reserves resulted in a higher equilibrium sex ratio. For all simulations the equilibrium sex ratio was higher than the starting condition of 3.46% male. The status quo simulation (18% reserves and no increase in fishing effort) had a mean of 9.45% male, a 173% improvement over the starting condition. The highest equilibrium value for sex ratio occurred with 100% reserves and no increase in fishing effort (20.7% male). For the proportional redistribution regime (Prop), the sex ratio response was dome-shaped (Fig. 3.5): sex ratio increased with increasing reserve size up to 51% reserves after which it declined. The sex ratio at the peak of the curve was 8.88% male, a 157% improvement over the starting condition.

The response by adult population to increasing the number of reserves was positive, but the response to increasing fishing effort was negative. For the four fixed effort regimes the response pattern was consistent but showed the opposite pattern for the proportional redistribution regime (Fig 3.6). In every simulation the equilibrium adult population was less than the starting condition of 861 adults. The equilibrium adult population for the status quo simulation was 517 adults, or 60% of the starting condition. The highest equilibrium population was obtained with 100% reserves and no increase in fishing effort (779 adults, 90% of starting condition). For the proportional redistribution regime, adult population decreased with increasing reserve size. The highest equilibrium population for the proportional redistribution regime occurred with no reserves (455 adults, 53% of starting condition). The population response was linear with respect to reserve size for all simulations, with similar positive slopes for the fixed regimes and a negative slope for the proportional redistribution regime ($p < 0.001$).

The proportional redistribution regime is a special case of effort change. As the size of reserves increases, fishable area decreases. Assuming that total effort by the fishery does not change, the fishing mortality rate experienced by vulnerable fish (those not protected by

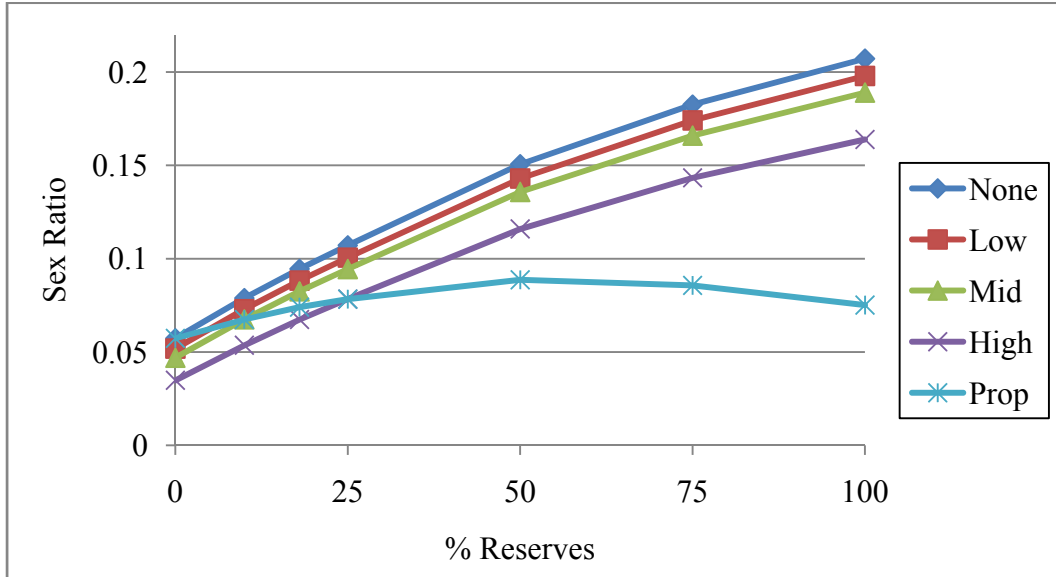


Figure 3.5. Male to female sex ratio response to increasing marine reserve size and the five fishing effort regimes defined in the text (initial sex ratio = 0.0346).

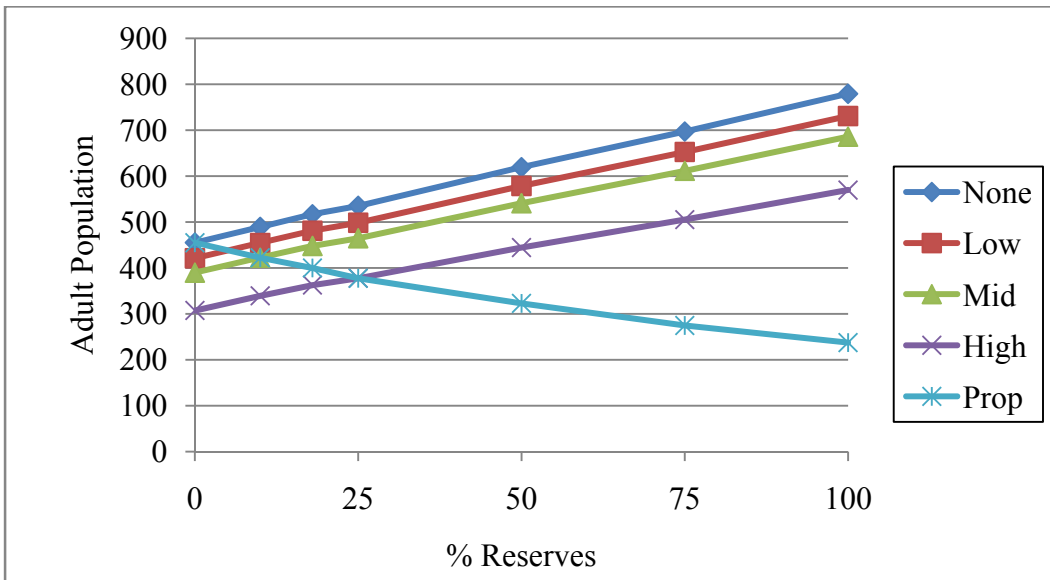


Figure 3.6. Adult population response to increasing marine reserve size and the five fishing effort regimes defined in the text (initial adult population = 861).

reserves) increases with increasing reserve size. This result is reflected in the values for sex ratio and adult population size at high reserve size: sex ratio increases to a point at which the magnitude of fishing outside reserves negates their influence, while adult population responds negatively for all reserve sizes.

The minimum size reserves necessary to maintain male sex ratio at the 5% and 10% sex ratio benchmarks increased as fishing effort increased (Fig. 3.7). When the change in fishing effort was small (0% or 5% increase), no reserves were needed to attain 5% males. If effort increased by more than 5%, only small reserves (less than the current amount of protection) were needed to attain the 5% males. In order to attain at least 10% males, reserves that protect at least 22% of spawning sites were needed, and the amount of protection increased linearly with increasing effort ($y = 0.685x + 21.89$; $r^2 = 0.998$). The results for the proportional redistribution regime are not included in this analysis because the equilibrium sex ratio for all effort regimes falls between the benchmarks; no reserves are necessary to attain 5% males in the population, but no amount of reserves attains 10%.

Fertilization success was identical between sites because it was a function of the population sex ratio, and followed the same general pattern as sex ratio: as reserve size increased, so did fertilization success and as the fishing mortality rate increased, fertilization success decreased (Fig. 3.8). For the fixed fishing effort regimes with more than 50% reserves the fertilization success rate did not vary significantly. The proportional redistribution regime reached a maximum fertilization success rate (98.6% success) at 51 % reserves. The fertilization success rate was most sensitive to simulations that had small sex ratio estimates: small reserve size and high fishing mortality. This result is due to the fact that fertilization success is a function of the population sex ratio and was scaled so that significant reductions in the fertilization success rate occurred only when the sex ratio fell below 5% male (see Fig. 2.3).

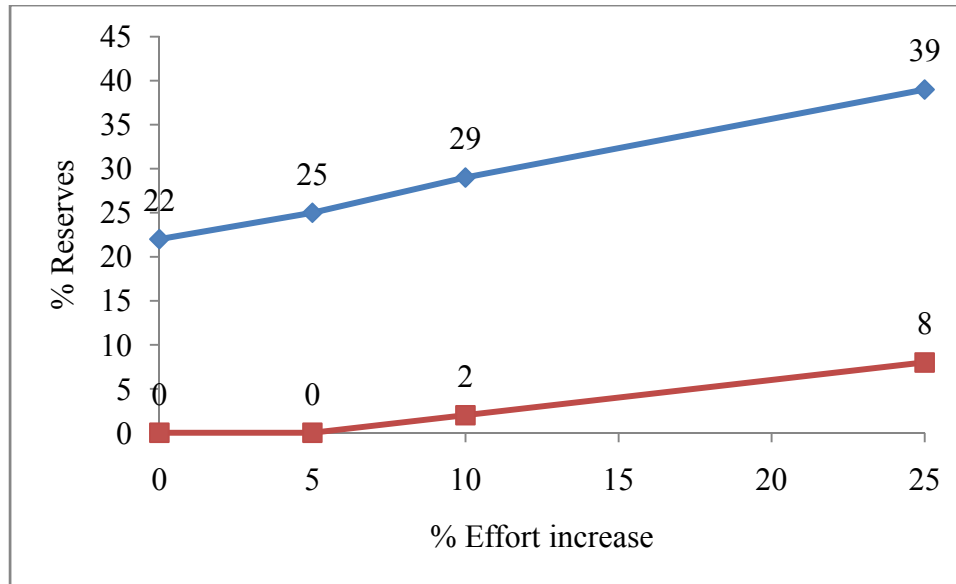


Figure 3.7. Minimum size reserves necessary to attain sex ratio of 5% (red line) and 10% (blue line). For the None and Low effort regimes the sex ratio was above the 5% benchmark with no reserves.

When the fishing mortality rate applied to the population changes without any reserves, both the sex ratio and the adult population declined as the mortality rate increased (Figs. 3.9 and 3.10). The maximum sex ratio (43.3% male) and the maximum adult population (3451 adults) occurred when the fishing mortality rate was zero. The only simulation to never reached equilibrium was when the fishing mortality rate doubled the current value ($fmult = 2.0$). While the population did not reach zero, at the end of 100 years the adult population equaled 6 and was still declining. The maximum value of the adult population with no fishing ($fmult = 0$) was approximately four times the starting condition for the adult population, comparable to the population size of the unfished population assumed in the calculation of the stock-recruitment parameters. Fertilization success declined as fishing mortality increased, due to the observed decline in sex ratio with increasing fishing mortality (Fig. 3.11).

There were clear patterns in the variability of the response variables (Fig. 3.12). For sex ratio, variability declined as reserve size increased, while variability increased as fishing effort

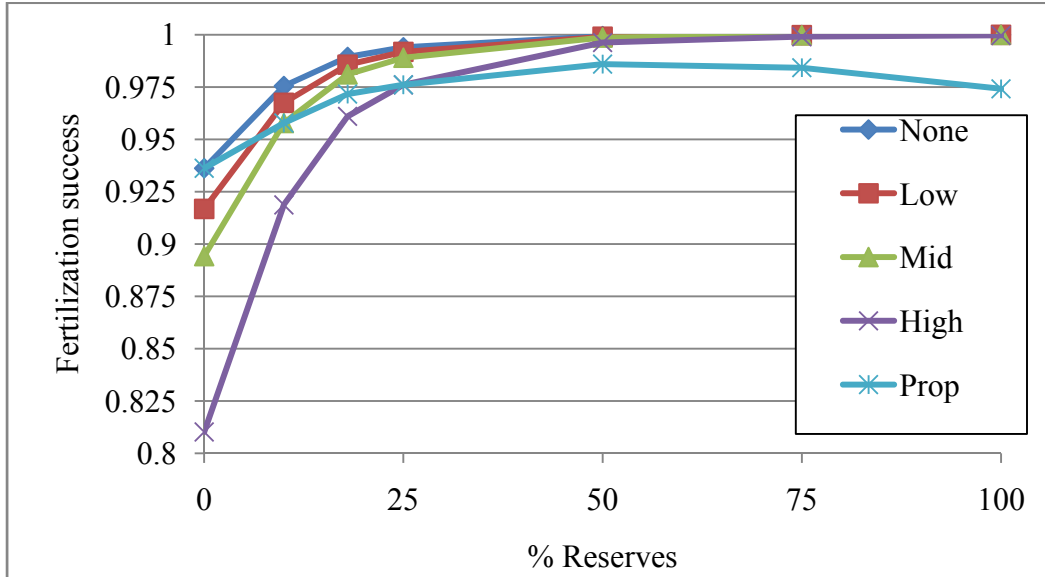


Figure 3.8. Fertilization success response to increasing marine reserve size and the five fishing effort regimes defined in the text; fertilization success is the mean of all sites for the final 20 years of simulations.

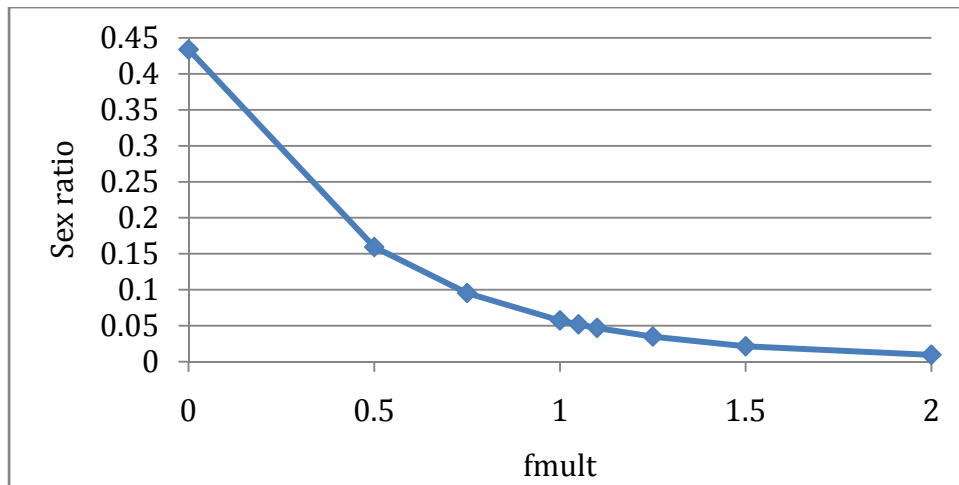


Figure 3.9. Response by the population sex ratio success to the range of fishing mortality rates described in the text (via f_{mult}) as applied to the total population.

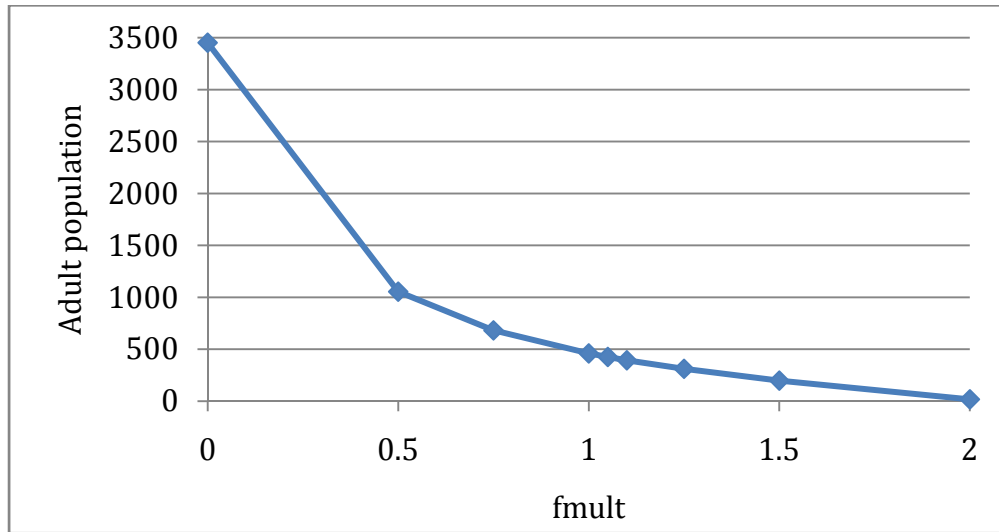


Figure 3.10. Response by the adult population size to the range of fishing mortality rates described in the text (via *fmult*) as applied to the total population.

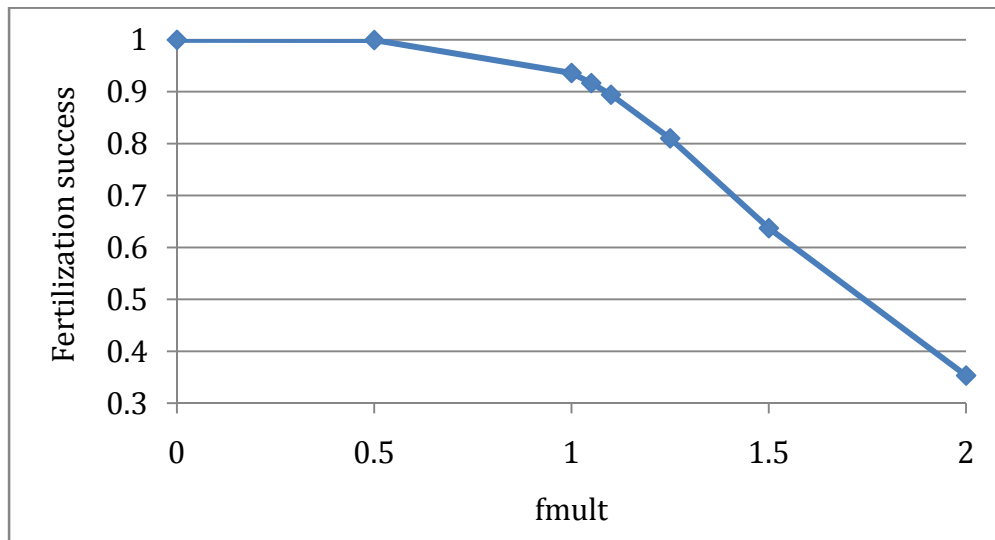


Figure 3.11. Response of the fertilization success to a range of fishing mortality rates described in the text (via *fmult*) as applied to the total population.

increased. For the adult population, the variability followed the same pattern as sex ratio. Overall variability in the adult population was less than the variability in sex ratio. The variability in sex ratio and adult population for the proportional redistribution regime showed the opposite pattern: variability increased with increasing reserve size. However, this result follows the pattern of variability in increasing fishing effort: increasing reserve size with proportional redistribution causes the fishing mortality to increase, so the variability also increases.

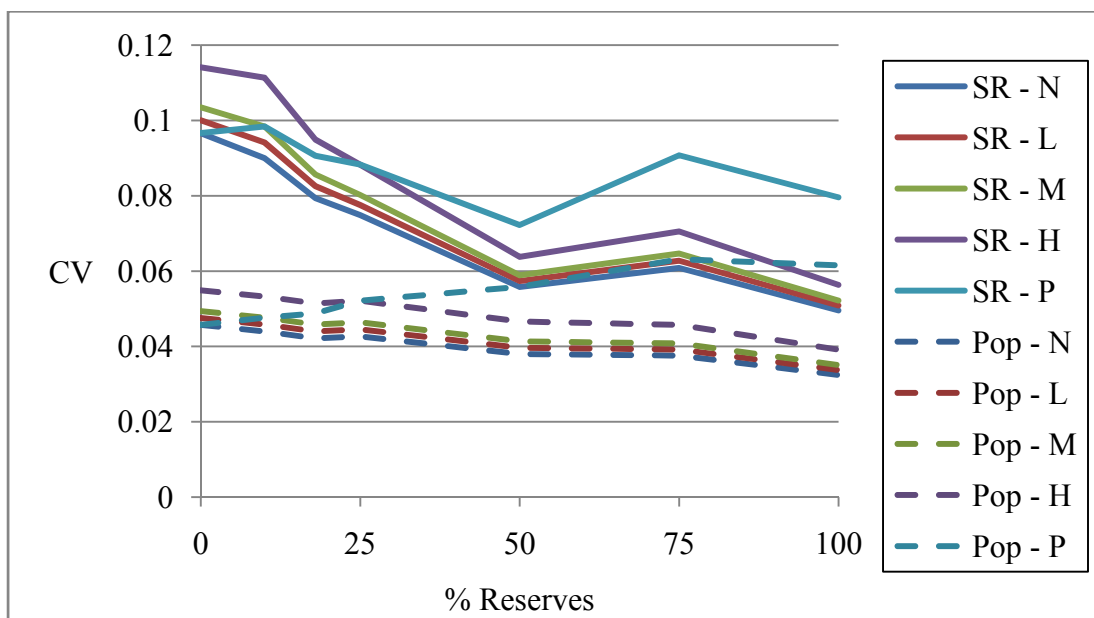


Figure 3.12. Variability in response variables sex ratio (SR) and adult population (Pop) for a range of marine reserve sizes by five fishing effort regimes expressed as a coefficient of variation (CV) calculated by dividing the standard deviation by the mean.

3.4. Discussion

Previously, a version of this model was used to determine how a size-selective fishery impacts the population dynamics of protogynous differently than dioecious populations (Alonzo and Mangel 2004). In their study the authors found that protogynous stocks collapsed at lower fishing mortality rates than comparable dioecious stocks, but that allowing some males in the protogynous stock to escape fishing pressure caused the protogynous population to decline less

slowly than the dioecious population for the same fishing mortality. In effect, reducing fishing mortality on older fish allowed the fishery to exert a higher fishing mortality rate on a protogynous stock and still maintain the same population size. The authors hypothesized that these results are due to sperm limitation in protogynous populations when high fishing mortality reduces the availability of males. Size-selective fishing pressure will disproportionately remove males from a protogynous stock and thus increase the likelihood that sperm limitation will occur. One mechanism that may allow males to escape fishing pressure is the use of marine reserves. For the particular life history of gag, marine reserves are thought to be especially beneficial if they can be designed to protect spawning aggregations, and thereby protect the male fish that stay at spawning sites year round (Koenig et al. 2000). Based on the description by Alonzo and Mangel (2004), I developed a gag-specific version of their IBM to explore the impact of marine reserves on a hypothetical stock of gag.

In general, the result of my modeling efforts support the hypothesis that protecting older fish can positively impact population sex ratio and adult population size. Protecting spawning sites from fishing pressure increased the percentage of male fish in the population, which in turn increased fertilization success ultimately leading to higher recruitment and a larger adult population. Even small reserves showed a positive impact on sex ratio and population size. Sex ratio appeared to respond quickly to increasing reserve size and later showed a slightly diminishing benefit as reserves approached 100% protection (Fig. 3.5). This is an obvious discrepancy from the response pattern from the age-structured model developed in Chapter 2, and the differences between these results are discussed in depth in Chapter 5. For the application of marine reserves in the management of gag, the IBM results suggest that the maximum benefit of reserves will be obtained at smaller sizes. This is an encouraging result for managers because

of the expected drop-off in yield that occurs with larger reserves due to the decrease in the availability of vulnerable fish (see Fig. 2.6).

The equilibrium sex ratio was higher than the starting condition for all reserve simulations; however the equilibrium adult population was less than the starting condition for all simulations. These results are especially interesting for small reserve size (less than 18%). For example, even in the absence of marine reserves the expected sex ratio based on current fishing mortality is 25% larger than the current sex ratio. While the predicted decline in the adult population supports the stock assessment's verdict that the gag population is currently undergoing overfishing, the higher sex ratio result is somewhat anomalous. The model results suggest that if the current fishing mortality is not reduced, the population will decline, and this pattern is intensified when fishing mortality increased further. However, given a decline in the adult population, it may be expected that the sex ratio would also decline. Instead the sex ratio actually increases, even with no reserves. A possible explanation for this result is that recent changes to the fishing mortality rate have yet to be reflected in the population sex ratio. The marine reserves currently in place in the GOM were implemented in 2000, and it is possible that not enough time has elapsed for the reserves to show benefits at the population, while changes in the age structure of the catch are being reflected in the fishing mortality estimates.

The maximum value of the sex ratio when fishing mortality was zero was 43.3% male. This value is higher than would be expected for gag, a species where the estimated sex ratio for the unfished population is about 20% male (McGovern et al. 1998; SEDAR 2006). This is similar to the result found using the age-structured model (sex ratio at $F=0$ was 35% male, see Chapter 2). The IBM results offer more support for the hypothesis that applying the sex change probability curve fitted to a fished population to an unfished simulation reveals a compensatory change in response to fishing. While there have not been observed changes in the length at first

or 50% sex change over time (SEDAR 2006), the rate at which fish change sex could have changed which was not detected by age and growth studies. The results from both the age-structured and the IBM suggest that sex change is variable in the population, and not fixed as it is treated in the models. Given that such changes in the rate of sex change are subtle and not easily detected or manipulated in the real population this is a clear opportunity for additional simulations to explore how density-dependence may affect the rate of sex change in the population. This work is discussed in Chapter 4.

This IBM was designed to allow for the relative comparison of management options and their impact on a population of gag grouper. The results showed that management options that protect older fish have a positive impact on both sex ratio and population size, essentially supporting the conclusions reached in Chapter 2. However, the benefits of using an individual based model stem from the impact of individual variation on population-level dynamics. For this model, individual variation was limited to maturation and sex change. Individuals were forced through probabilities that were calculated based on population-level observations. By fixing site allocation for the life of individuals, this would allow for variation in the density and in the sex ratio between spawning sites. However, the calculation for fertilization success was based on the population sex ratio, which effectively ignores the impact that variation in site-specific fertilization success may have on population dynamics. While the model was effective in exploring the broader question of the utility of marine reserves for managing gag, integrating density effects into the sex change probability and fertilization success may improve results.

CHAPTER 4: DENSITY-DEPENDENT SEX CHANGE

4.1. Introduction

During the decision process regarding the potential use of marine reserves in the management of gag, the Gulf Council was forced to consider the controlling mechanism of sex change in gag (GMFMC 1999). Two hypotheses were identified as possible mechanisms of control over sex change: socially induced sex change and size induced sex change. While it is unknown the extent to which each mechanism acts on the gag population, general patterns should be apparent by tracking the population through time. What is evident that the gag population has suffered a large decline in proportion of males in the population (see Chapter 1), but less clear is how the population has responded this decline over time. If sex change is socially-induced, a decline in the male to female sex ratio should be followed by a decrease in the mean size at transition (measured as the size at which 50% of fish are male). As sex ratio declines, individuals change sex at an earlier age to replace males lost to harvest. If this is the case for gag, the observed decline in sex ratio should have been buffered by a compensatory shift in transition size. Alternatively, if sex change is size-induced, a decline in sex ratio should not be expected to alter the transition rate of individual fish. A size-induced population under high size-selective fishing pressure would experience a disproportionate loss of males from the population that would not be buffered by a compensatory response. High fishing mortality on large females will also drive down the sex ratio by removing those individuals most likely to change into males.

The two mechanisms of control affect which management options are most effective. For a size-induced population the goal of management should be to reduce overall fishing mortality on the population. This will increase the chance that young fish will survive long enough to change sex as well as increasing the survival of older fish. While a socially-induced

population will benefit from an overall reduction in fishing mortality, it is also important to utilize management actions that protect the social structure of the population to ensure social cues are properly transmitted. For gag in the GOM these management options manifest as catch limits and spatial or time closures. The Gulf Council ultimately determined that, despite lacking conclusive evidence for either size or social mediation of sex change in gag, heavy fishing on spawning aggregations had the effect of both high size-selective mortality and the disruption of social structure and approved the use of marine reserves for management (GMFMC 1999).

Data available from the stock assessments for the GOM gag population can be useful in determining indicate how changes to the population caused by size-selective fishing can cause changes to the rate of sex change. The most recent stock assessment, completed in 2006, indicated that there has not been any significant change in the mean length of sex changing fish since 1992 (1100 mm; SEDAR 2006). However, the sex change function described by the 1997 gag stock assessment and the function described in the 2006 assessment are different (Fig. 4.1). Both curves were based on a logistic regression of observed proportions of female fish from age and growth studies and were modeled using a Gompertz logistic function shown in equation 1, where β_0 and β_1 are constants fitted with the regression and TL is the total length of fish (Collins et al. 1998; SEDAR 2006):

$$(1) \quad \text{Proportion male} = 1 - [\exp(-\exp^{-(\beta_0 - \beta_1 TL)})]$$

The male to female sex ratio was not reported in the 1998 report by Collins et al., but an age-structure study of gag caught from 1997 to 1999 reported a sex ratio of 4.65% male for the northeastern GOM (Fitzhugh et al. 2003). From the observed proportions used to fit the logistic regression in 2006, the sex ratio was 3.46% male. A visual examination of the curves in Figure 4.1 suggests that as the population sex ratio has declined, the slope has decreased slightly and the mean age at transition has increased (decreasing the slope parameter causes the curve to be

shallower). Smaller fish have a slightly greater chance of switching sex in 2006, but the population will also have larger females in 2006 than in 1997.

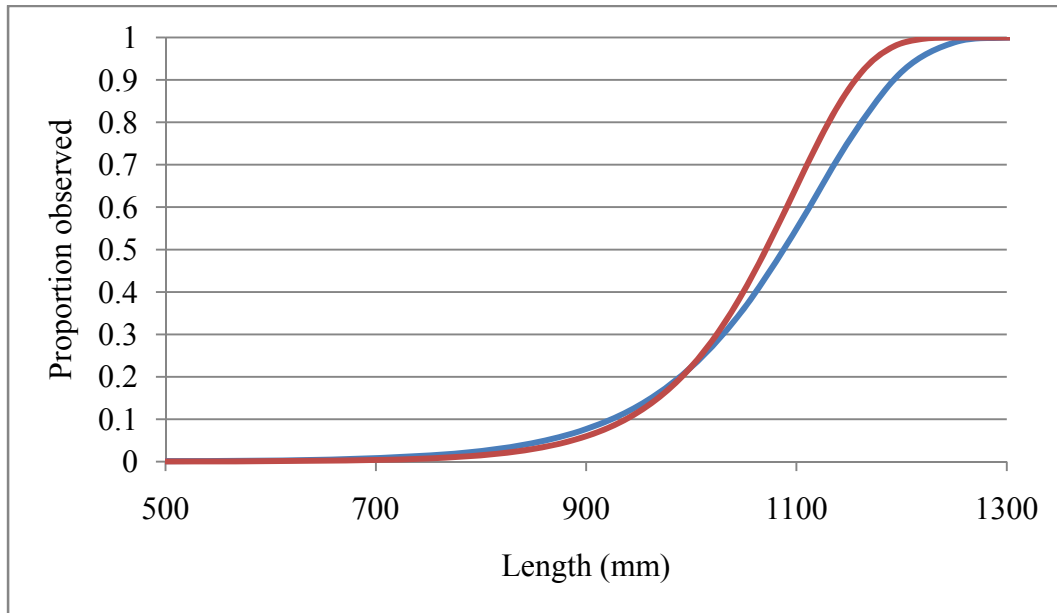


Figure 4.1. Proportion male in population based on logistic regression of observations from 1997 (red line) and 2004 (blue line).

While the 2006 assessment states that the data “showed no evidence of temporal changes in size and age at transition” for gag in the GOM, plotting the published transition equations from new and old assessments suggests otherwise (SEDAR 2006). In addition, gag show a number of characteristics that suggest socially-induced sex change. The number of transitional gag (individuals that are undergoing sex change) caught increases post-spawning, suggesting that social cues transmitted during aggregation initiate sex change (Hood and Schleider 1992; Collins et al. 1998). Relevant cues regarding the composition of sex structure are only available during spawning as females migrate back to shallow water and males remain at spawning sites (McGovern et al. 1998). Gag form large permeable social groups, another quality identified by Ross (1990) as a necessary condition for inductive sex change. According to Ross (1990), fish

must also be able to distinguish the sex of other individuals in order for inductive cues to be possible. Gag show a coloration change following sex change where the belly appears darker. This 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). Given these characteristics it is likely that social cues help to induce sex change in gag.

Another motivation for exploring socially-induced sex change came from the results of the age-structured model and the IBM when fishing mortality equaled zero. The equilibrium sex ratio for the age-structured model when fishing mortality equaled zero was 36.7% male and the equilibrium sex ratio for the IBM was 43.3% male, both of which are significantly greater than the estimate of sex ratio for an unfished population (22% SEDAR 2006). In their version of the age-structured model, Heppell et al. (2006) found the same result: when fishing mortality is set equal to zero the equilibrium sex ratio was about 33% male. The authors also found that shifting the age at first transition (the q parameter in the age-structured model) older by three years and decreasing the slope (via the slope parameter r) resulted in an equilibrium sex ratio of about 20%, closer to the expected value. However, they did not explore how this shift may manifest in the model population. Because the models are used to explore management options that intend to increase the sex ratio in the population, success in a real population would result in an increase in the sex ratio and a shift in the rate of sex change if sex change is indeed socially-induced. Such change should be reflected in the models with a corresponding shift in the parameters that control sex change.

This chapter describes how I modeled socially-induced sex change by adding density-dependence to the sex change functions in the age-structured model and the IBM. The ultimate goal was to explore how socially-induced sex change acting on a population of gag grouper will alter estimates of sex ratio and affect the expected success of marine reserves as a management

tool for the fishery. The specific functions controlling sex change are slightly different between the models and therefore the method for adding density-dependence was specific to each model. To further differentiate between the two models, fertilization success in the IBM was allowed to vary based on the site-specific sex ratio. Where previously fertilization success was a function of the population sex ratio, adding site-specific variability more fully explores the impact that changes in sex ratio have on the population.

4.2. Methods

For the remainder of the model description and results, functions that model socially-induced sex change are referred to as density-dependent functions. The results of simulations that include the density-dependent functions are contrasted with results from the previously discussed models which are referred to as using fixed functions. When marine reserve scenarios are described, the age-structured model reserve size refers to the percentage of spawning aggregation area assumed closed to fishing pressure, while the IBM reserve size refers to the number of spawning sites that are closed to fishing (total number of spawning sites is 100). In both cases reserves decrease fishing mortality experienced by the associated portion of the population.

4.2.1. Age-Structured Model

In the age-structured model described in Chapter 2, the probability of sex change is calculated for each age class. This probability, although calculated at each time step, is fixed for the duration of each simulation. The sex change probability calculation for the age-structured model is shown in equation 2: the probability of sex change at age i , where r and q are parameters obtained from fitting a logistic regression to observed proportions at age as described in Chapter 2 (see Table 4.1 for parameter values):

$$(2) \quad P_{\text{change},i} = 1 - \exp^{-r(i-q)}$$

In the real gag population, I assume that density-dependence will act on both parameters: the magnitude of the probability of sex change for a given age will change via r , and the age when fish start to change sex will change via q . For the shape-parameter r , I assume that the relationship is negative with respect to male density. As the percentage of males in the population increases, the magnitude of the probability of change for a given age increases (fish become more likely to change sex). To model this relationship I used an inverse transformation (equation 3; Fig. 4.2), which assumes that r is inversely proportional to density, so that the density effect is greatest when the number of males is small. Density is represented by the variable $pmale$, which is a measure of the proportion of males in the population calculated at the end of each time step, so that the value of $pmale$ used is the proportion of males in the population at the end of the previous year ($pmale_{t-1}$). The value for c was obtained by multiplying the fixed value of r by the value of $pmale_0$ calculated as the density of males at the end of the status quo simulation (status quo condition is 18% reserves and no change in fishing effort, see Table 4.1).

$$(3) \quad r' = c / pmale_{t-1}$$

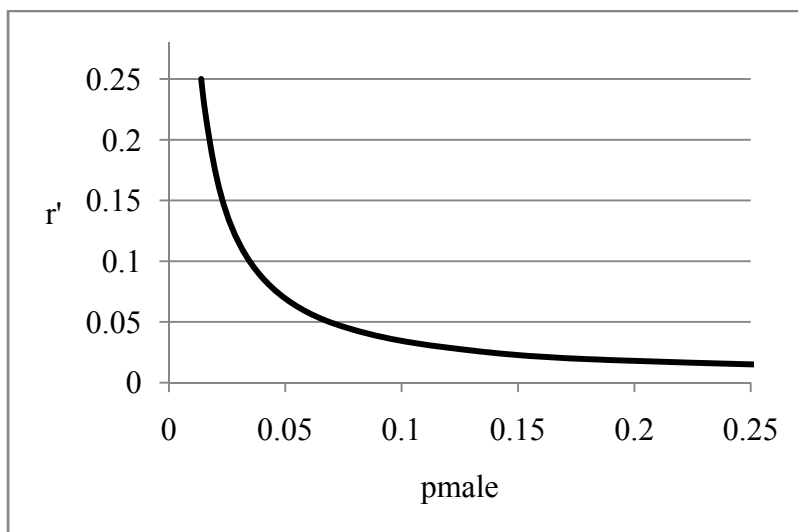


Figure 4.2. Change in the density-dependent sex change function shape parameter r' over a range of estimated densities measured as the proportion of males in the population.

For the intercept-parameter q , I assumed that the age at first sex change will increase with increasing density. I assumed that this relationship was positive, but non-linear (see Fig. 4.3), and that there is some minimum age that fish must reach before they can change. This minimum size threshold is reflected in the population data, where no males less than 800 mm (or about 6.5 years) are found in the catch (SEDAR 2006). To model the relationship between q and density, I used the transformation in equation 3, where q_{min} is the minimum size at first change and d is a constant calculated with the equation shown in Table 4.1:

$$(4) \quad q' = q_{min} + d (p_{male_{t-1}})^{0.5}$$

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

$$(5) \quad P_{change,i} = 1 - \exp [-(c / p_{males_{t-1}}) (i - (q_{min} + d p_{males_{t-1}}^{0.5}))]$$

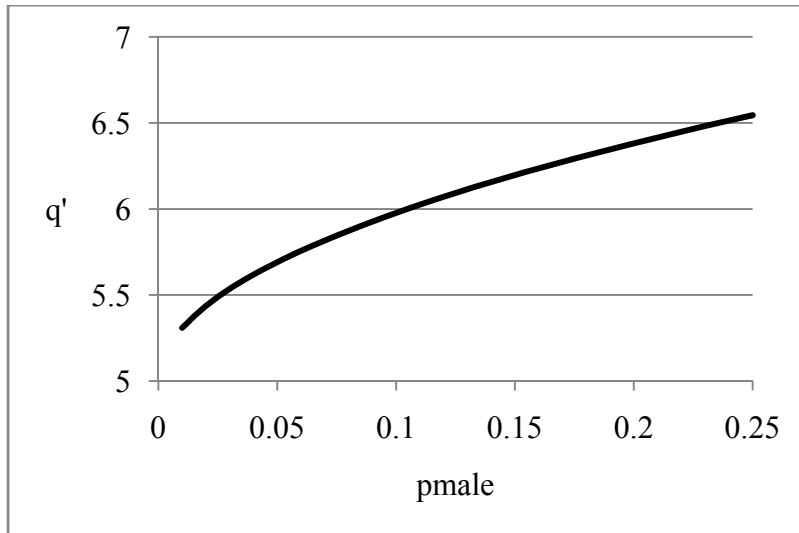


Figure 4.3. Change in the density-dependent sex change function shape parameter q' for a range of estimated densities measured as the proportion of males in the population.

No other model functions or parameters were changed for the socially-induced sex change simulations. All 30 simulations that were tested in Chapter 2 (six reserve scenarios with

five effort regime changes), plus the simulations of changing fishing mortality without reserves, were repeated with the inclusion of the socially-induced sex change function. The same response variables (sex ratio, adult population, and fishery yield) were output for each year and reported as the mean of the final 20 years for all 500 replicates. Given that this part of my study is hypothetical, there is a potentially high amount of uncertainty in the chosen parameters. Therefore, a proportional sensitivity analysis was performed for each of the three density-dependence parameters: c , d , and q_{min} . For the analysis, the parameters were tested with the status quo simulation where all other parameters were fixed and each of the density-dependent parameters varied independently by plus or minus 5%. Sensitivity was calculated with equation 6, where p is the parameter that varied and var is the response variable:

$$(6) \quad \text{sensitivity} = (\text{var}_{p+5\%} - \text{var}_{p-5\%}) / (0.1 \text{ var}_p)$$

4.2.2. Individual Based Model

In order for the IBM to better represent changes to fertilization success that occur at the site level, the density parameter in the fertilization success function was modified to vary by site. In the original IBM described in Chapter 3, the proportion of males was calculated as a population variable and then used to modify the number of eggs that were ultimately fertilized (see equation 7: the percentage of eggs fertilized per site j). This relationship was based on evidence that about 10% of females failed to spawn when the sex ratio fell below 5% based on catch data from 1998 to 2004 (SEDAR 2006). In the original IBM the population sex ratio was used to calculate P_{fert} . To model the variability in fertilization success between spawning sites the population sex ratio parameter was replaced with the site-specific sex ratio calculated at the beginning of each time step. The updated function is shown in equation 8, where $ratio$ is the site specific male sex ratio for all sites j :

$$(7) \quad P_{fert,j} = 1 - \exp^{(-\Theta \text{ pmale})}$$

$$(8) \quad P_{\text{fert},j} = 1 - \exp^{(-\Theta \text{ratio}_j)}$$

The IBM was first used to investigate the effect of site-specific density of fertilization success on the population sex ratio and total adult population size for all the simulations described in Chapter 3 (six marine reserve scenarios with five fishing effort regimes), independent of any other changes. Site-specific fertilization success was retained for the density-dependent sex change portion of the study described below.

The probability of sex change function used in the IBM was calculated based on length using equation 9, where r and L_c are constants calculated by the logistic regression of observed proportions at age from the stock assessment (SEDAR 2006):

$$(9) \quad P_{\text{change},L} = 1 / [1 + \exp^{-(r(L - L_c))}]$$

For the IBM, I assumed that density-dependence acts only on the slope parameter r . The value of L_c represents the mean length of sex change, or the length at which individual fish have a 50% probability of switching sex. The stock assessment reports that this parameter has not changed significantly in the GOM gag population, so I chose to leave L_c fixed (SEDAR 2006; see the Discussion for more information regarding the development of this function). The slope parameter r alters the rate of the probability that fish will switch sex. I assumed that the relationship between r and male density was positive and non-linear: r increases with density, but increases more slowly as density gets large (Fig. 4.4). Density is represented by the parameter $ratio$, the site-specific sex ratio described above. The transformation of r is shown in equation 10, for all spawning sites j during time t :

$$(10) \quad r' = ta (\text{ratio}_{j,t}^{0.5})$$

The value of ta was calculated by dividing the fixed value of r by the square root of the median $ratio$ value obtained from the status quo simulation (see Table 4.1). The complete sex change

function follows equation 11 shown below, and Figure 4.5 shows a general sex change probability curve for a range of density values:

$$(11) \quad P_{\text{change},L} = 1 / [1 + \exp^{((-\tau a (\text{ratio}_j^{0.5})) (L - L_c))}]$$

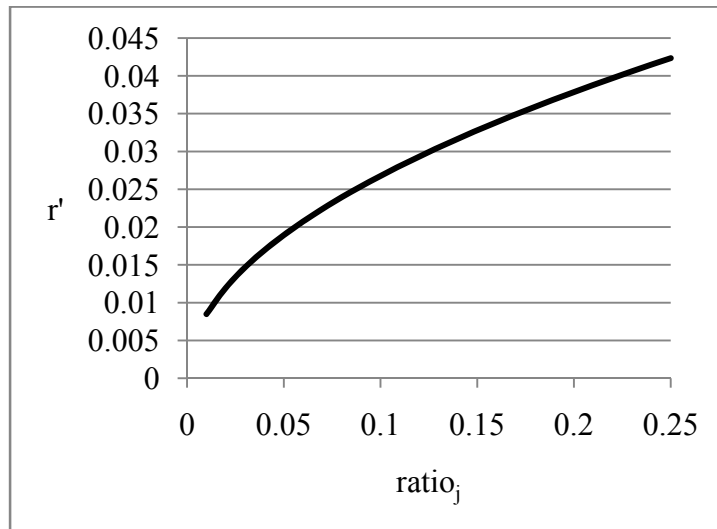


Figure 4.4. Change in the density-dependent sex change function shape parameter r' for a range of estimated densities measured as the site-specific sex ratio.

All simulations tested in Chapter 3 were replicated with the IBM including density dependent sex change (six marine reserve scenarios by five fishing effort regimes, and change in fishing mortality rate without marine reserves). No other parameters or function were altered (except for the calculation of site-specific fertilization success described above).

4.3. Results

The addition of density-dependence to the sex change functions did not significantly change the general pattern of the sex ratio response to marine reserve scenarios and fishing effort regimes for either model: sex ratio increased with increasing reserves and decreased with increasing fishing effort. However, the magnitude of the sex ratio response changed when compared to the fixed function. Marine reserves had a positive impact on the male to female sex

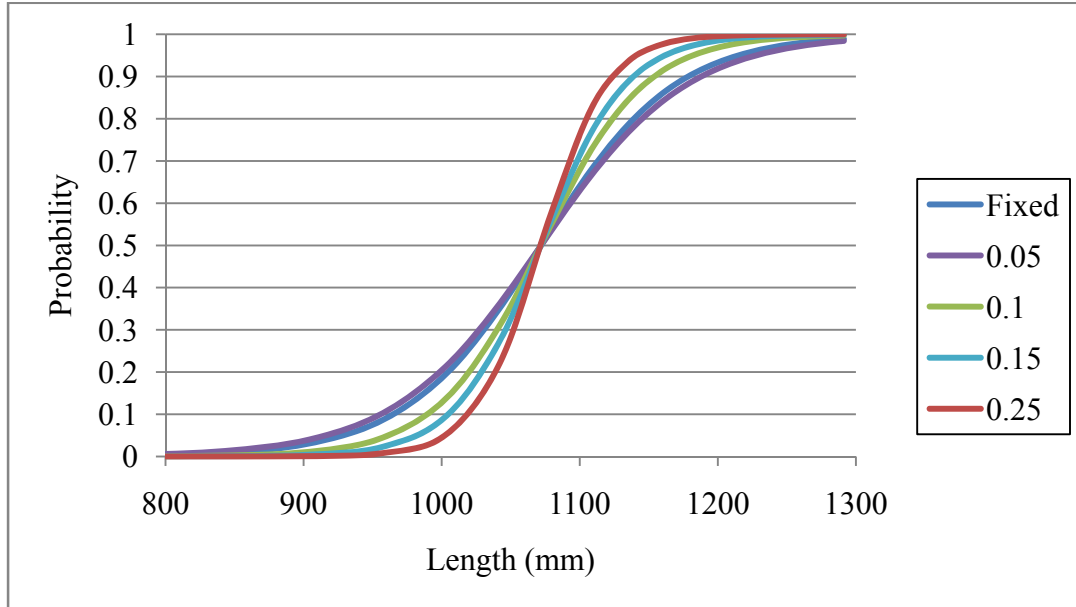


Figure 4.5. Sex change probability curves for a range of estimated densities based on the density-dependent transformation (“Fixed” is the fitted curve from Chapter 3).

Table 4.1. Parameters referred to in this chapter, the model they are used in (A.S. is the age-structured model), their source (reference or the equation used to calculate constants) and values.

Parameter	Description / Model	Source	Value
r	Slope parameter, A.S.	Fitted to observed proportions	0.0597
q	Age at first change, A.S.	Fitted to observed proportions	5.745
c	Slope adjustment, A.S.	$r (p_{\text{male}0})$	0.00338
d	Age adjustment, A.S.	$(q - q_{\text{min}}) / (p_{\text{male}0}^{0.5})$	3.13
pmale0	Mean value of population sex ratio	Status quo simulation	0.058
q_{min}	Minimum age at first change, A.S.	“best guess” (my estimate)	5.0
Θ	Fertilization parameter, both models	“best guess” (my estimate)	50
r	Slope parameter, IBM	Fitted to observed proportions	0.0206
ratio₀	Median value of ratio, IBM	Status quo simulation	0.0591
ta	Slope adjuster, IBM	$r / (\text{ratio}_0^{0.5})$	0.0847

ratio which was used as the proxy for density, so small reserves coincided with low density. At low male density (or small reserves) the addition of density-dependence improved the estimates of sex ratio when compared to the fixed function. With large reserves, the addition of density-dependence returned lower estimates of sex ratio when compared to the fixed function.

4.3.1. Age-Structured Model

The pattern for sex ratio, adult population, and yield were the same with and without density dependence in the sex change function. However, the magnitude of response was only notably different for sex ratio, so results are only these results are presented (Fig. 4.6). The influence of density-dependent sex change on the equilibrium sex ratio was dependent on the reserve scenario tested because reserve size was positively correlated to sex ratio within a given fishing effort regime. For small reserves, the addition of density-dependence resulted in a higher equilibrium sex ratio when compared to the fixed sex function. For large reserves, adding density-dependence resulted in a lower equilibrium sex ratio when compared to the fixed function. This pattern is most apparent in the calculation of the minimum size reserves needed to reach the 5% and 10% male benchmarks (Fig. 4.7). With density-dependent sex change, smaller reserves are needed to attain 5% males in the population and larger reserves were needed to attain 10% males.

Changes in fishing effort tended to amplify the effects of density-dependence for the small reserve scenarios. Considering the two examples plotted in Figure 4.8, with no change in fishing mortality the difference between the equilibrium sex ratio with and without density-dependent sex change with no reserves was 5.8% but the difference with 100% reserves was 38.3%. For the “High” effort regime (a 25% increase in fishing mortality), the difference in the equilibrium sex ratio with no reserves was 31.6% and with 100% reserves was 32.9%. For all effort regimes, the equilibrium sex ratio without density-dependent sex change started below the

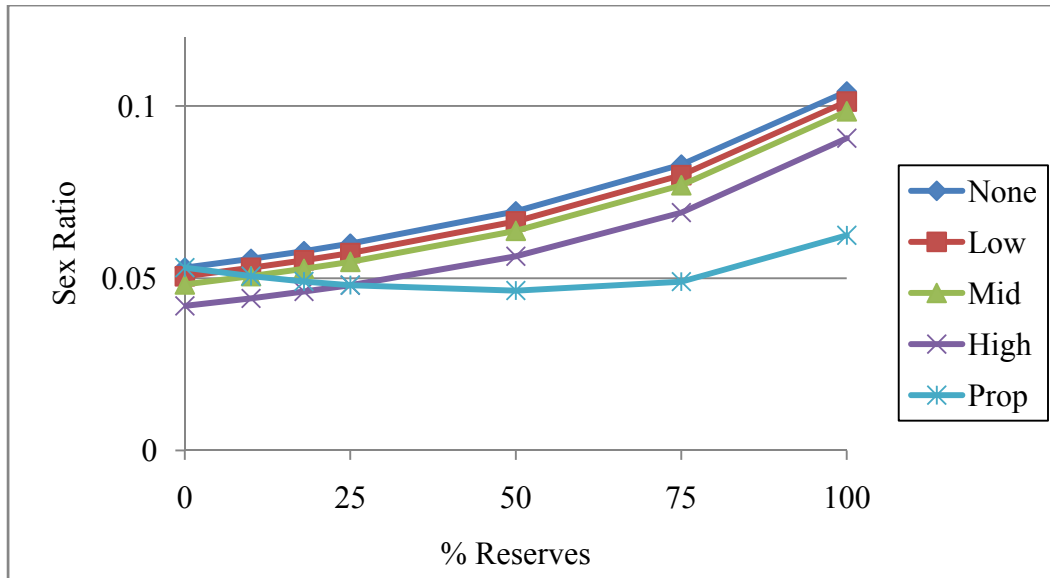


Figure 4.6. Sex ratio response to increasing marine reserve size for the five fishing effort regimes described in the text with the inclusion of density-dependence to the sex change function.

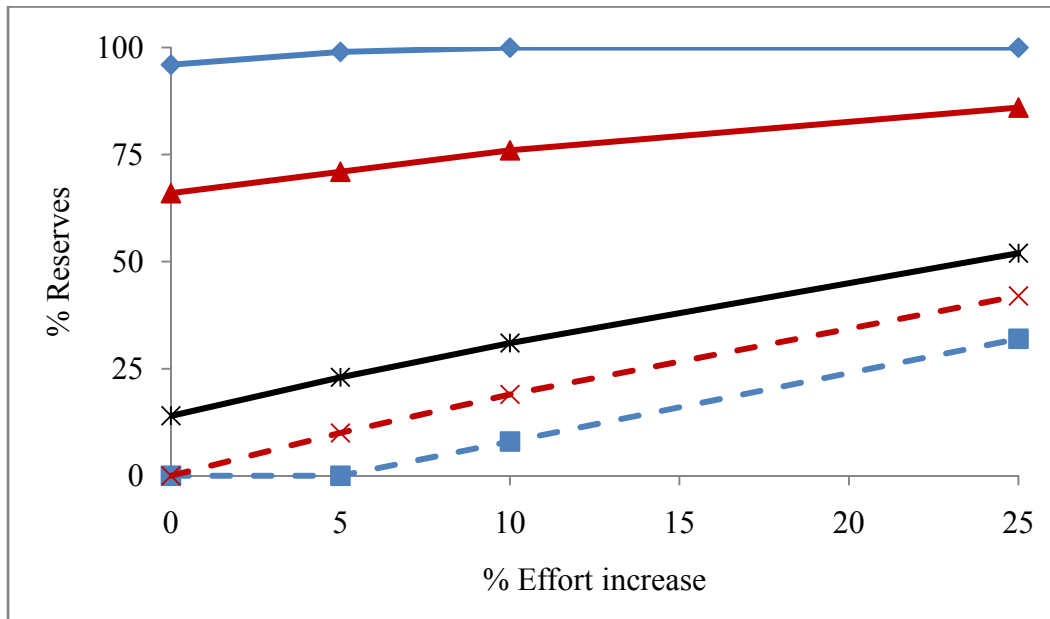


Figure 4.7. Minimum reserve size needed to attain sex ratio benchmarks of 5% (dashed line; red= no density, blue = with density) and 10% males (solid lines). The black line indicates the reserve size necessary to attain 5.67% male, the ratio at which the density-dependent function was equal to the fixed function.

density-dependent curve but finished above as reserve size increased (Fig. 4.8). The sex ratio response curves with and without density-dependent sex change crossed at approximately 5.67% males for all effort regimes. The reserve size needed to attain 5.67% reserves increased with increasing fishing effort as shown by the black line in Figure 4.7.

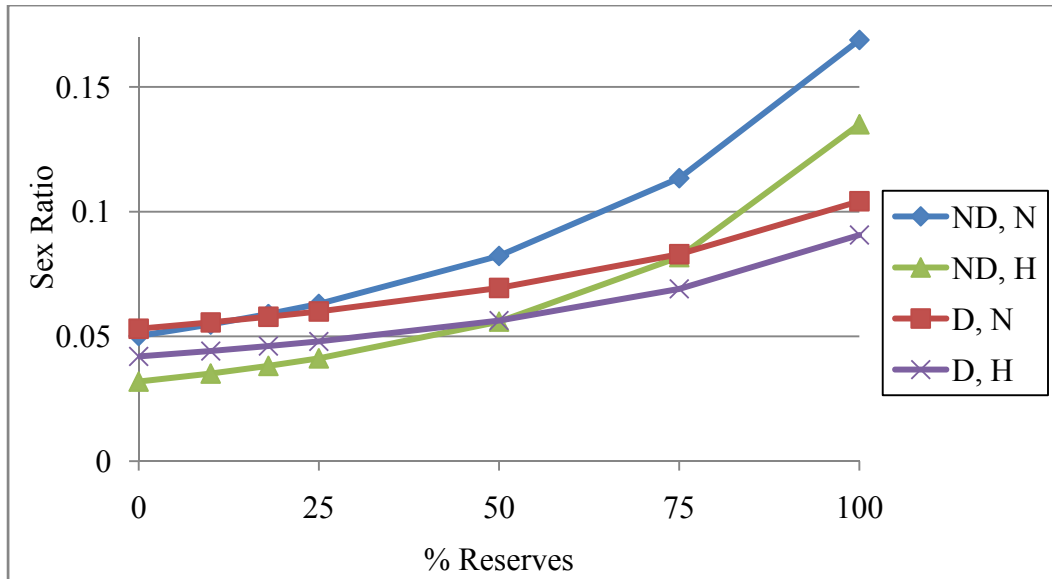


Figure 4.8. Sex ratio response with (D) and without (ND) density-dependent sex change for increasing marine reserve size and two the None (N) and High (H) effort regimes.

For the proportional redistribution regime the inclusion of density-dependence to the sex change function improved the equilibrium sex ratio up to 92% reserves, at which point the sex ratio was 5.67% (Fig. 4.9). The sex ratio response curve crossed the 5% benchmark at 12% reserves and again at 77% reserves. No scenarios attained the 10% male benchmark. The inclusion of density-dependence for the proportional redistribution regime appeared to flatten the sex ratio response curve, suggesting that density-dependence may reduce natural fluctuations in sex ratio.

The sex ratio response when fishing mortality rate changed without any reserves is shown in Figure 4.10. The addition of density dependence to the sex change function yielded a much

smaller estimate of the equilibrium sex ratio with no fishing than for the fixed function: 19.8% males with density-dependence versus 36.7% males for the fixed function. The two response curves crossed when f_{mult} equaled 1.0, or the current mortality rate, indicating that density-dependence resulted in a larger equilibrium sex ratio at high fishing mortality. Density-dependent sex change also appeared to make the population more resistant to “crashing”, defined as an equilibrium population size less than 10% of the initial adult population. With density-dependent sex change the population crashed when the fishing mortality rate was 1.6 times the current estimate while with fixed sex change function the population crashed when the mortality rate was 1.46 times the current estimate.

The results of the sensitivity analysis are shown in Table 4.2. The negligible impact of the density-dependent sex change function on adult population and yield is shown by the extremely low sensitivity of these two response variables to change in the density parameters. The only parameter that showed a significant sensitivity (>1 , shown in bold) was q_{min} for sex ratio.

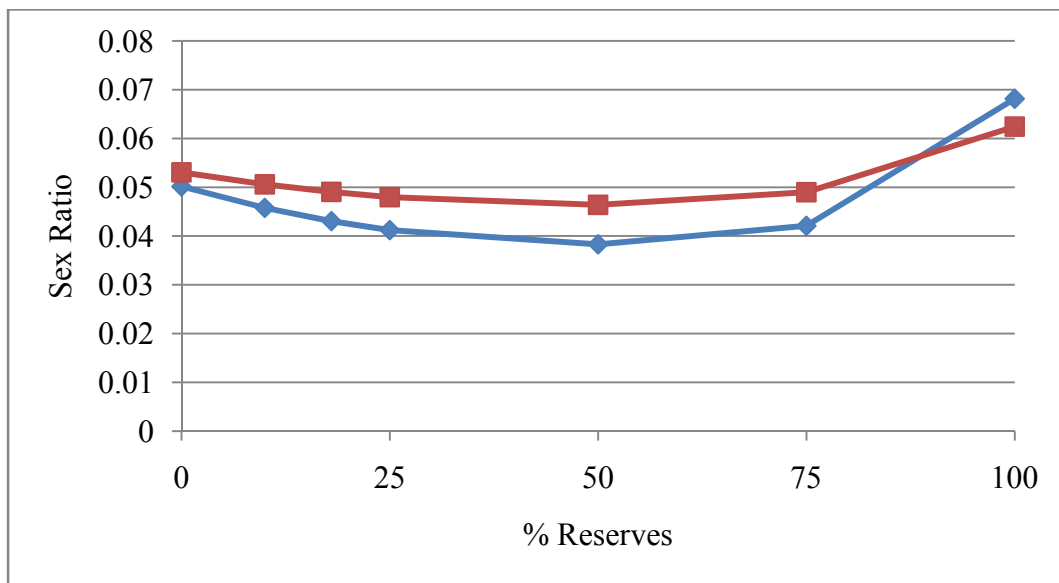


Figure 4.9. Sex ratio response to increasing marine reserve sizes for the proportional redistribution regime with density-dependent sex change (red line) and without (blue line).

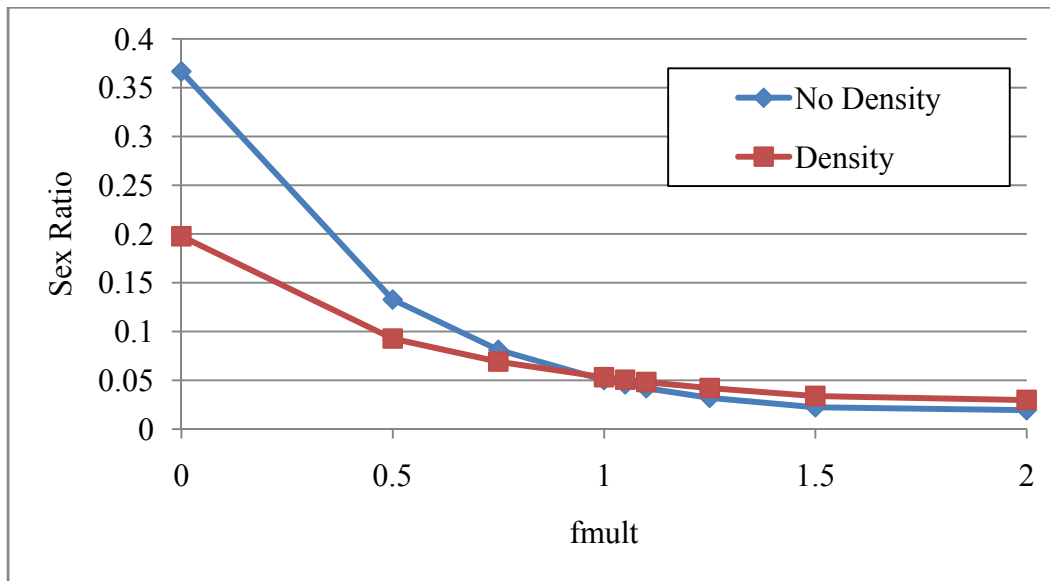


Figure 4.10. Sex ratio response to increasing fishing mortality rate for no marine reserves with density-dependent sex change and fixed sex change.

Table 4.2. Sensitivity analysis for the age-structured model with density-dependent sex change parameters.

Parameter	Adult Population	Sex Ratio	Yield
c	0.00388	0.359	0.000601
d	-0.00243	-0.226	-0.000767
q_{min}	-0.0158	-1.45	-0.00498

4.3.2. Individual Based Model

When fertilization success was allowed to vary according to site-specific male density, fertilization success expressed as the mean of all sites for the final 20 years of simulations transformed from curved (see Fig. 3.8) to linear (Fig. 4.11), and converged near 1 with 100% reserves for all four fixed effort regimes. Response by sex ratio and adult population size to site-specific fertilization success was not notably different than for population-specific fertilization success. Because of this result, all subsequent changes in sex ratio or population were attributed to changes in the sex change function.

As in the age-structured model, the addition of density-dependence to the sex change function did not alter the general pattern of the sex ratio response (Fig. 4.12). Equilibrium sex ratio increased with larger reserves, and decreased with increased fishing effort. The curves continue to show a slightly diminishing trend in sex ratio increase as reserves approached 100%, suggesting that the greatest benefit may be experienced with smaller reserves. Proportional redistribution remained the “worst case” regime where benefits to sex ratio for reserves larger than 25% were effectively negated by the redistribution of effort.

Similar to the age-structured model, the addition of density-dependence to the sex change function improved estimates of equilibrium sex ratio when male density was low as compared to the fixed function, and reduced the equilibrium sex ratio when male density was high. For the two examples plotted in Figure 4.13, with no change in fishing effort the difference in the equilibrium sex ratio between the density-dependent sex change and the fixed sex change was 28.8% with no reserves and 13.5% with 100% reserves. For the “High” effort regime the difference in the equilibrium sex ratio was 74.7% with no reserves and 12.1% with 100% reserves. Density-dependence seemed to have a larger effect on sex ratio for small reserves. As fishing effort increased, the reserve size at which the equilibrium sex ratio for fixed sex change

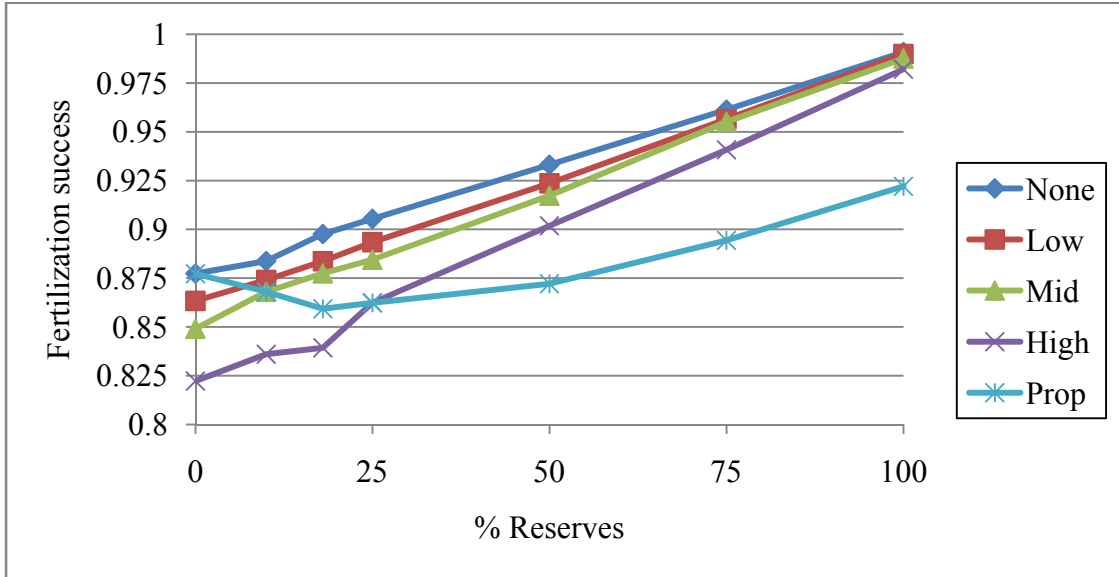


Figure 4.11. Fertilization success response to increasing marine reserve size and the five fishing effort regimes defined in the text with the inclusion of density-dependence in the sex change function.

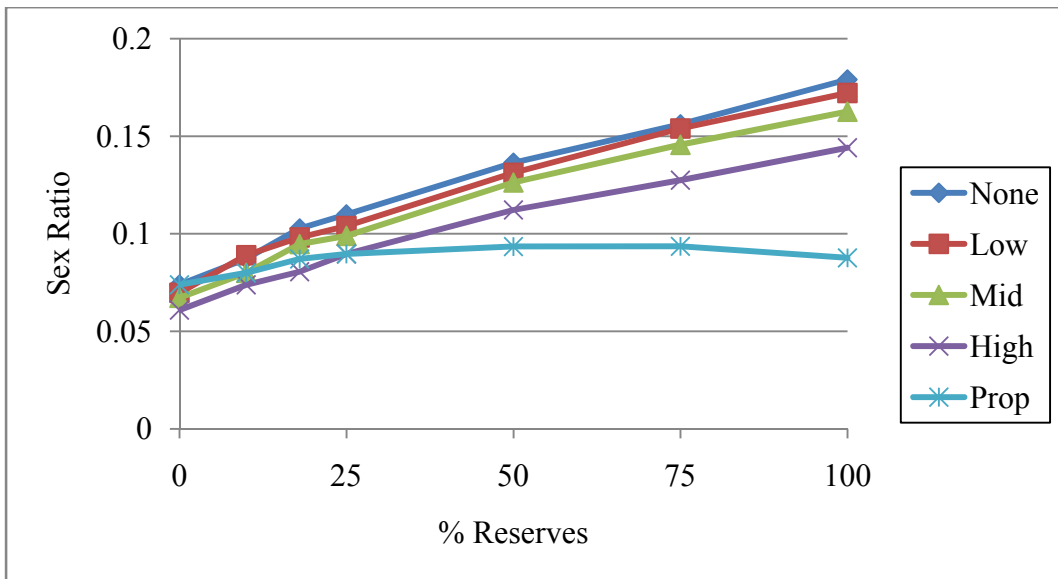


Figure 4.12. Sex ratio response to increasing marine reserve size and the five fishing effort regimes described in the text with the inclusion of density-dependence in the sex change function.

was larger than the equilibrium sex ratio with density-dependence also increased (shown as the black line in Fig. 4.14). For all density-dependent simulations the equilibrium sex ratio with no reserves was greater than the 5% benchmark. The minimum size reserves needed to attain the 10% male benchmark increased with increasing effort and was larger than with the fixed sex change function (Fig. 4.14). Equilibrium sex ratio for the proportional redistribution regime was between the 5% and 10% benchmarks for all reserve simulations, indicating that other management options are required to substantially increase the sex ratio if effort remains constant as reserve size increases.

The equilibrium adult population response to increasing reserve size with density-dependent sex change followed the same pattern with as with fixed sex change (see Fig. 3.6). Equilibrium adult population size increased linearly with increasing reserve size for the four fixed effort regimes and decreased linearly for the proportional redistribution regime. Fertilization success did not change with the addition of density-dependence to the sex change function; it remained linear for the four fixed redistribution regimes and convex for the proportional redistribution regime (see Fig. 4.11).

When fishing mortality changed without marine reserves the pattern of the sex ratio response was similar to the age-structured model but the impact of density-dependence was smaller (Fig. 4.15). The equilibrium sex ratio with no fishing was 40% male, outside of the range of expected values for the sex ratio of an unfished population of gag. The addition of density-dependence did make the population slightly more resilient to crashing at high fishing mortality: with fixed sex change the population crashed when fishing mortality was 1.7 times the current rate, while with density-dependent sex change the population crashed when fishing mortality was 1.76 times the current rate.

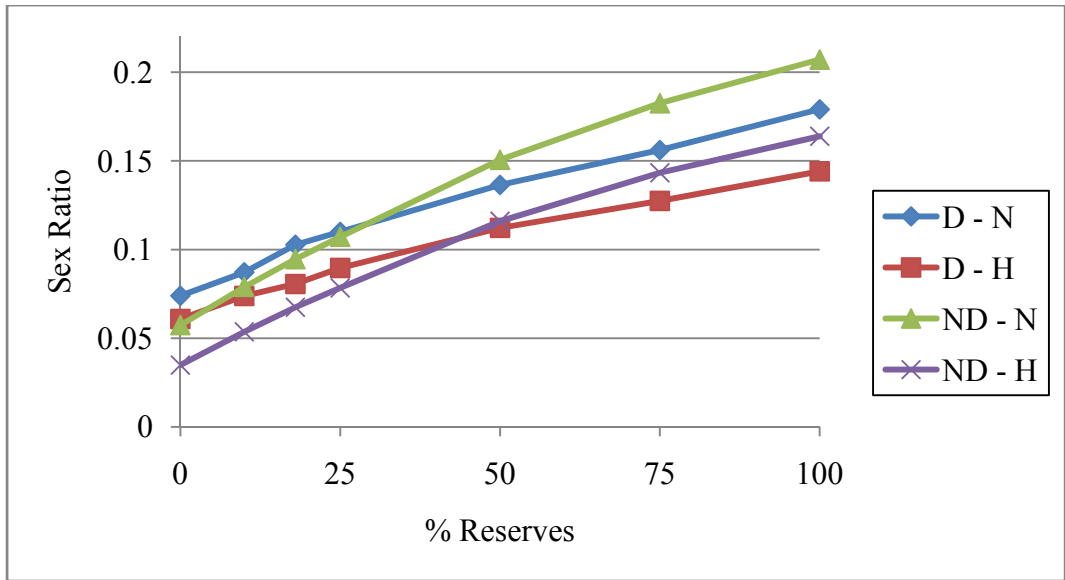


Figure 4.13. Sex ratio response for the “None” (N) and “High” (H) fishing effort regimes with (D) and without (ND) density-dependent sex change for increasing marine reserves.

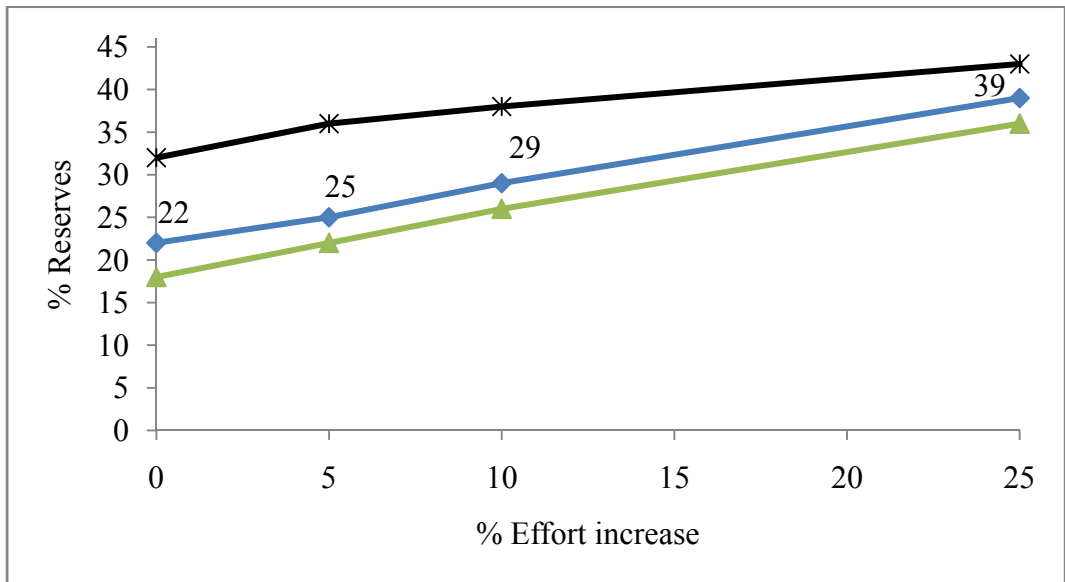


Figure 4.14. Minimum reserve size needed to attain the 10% male benchmark with density-dependent sex change (blue line) and fixed sex change (green line) for increasing fishing effort. The black line depicts the reserve size at which the equilibrium sex ratio without density-dependence equaled the sex ratio with density-dependence.

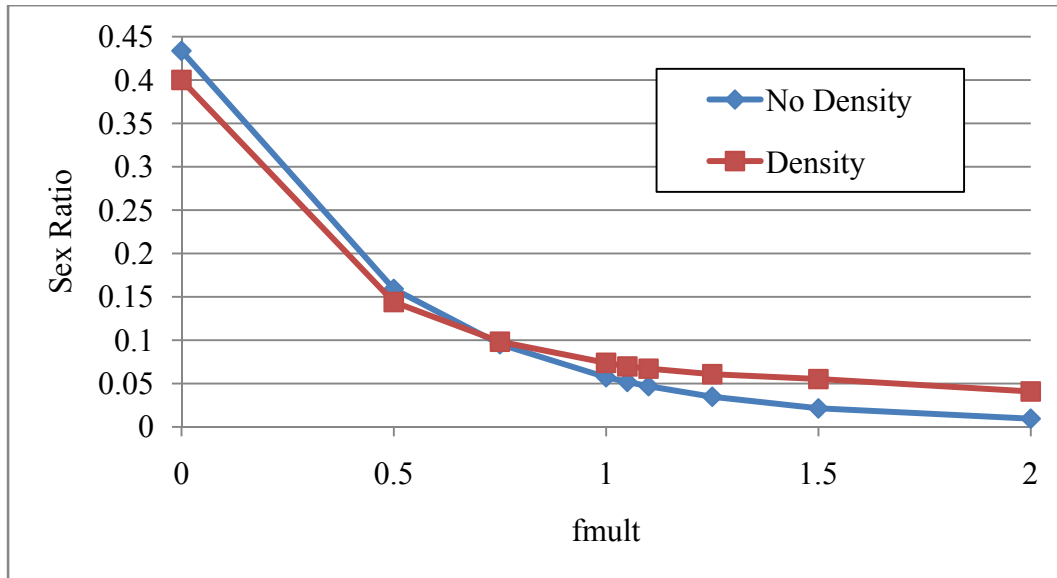


Figure 4.15. Equilibrium sex ratio response to changing the fishing mortality rate with no marine reserves; the red line shows the simulations with density-dependent sex change (Density) and the blue line shows simulations with fixed sex change (No Density).

4.4. Discussion

The addition of density-dependence to the sex change functions in the two models was the most theoretical part of my study but also the most interesting. My discussion will first describe the development process for the density-dependent sex change functions, briefly elaborate on some implications of the results, and conclude with a general discussion of possible future applications of these functions.

4.4.1. Age-Structured Model

The addition of density-dependence to the sex change function in the age-structured model was relatively straightforward. The three density-parameters added to the model approximated the expected effect that socially-induced sex change would have on a population. The use of the square root on the density variable $pmale$ in the transformation of the intercept parameter was chosen arbitrarily as I assumed that the density effect would be non-linear and would decrease as male density increased. Lacking specific information regarding the effect of

male density on either the shape or the intercept parameter, patterns of density effects were limited to coarse representations.

The sensitivity analysis revealed that the model was most sensitive to small changes in the age at first sex change, represented by the q_{min} parameter. One possible cause for the insensitivity to the density parameters c and d is because the calculation of these parameters was based on information from the fixed model simulations. However, the q_{min} value was added to represent an assumed physiological minimum, and was included to improve the estimation of the intercept value q' . The low sensitivity of both population size and yield to changes in the density parameters was reflected by the lack of any significant change in the response curves when density-dependence was added. Heppell et al. (2006) found that their model results were similarly insensitive to small changes in fertilization success. In the model fertilization success is a function of the population sex ratio and ultimately impacts the population size and yield via changes in recruitment. That recruitment appeared to be insensitive to small changes in fertilization success driven by sex ratio is not surprising given the stochastic component of recruitment. The stock assessment concluded that extremely high variability in the stock-recruitment relationship in effect made recruitment independent of the stock size (SEDAR 2006). The stochastic function used in the model was fitted to recruitment estimates found in the stock assessment, so the model stock-recruitment function also contained a high amount of variability which had the effect of masking any small changes in fertilization success caused by management options and changes in fishing effort. While this caused little apparent change in the response of population size and yield with the addition of density-dependence, sex ratio was sensitive to density-dependent sex change.

In general the addition of density-dependence to the sex change function approximated the expected effect that socially-induced sex change would have on a heavily fished protogynous

population. Socially-induced sex change should act as a buffer against high fishing mortality by increasing the probability that fish will change sex as the sex ratio is driven down by size-selective fishing. The model results showed exactly this pattern for sex ratio. The buffering effect on the population size with high fishing mortality can be interpreted as an extension of the sex ratio effect: as high fishing pressure depletes the population, density-dependent sex change serves to maintain enough males in the population to limit fertilization failure.

4.4.2. Individual Based Model

The development of the density-dependent sex change function used in the IBM was more complicated than for the age-structured model. When developing the function for the IBM, I followed the same methodology as I used for the age-structured model. Initially I assumed that density-dependence would alter both the rate of change and the mean age of change. The initial transformation based on these assumptions included four density parameters: ta altered the shape parameter as an inverse relationship with density; tb altered the mean age of change as a positive but non-linear relationship with density; tc was a constant representing the minimum age at first change; and td altered the mean age at change based on density similar to tb . The full function appears below in equation 12 for length L as a function of the site-specific sex ratio $ratio_j$:

$$(12) \quad P_{\text{change},L} = 1 / [1 + (\exp^{(-ta (ratio_j^{0.5}))}) (L - (tc + tb (ratio_j^{0.5}) + (tc) (ratio_j^{0.5})))]$$

Figure 4.14 depicts probability curves derived from this transformation for four different estimated densities. Upon first examination, the model appears to all fit the assumptions made concerning the effect of density on the probability of sex change. However, the probability curves derived from the transformation caused the probability of sex change for young fish to increase slightly with increasing density, opposite of the expected pattern. In addition, this full transformation included four parameters, all based on assumptions made by approximating

patterns observed from the stock assessments. I wanted to test whether a simpler model could be used to reduce the number of assumptions made. Using the transformation described earlier in the Methods section, I reduced the number of density parameters to just one that altered the shape of the curve. Exploratory simulations revealed that the sex ratio response followed roughly the same pattern for both the full transformation and the single-parameter transformation (based on results of the age-structured model that used the same assumptions; Fig. 4.15). These exploratory results indicated that reducing the number of parameters did not affect the shape or magnitude of the response when compared to the full transformation (Fig 4.15), so I chose to use the simpler model with the fewest assumptions.

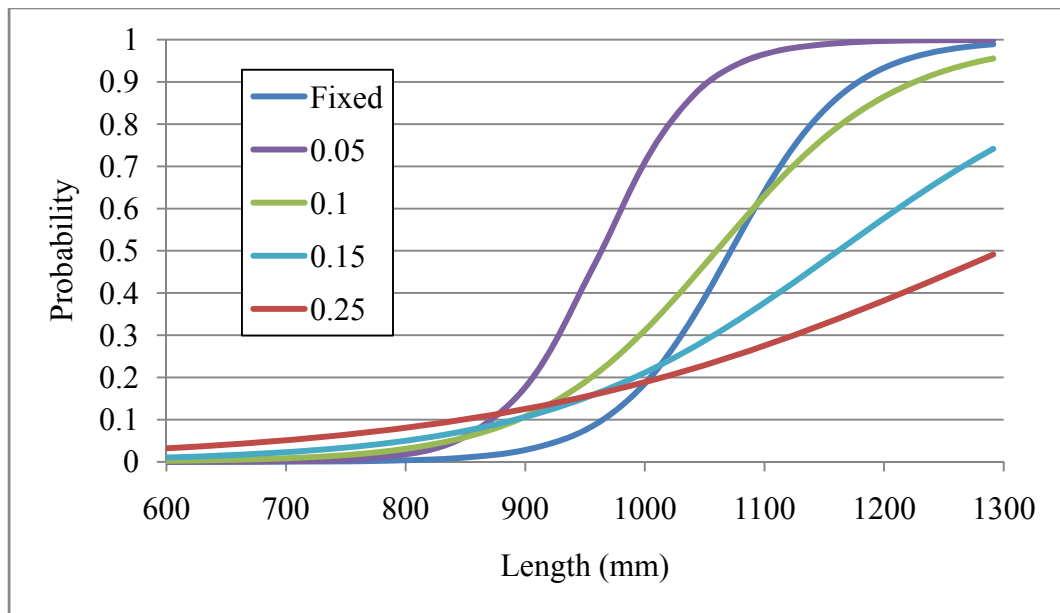


Figure 4.16. Five sex change probability curves for a range of estimated densities for the full, four parameter density-dependent sex change transformation, where the notation “Fixed” represents the fitted curve from Chapter 3.

In general the addition of density-dependence to the sex change function in the IBM reflected the expected effect that socially-induced sex change would have on a heavily fished protogynous population. The same patterns apparent in the age-structured model results

appeared in the IBM results. Socially-induced sex change appeared to act as a buffer against high fishing mortality resulting in higher sex ratio when the density was decreased by fishing pressure. The IBM results also showed the buffering effect on the population size at high fishing mortality rates.

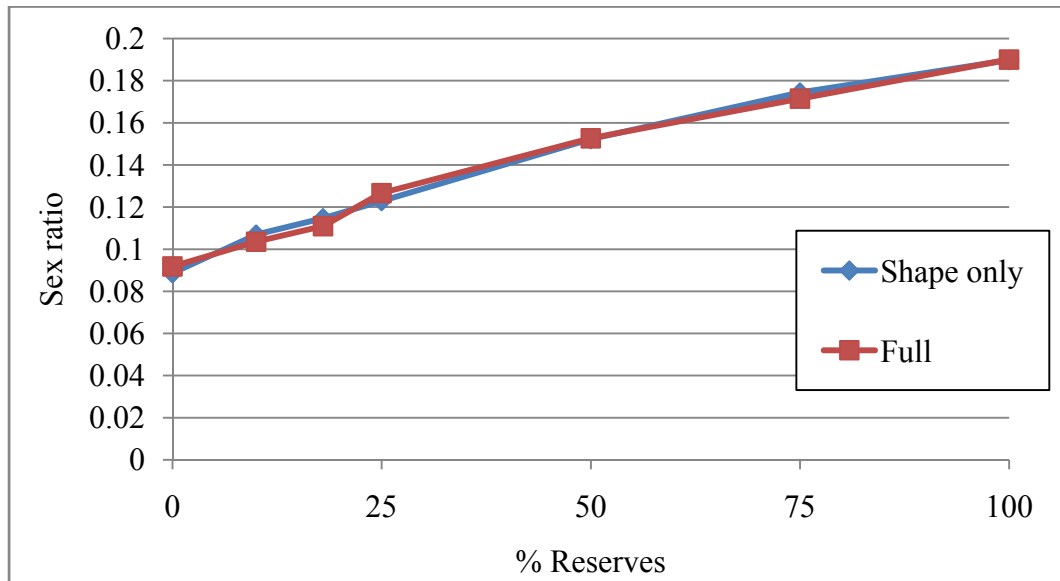


Figure 4.17. Response curves for two iterations of the sex change function: the full transformation and the single-parameter transformation (Shape Only) to increasing marine reserves with no change in fishing effort.

4.4.3. General Considerations

The results of modeling socially-induced sex change with the addition of density-dependent parameters to the sex change functions in the models revealed at least two outcomes that would be popular for fishery managers. The first is the improvement of sex ratio estimates at low male density. This result could be used to support the use of marine reserves as the inclusion of density-dependence improved estimates of sex ratio at low male density. However, it must be noted that the exact magnitude of the density-dependent effect as modeled here was essentially arbitrarily chosen. Although the assumptions regarding the performance of density parameters were informed by observations from the real population, in the end they are rough

approximations of observed patterns. While the results from the models suggest that density-dependent sex change may improve the ability of marine reserves to increase the population sex ratio, the actual response to reserves is uncertain. Nevertheless, this result suggests that more studies regarding socially-induced sex change could be beneficial to understanding the impact of management options on the fishery.

The second result that may prove attractive to fishery managers is the increase in resilience to high fishing mortality shown with the inclusion of density-dependence. In a fishery that aims to maximize long term yield, it is necessary to understand the mechanisms that influence the number of fish available for harvest, and also how harvest affects the population. The result that density-dependent sex change may make the population more resilient to fishing pressure should provide the motivation for more studies that explore the specific mechanisms controlling sex change. Improving understanding of these processes will better inform the magnitude of the density-dependent effect and ultimately improve fishery-specific population targets. The recognition that female-only measures of spawning stock may be underestimating fishery impacts on protogynous populations is the first step towards improving assessment models. Other modeling studies have suggested including a measure of male biomass to MSY-based assessment measures (Brooks et al. 2008), and Alonzo and Mangel (2005) used a version of this IBM to show that Spawner-Per-Recruit measures could be improved with knowledge of the mechanism controlling of sex change. For gag, where it is assumed that social cues play at least some part in controlling sex change, the results from this modeling work suggest that including an approximation of the effect of socially-induced sex change could further improve assessment measures for protogynous populations.

CHAPTER 5: MODEL COMPARISON AND CONCLUSION

The two models developed for this thesis, the age-structured model and the IBM, were used to describe a similar population experiencing the same management actions and changes in fishing effort. Because of the differences in the methods between the two models comparing results may reveal unexpected patterns that could be indicative of coding errors or particularly sensitive parameters or functions that were not accounted for. While the comparison did not reveal any coding errors, the differences in the results raise a number of questions regarding how well the two models actually represent the functions that take place in the population. First I will compare the model results for the fixed sex change simulations, and then for the density-dependent sex change simulations. I then include some management recommendations based on the modeling results, which is difficult due to the fact that there are no specific standards for how the sex ratio in the gag population should be managed other than to keep it above some undefined minimum. The model results were also highly sensitive to changes in fishing effort as well as the pattern of effort change, so all recommendations must consider the expected changes to fishing effort through time. Finally, I offer some brief concluding statements.

5.1. Model Comparison

5.1.1. Fixed Sex Change

Both the age-structured model and the IBM simulated a model gag population with similar results. To compare the results of the two different models with each other, estimates of adult population size and sex ratio were corrected relative to the value of the status quo simulation (18% reserves and no change in fishing effort). The plot of the relative adult population size was similar for both models: both show a linear response to increasing marine reserves with the magnitude of the relative change from the status quo about the same for a given reserve size (Fig. 5.1). The slopes of the response lines for increasing reserve size were larger

for the IBM results than for the age-structured model results. This pattern is visible in the plot (see Fig. 5.1), where the values from the age-structured model were greater than those from the IBM with 0% reserves, but less than with 100% reserves.

For fishery yield, the results from the different models were corrected relative to the yield at the current fishing mortality rate ($fmult = 1.0$). The plot of the relative yield shows that the two lines were nearly identical and approximate a typical surplus production curve (Fig. 5.2). Both curves had a maximum value at about the same value of fishing mortality ($fmult = 0.44$ at MSY for the age-structured model; $fmult = 0.43$ at MSY for the IBM). The age-structured model crashed when $fmult$ was greater than 1.46, but the IBM did not crash until $fmult$ was greater than 1.7. This discrepancy is visible in the plot of the two yield curves where the age-structured model curve drops below the IBM curve suddenly while the IBM curve does not indicate any yield crash.

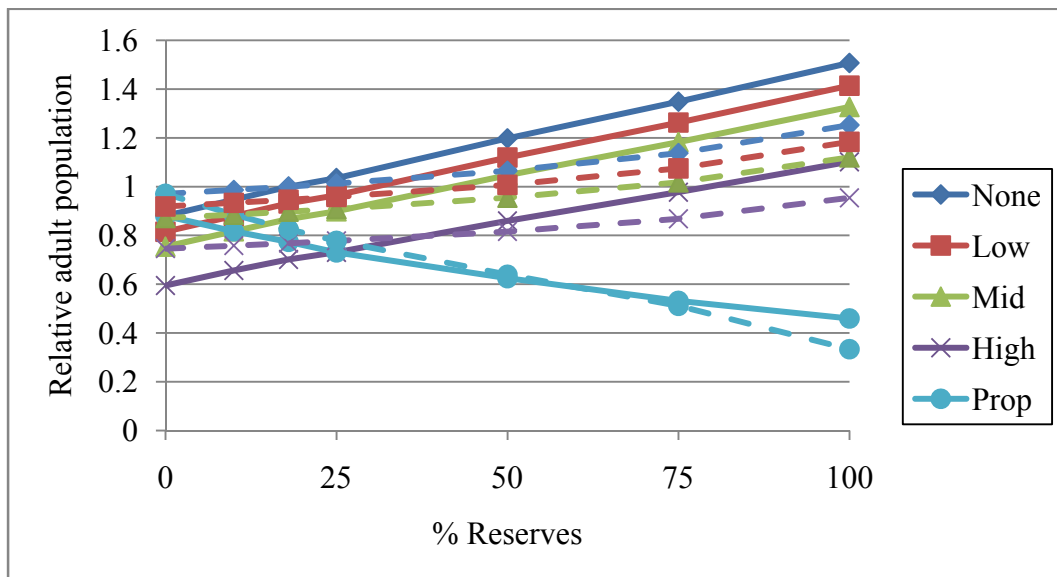


Figure 5.1. Adult population size relative to the status quo simulation for increasing marine reserve size and fishing effort regimes described in the text. Solid lines indicate results from the IBM and dashed lines indicate results from the age-structured model.

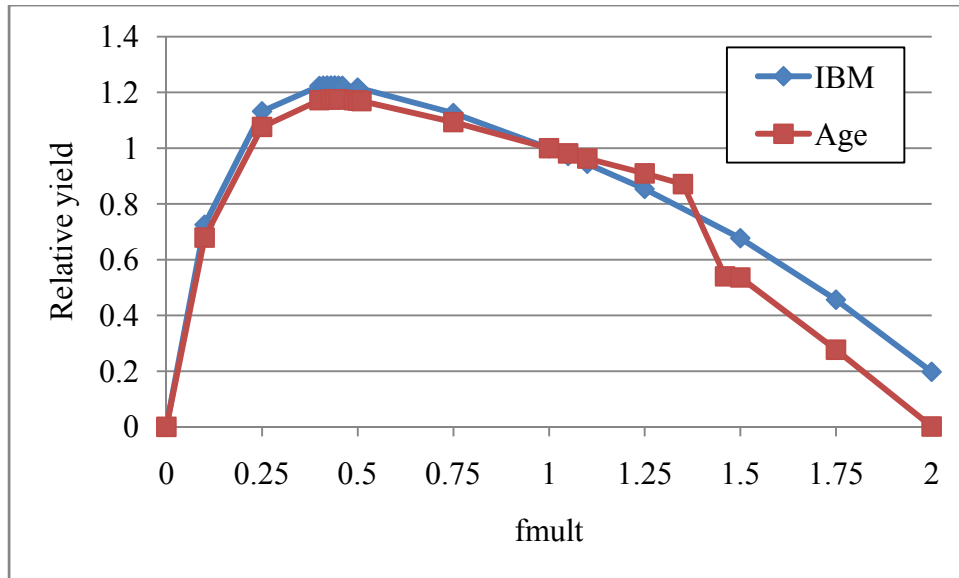


Figure 5.2. Yield curves for the age-structured model and the IBM where the values plotted are equilibrium yield values relative to yield at $fmult = 1.0$ (the current fishing mortality rate).

While the relative response curves for adult population size and yield were similar for both models, the sex ratio response curves for increasing marine reserve size were distinctly different between the two models (Fig 5.3). The shape of the sex ratio response curve for the age-structured model was convex, while the sex ratio response curve for the IBM was concave. The difference in shapes resulted in closer estimates of sex ratio for small and large sized reserves but a much larger difference in estimates for middle-range reserves. When the sex ratio results from the two models are adjusted relative to the equilibrium sex ratio value from the status quo simulation, the two curves overlap much more (Fig. 5.4). The general shapes (IBM concave and age-structured convex) are retained, but the changes in magnitude are more revealing. For the 100% reserve size the age-structured model estimates were much higher relative to the status quo than estimates from the IBM.

The two models used different functions and methods to model sex change. In the age-structured model, the number of females that changed sex each time step was calculated as a

percentage of the total female population of that age. This age-specific percentage that changed was based on the probability curve fitted to observed proportions of fish post-mortality (Fig. 5.5). Of the number of fish in each age class that survived that year and were mature females a fixed proportion switched sex each time step. In the IBM the probability of changing sex was calculated for individual fish and based directly on the observed proportion curve (see Fig. 4.1). Each female fish that survived in a given year was then given a probability of sex change based on this curve. However, because the function works on individuals and not the population, the number of fish that actually change each year was not necessarily the number that would fulfill the expected proportion. In both models only females changed sex, once fish were males they stayed males, and the number of males did not influence the probability that remaining females would change sex.

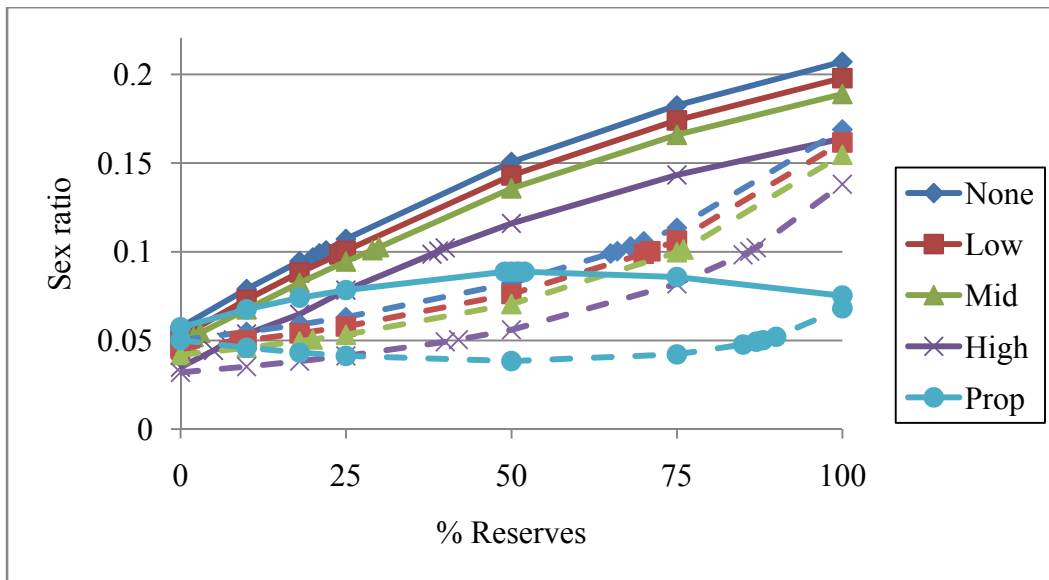


Figure 5.3. Absolute sex ratio values for simulations the modeled increasing marine reserve size and five fishing effort regimes, solid lines represent results from IBM and dashed lines represent results from the age-structured model.

Of the two methods, the IBM approach probably does a more realistic job replicating how sex change occurs in the population. Individual fish face differential probabilities of sex change based on specific social and non-social cues; they do not necessarily follow the probability that would result in an expected proportion. In the IBM the number of new males each year will vary even with equal sized cohorts, while in the age-structured model the number of new males will be the same each year given equal sized cohorts. However, the IBM function would require some additional modification so that on average the function returns a proportion that replicates the observed data. This additional step was not taken, but the difference between the two methods deserves some additional consideration. Overall, I think that while neither approach is perfect, that the IBM is more realistic by virtue of including some variability in sex change from year to year.

The comparison of the results of the two models indicates that general population dynamics were modeled similarly but the specific sex structure of the population was different. The population curves indicate that the models effectively recreated similar effects in terms of the number of individuals in the population. The populations in both models were driven by the same Beverton-Holt stock recruitment function, so comparable patterns seen the results make sense. Likewise the functions used to calculate fishery yield were the same between the two models. The difference in the sex ratio results between the models can be explained by the differential treatment of sex change. This difference could have implications for a real fishery in terms of the fertilization success which was a function of the sex ratio. However both models were insensitive to small changes in fertilization success, mainly due to the stock-recruitment functions, so these patterns were not seen in the results. Adjusting the stock-recruitment function to make the model more sensitive to small changes in the stock size could help to better understand how the sex ratio affects the population through time.

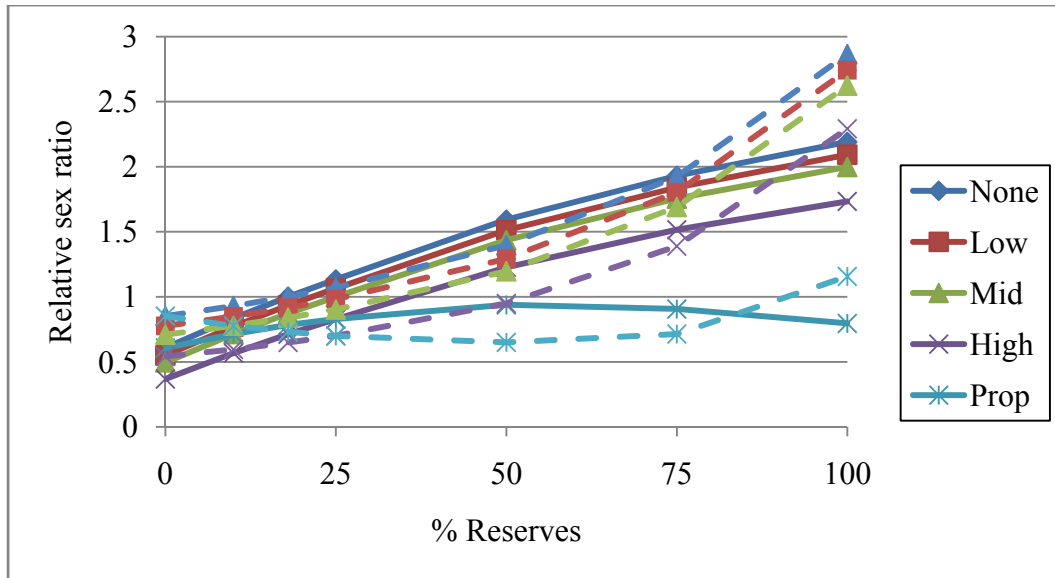


Figure 5.4. Sex ratio values relative to the equilibrium values for the status quo simulation for increasing marine reserve size and five fishing effort regimes, solid lines represent results from IBM and dashed lines represent results from the age-structured model.

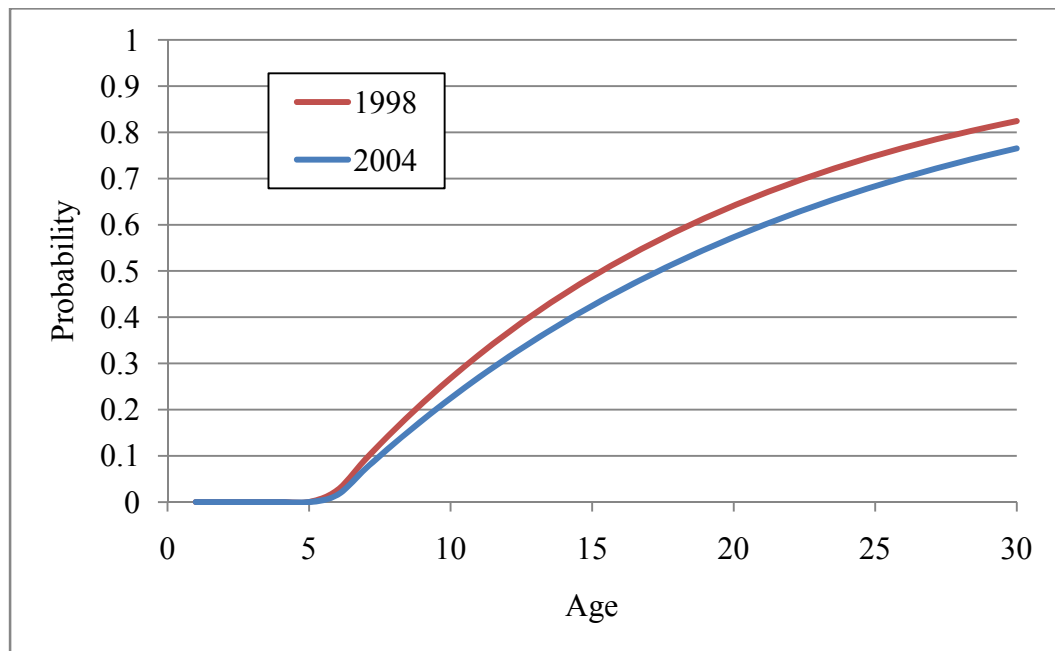


Figure 5.5. Probability of sex change for the age-structured model, fitted to observed proportions at age in the catch based on the method described in Heppell et al. (2006; SEDAR 2006).

5.1.2. Density-Dependent Sex Change

The addition of density-dependence to the models followed the same assumption: as the density of males increases in the population, the rate at which females switch sex will decrease. The specific mechanism for the density-dependent relationship in each model was different mainly due to the inherent differences in the way that sex change was treated between the models as explained above. Despite these differences, density-dependent sex change altered the model results in the same way.

The specific pattern of density-dependent added to the models was largely hypothetical due to a lack of specific data regarding how the rate of sex change is influenced by the density of males in the population. Sex change functions were fitted to observed proportions of fish from the age and growth study done for the 2006 gag stock assessment (SEDAR 2006), but in the age-structured model the probability curve was fitted to observed proportions post-mortality, while the IBM used the proportions at length curve directly. Another way to interpret this is the age-structured model followed a probability curve, while the IBM followed a proportion. When the age-structured sex change function from my model was compared to the function used in a previous version of the model (described in Heppell et al. 2006 and using data from 1998), there is a clear difference between the two curves (Fig. 5.5). In their version of the model, Heppell et al. (2006) fit the probability curve to observations of the proportions of males and females from study of gag in the Atlantic conducted in 1994 and 1995 (McGovern et al. 1998). This curve is contrasted to the probability curve fit to observations from gag in the GOM in 2004 (SEDAR 2006). The two curves have a similar intercept-value (representing the age at which fish first change sex), but the updated curve has a smaller slope parameter resulting in a lower probability that a fish of a given age will change sex. Similar changes were observed in the fitted proportions at length curves used in the IBM from 1997 and 2004 (see Fig. 4.1).

Both the probability curve used in the age-structured model and the proportions at length curve used in the IBM showed that changes in the rate of sex change are observable in the real population through time. More age and growth studies specifically designed to track such changes would help to better inform a density-dependent sex change function. Including such a function in the models caused different estimates of the sex ratio, which would in turn have an effect on the fertilization success of the fishery and ultimately population size and fishery yield. Because of this, including density-dependent sex change in population dynamics models used by the stock assessment could better inform measures of fishery production.

5.2. Management Recommendations

Management options that increased sex ratio also resulted in a larger adult population. However, these options did not always maximize yield. In the case of gag, maximizing long term yield necessitates the avoidance of sperm limitation, even at the cost of short term yield. Efforts to increase the population sex ratio are preventative in that they aim to maintain population structure to prevent future reproductive failure. For the gag population in the GOM, using marine reserves that protect spawning aggregations appears to be the best option to increase sex ratio. Should fishing mortality increase, either due to effort displaced by large reserves or from a general upward trend in fishing effort, larger marine reserves would be necessary to maintain the sex ratio.

Managing fisheries with spatial management actions like marine reserves is an uncertain exercise. There is little specific information regarding the response by fishers to large area closures, and describing the movement patterns of adult fish is also uncertain. Effective gag reserves should encompass entire spawning aggregations making it unlikely that associated spawners leave the reserve during spawning. In the models, I assumed that marine reserves were effective at protecting fish: reserves were correctly placed and sized as to result in realized

protection for male gag. Real world experience with marine reserves suggests that implementation does not necessarily result in assumed protection. For example, the existing gag spawning reserves in the GOM protect approximately 18% of known gag spawning sites (GMFMC 1999), but this is based on an estimate of the total spawning area. The amount of realized protection is likely to be less than 18%.

Results from both models suggest that reserves covering at least 18% of spawning area should be adequate to maintain sex ratio at 5% male under the current fishing patterns. Low confidence in the amount of actual protection currently afforded by reserves suggests that more spawning area may require protection. Table 5.1 shows the management options that improve upon the status quo in terms of the relative adult population and sex ratio. The yield response to increasing marine reserves was essentially flat up to a point after which it began to decline (see Fig. 2.7). For example, from the age-structured model the difference between yield with no reserves and the maximum yield with respect to reserve size at current fishing mortality was four metric tons (2625 metric tons with no reserves and 2629 metric tons at 20% reserves). Focusing on only adult population and sex ratio, the table shows that more than 18% reserves should maintain or even increase both the adult population, but also shows that the sex ratio was dependent on the pattern of fishing effort.

Specific recommendations for marine reserve use in the fishery depend on expected changes in fishing effort: if effort is assumed to be relatively stable, reserves that protect less than 50% of the spawning area are likely to be adequate. However, if effort is expected to increase over time, larger reserves would be needed if marine reserves were the sole focus of management. The simulations I tested did not account for changes in more traditional management options such as size and bag limits. The entire suite of management actions used by managers to control harvest in the fishery all influence the pattern of fishing mortality

experienced by the population, which was the main driver of sex ratio. All management options must be considered when making management recommendations, and the models I have presented offer two solutions to modeling potential responses to spatial management.

Table 5.1. Relative adult population size and sex ratio for increasing marine reserve size and fishing effort regimes shown for a) the IBM, and b) the age-structured model. Values greater than 1 represents improvement over the status quo and are shown in bold and simulations with both values greater than 1 are shown in bold and underlined.

a. IBM:

Fishing Effort	0	10	18	% Reserves 25	50	75	100
None	.88, .61	.95, .83	<u>1.0, 1.0</u>	<u>1.04, 1.13</u>	<u>1.20, 1.59</u>	<u>1.35, 1.93</u>	<u>1.51, 2.19</u>
Low	.81, .55	.88, .77	.93, .95	.97, 1.06	<u>1.12, 1.51</u>	<u>1.26, 1.84</u>	<u>1.41, 2.09</u>
Mid	.75, .50	.82, .71	.87, .89	.90, .99	<u>1.05, 1.44</u>	<u>1.18, 1.75</u>	<u>1.33, 2.0</u>
High	.59, .37	.67, .57	.70, .77	.73, .83	.86, 1.22	.98, 1.52	<u>1.10, 1.73</u>
Prop	.88, .61	.82, .71	.77, .83	.73, .83	.62, .94	.53, .91	.46, .80

b. Age-structured model:

	0	10	18	25	50	75	100
None	.97, .85	.99, .93	<u>1.0, 1.0</u>	<u>1.01, 1.07</u>	<u>1.07, 1.40</u>	<u>1.14, 1.92</u>	<u>1.25, 2.87</u>
Low	.92, .78	.93, .85	.95, .92	.96, .98	<u>1.01, 1.29</u>	<u>1.08, 1.80</u>	<u>1.18, 2.74</u>
Mid	.87, .71	.89, .78	.90, .84	.91, .91	.95, 1.19	<u>1.02, 1.69</u>	<u>1.12, 2.65</u>
High	.75, .54	.76, .60	.77, .65	.78, .70	.82, .95	.87, 1.39	.95, 2.29
Prop	.97, .85	.89, .78	.83, .73	.78, .70	.64, .65	.51, .71	.33, 1.16

5.3. Conclusion

Both models developed for my thesis modeled the population dynamics of gag grouper in the GOM and showed that marine reserves may be effective as a fishery management tool for increasing the male to female sex ratio in the population. Each model simulated the population differently, but for the most part the results agreed. The age-structured model was perhaps most effective at simulating the population response to changing fishing patterns. The benefit of using

the age-structured approach is in its similarity to assessment models and the ability to simulate large scale patterns based on changes in fishing effort and mortality rates. The IBM was most effective at describing population change in response to increasing or decreasing variability of the various population drivers, such as density-dependent sex change. The benefit of using the IBM approach is in the flexibility at changing parameters to model hypothetical changes to the population over time. Using both models helped to better understand the specific dynamics of the population. For specific applications of hypothetical patterns, I would first use the IBM approach to explore the specific population response. That information could then be used to better inform an age-structured approach that is designed to replicate the population. The method of utilizing multiple models was discussed in the 2006 stock assessment (SEDAR). While neither model as I have presented them is specifically appropriate for use in future stock assessments, perhaps some of the modeling of density-dependent sex change could one day be incorporated to improve stock assessments in the future.

REFERENCES

- Alonzo, S. H., and M. Mangel. 2004. The effects of size-selective fisheries on stock dynamics of and sperm limitation in sex-changing fish. *Fish. Bull.* 102: 1-13.
2005. Sex-change rules, stock dynamics, and the performance of spawning-per-recruit measures in protogynous stocks. *Fish. Bull.* 103: 229-245.
- Armstrong, P. R. 2001. The effects of fishing on a protogynous hermaphrodite. *Can. J. Fish. Aquat. Sci.* 58: 568-578.
- Bannerot, S., W. W. Fox, Jr., and J. E. Powers. 1987. Reproductive strategies and the management of snappers and groupers in the Gulf of Mexico and the Caribbean. *In Tropical snappers and groupers: biology and fisheries management* (J. J. Polovina, and S. Ralston, eds.), p. 561-603. Westview Press, Boulder, CO.
- Barrowman, N. J., and R. A. Meyers. 2000. Still more spawner-recruitment curves: the hockey stick and its generalizations. *Can. J. Fish. Aquat. Sci.* 57: 665-676.
- Beets, J. and A. Friedlander. 1994. Stock analysis and management strategies for red hind, *Epinephelus guttatus*, in the US Virgin Islands. *Proc. Gulf. Carib. Fish. Inst.* 42: 66-79.
- Bohnsack, J. A., and J. S. Ault. 1996. Management strategies to conserve marine biodiversity. *Oceanography.* 9(1): 73-82.
- Brooks, E. N., K. W. Shertzer, T. Gedamke, D. S. Vaughan. 2008. Stock assessment of protogynous fish: evaluating measures of spawning biomass used to estimate biological reference points. *Fish. Bull.* 106: 12-23.
- Buxton, C. D. 1992. The application of yield-per-recruit models to two South African sparid reef species, with special consideration to sex change. *Fish. Res.* 15: 1-16.
- Casey, J. P., G. R. Poulakis, and P. W. Stevens. 2007. Habitat use by juvenile gag, *Mycteroperca microlepis* (Pisces: Serranidae), in subtropical Charlotte Harbor, Florida (USA). *Gulf. Caribb. Res.* 19: 1-10.
- Claudet, J., C. W. Osenberg, L. Benedetti-Cecchi, P. Domenici, J. García-Charton, Á. Pérez-Ruzafa, F. Badalamenti, J. Bayle-Sempere, A. Brito, F. Bulleri, J. Culioli, M. Dimech, J. M. Falcón, I. Guala, M. Milazzo, J. Sánchez-Meca, P. J. Somerfield, B. Stobart, F. Vandeperre, C. Valle, and S. Planes. 2008. Marine reserves: size and age do matter. *Ecol. Lett.* 11: 481-489.
- Coleman, F. C., C. C. Koenig, and L. A. Collins. 1996. Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Env. Biol. Fish.* 47: 129-141.

- Coleman, F. C., P. B. Baker, and C. C. Koenig. 2004. A review of Gulf of Mexico marine protected areas: successes, failures, and lessons learned. *Fisheries*. 29(2): 10-21.
- Colin, P. L. 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental condition. *Env. Biol. Fish.* 34: 357-377.
- Collins, A. L., A. G. Johnson, C. C. Koenig, and M. S. Baker Jr. 1998. Reproductive patterns, sex ratio, and fecundity in gag, *Mycteroperca microlepis* (Serranidae), a protogynous grouper from the northeastern Gulf of Mexico. *Fish. Bull.* 96: 415-427.
- DeAngelis, D. L., and W. M. Mooij. 2005. Individual-Based Modeling of ecological and – evolutionary processes. *Ann. Rev. Ecol. Evol. Syst.* 36:147-168.
- Domeier, M. L. 2004. A potential larval recruitment pathway originating from a Florida marine protected area. *Fish. Ocean.* 13(5): 287-294.
- Domeier, M. L., and P. Colin. 1997. Tropical reef fish spawning aggregations: Defined and reviewed. *Bull. Mar. Sci.* 60(3): 698-726.
- Fitzhugh, G. R., C. C. Koenig, F. C. Coleman, C. B. Grimes, and W. Sturges III. 2005. Spatial and temporal patterns in fertilization and settlement of young gag (*Mycteroperca microlepis*) along the West Florida Shelf. *Bull. Mar. Sci.* 77(3): 377-396.
- Gerber, L. R., L. W. Botsford, A. Hastings, H. P. Possingham, S. D. Gaines, S. R. Palumbi, and S. Andelman. 2003. Population models for marine reserve design: a retrospective and prospective synthesis. *Ecol. App.* 13(1): S47-S64.
- Gerber, L. R., S. S. Heppell, F. Ballantyne, and E. Sala. 2005. The role of dispersal and demography in determining the efficacy of marine reserves. *Can. J. Fish. Aquat. Sci.* 62: 863-871.
- Ghiselin, M. T. 1969. The evolution of hermaphroditism among animals. *Quart. Rev. Biol.* 44: 189-208.
- Gilmore, R. G., and R. S. Jones. 1992. Color variation and associated behavior in the Epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* (Jordan and Swain). *Bull. Mar. Sci.* 51(1): 83-103.
- GMFMC. 1999. Regulatory amendment to the reef fish fishery management plan to set 1999 gag/black grouper management measures (revised). Gulf of Mexico Fishery Management Council, Tampa, Florida. 84 p.
- Gulf of Mexico Fishery Management Council (GMFMC). 2003. Amendment 21 to the reef fish management plan. Gulf of Mexico Fishery Management Council, Tampa, Florida. 220 p.

- Gulf of Mexico Fishery Management Council (GMFMC). 2008. Amendment 30B to the reef fish management plan. Gulf of Mexico Fishery Management Council, Tampa, Florida. 462 p.
- Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. *Ecol. Lett.* 5: 361-366.
- Heinsich, B. V., and W. A. Fable, Jr. 1999. Movement of gag, *Mycteroperca microlepis*, in and from St. Andrew Bay, Florida. *Bull. Mar. Sci.* 64(3): 501-508.
- Heppell, S. S. S. A. Heppell. F. C. Coleman. C. C. Koenig. 2006. Models to compare management options for a protogynous fish. *Ecol. Appl.* 16(1): 238-249.
- Hinckley et al. 1996. Development of a spatially explicit, individual-based model of marine fish early life history
- Hood, P. B., and R. A. Schlieder. 1992. Age, growth, and reproduction of gag, *Mycteroperca microlepis* (Pisces: Serranidae), in the eastern Gulf of Mexico. *Bull. Mar. Sci.* 51(3): 337-352.
- Hunstman, G. R., and W. E. Schaaf. 1994. Simulation of the impact of fishing on reproduction of a protogynous grouper, the graysby. *N. Amer. J. Fish. Man.* 14: 41-52.
- Keener, P, G. D. Johnson, B. W. Stender, E. B. Brothers, and H. R. Beatty. 1988. Ingress of postlarval gag, *Mycteroperca microlepis* (Pisces: Serranidae), through a South Carolina barrier island inlet. *Bull. Mar. Sci.* 42(3): 376-396.
- Kellner, J. B., I. Tetreault, S. D. Gaines, and R. M. Nisbet. 2007. Fishing the line near marine reserves in single and multispecies fisheries. *Ecol. App.* 17(4): 1039-1054.
- Kenchington, T. J. 1999. Management of the Gulf of Mexico Gag Grouper fishery: a reconsideration. Gadus Associates, Musquodoboit Harbour, Nova Scotia. 46 p. A report prepared for the Southeastern Fisheries Association, Inc.
- Koenig, C. C., F. C. Coleman. 1998. Absolute abundance and survival juvenile gag, *Mycteroperca microlepis*, in seagrass beds of the eastern Gulf of Mexico. *Trans. Am. Fish. Soc.* 127:44-55.
- Koenig, C. C., F. C. Coleman, C. B. Grimes, G. R. Fitzhugh, K. M. Scanlon, C. T. Gledhill, and M. Grace. 2000. Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf-edge reefs of Florida. *Bul. Mar. Sci.* 66(3): 593-616.
- Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile and adult fish: A comparison of natural ecosystem and aquaculture. *J. Fish. Biol.* 49: 627-647.

- McErlean, A. J. 1963. A study of the age and growth of the gag, *Mycteroperca microlepis* Goode and Bean (Pisces: Serranidae) on the west coast of Florida. Fla. Board Conserv. Mar. Lab. Tech. Ser. 41: 1-29.
- McGovern, J. C., D. M. Wyanski, O. Pashuk, C.S. Manooch II, and G.R. Sedberry. 1998. Changes in the sex ratio and size at maturity of gag, *Mycteroperca microlepis*, from the Atlantic coast of the southeastern United States during 1976 - 1995. Fishery Bulletin 96:797-807.
- McGovern, J. C., G. R. Sedberry, H. S. Meister, T. M. Westendorff, D. M. Wyanski, and P. J. Harris. 2005. A tag and recapture study of gag, *Mycteroperca microlepis*, off the southeastern U.S. Bull. Mar. Sci. 76(1): 47-59.
- Moe, M. A. 1966. Tagging fishes in Florida offshore waters. Fla. Bd. Conserv. Mar. Lab. Tech. Ser. 49: 1-40.
- Nowlis, J. S. 2006. Virtual Population Analysis of the Gulf of Mexico gag grouper (*Mycteroperca microlepis*) stock: the continuity case. National Oceanic and Atmospheric Administration, Southeast Fisheries Science Center. Sustainable Fisheries Division Contribution SFD-2006-022.
- Punt, A. E., P. A. Garratt, and A. Govender. 1993. On an approach for applying per-recruit methods to a protogynous hermaphrodite, with an illustration for the slinger *Chrysolephus puniceus* (Pisces: Sparidae). S. Afr. J. Mar. Sci. 13: 109-119.
- Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery. Numerical Recipes: The Art of Scientific Computing. New York: Cambridge University Press, 2007.
- Renan, X., T. Brule, and R. Lecomte-Finiger. 2006. First evidence of a nursery habitat for juvenile gag in the southern Gulf of Mexico. Trans. Am. Fish. Soc. 135: 595-603.
- Ross, R. M. 1990. The evolution of sex-change mechanisms in fishes. Env. Biol. Fish. 29: 81-93.
- Ross, S. W., and M. L. Moser. 1995. Life history of juvenile gag, *Mycteroperca microlepis*, in North Carolina estuaries. Bull. Mar. Sci. 56(1): 222-237.
- Russ, G. R., A. J. Cheal, A. M. Dolman, M. J. Emslie, R. D. Evans, I. Miller, H. Sweatman, and D. H. Williamson. 2008. Rapid increase in fish numbers follows creation of world's largest marine reserve network. Curr. Biol. 18(12): 514-515.
- Sadovy de Mitcheson, Y., and M. Liu. 2008. Functional hermaphroditism in teleosts. Fish and Fisheries. 9: 1-43.
- Scheffer, M., J. M. Baveco, D. L. DeAngelis, K. A. Rose, and E. H. van Nes. 1995. Super-individuals a simple solution for modeling large populations on an individual basis. Ecol. Model. 80: 161-170.

- Smith, M. D., J. Zhang, and F. C. Coleman. 2008. Econometric modeling of fisheries with complex life histories: avoiding biological management failures. *Journ. Env. Econ. Man.* 55: 265-280.
- Southeast Data, Assessment, and Review (SEDAR). 2006. SEDAR 10 Stock Assessment Report: Gulf of Mexico Gag Grouper.
- Southeast Data, Assessment, and Review (SEDAR). 2007. Analyses of Gulf of Mexico Gag Grouper in Response to Recommendations of the SEDAR Grouper Assessment Review Evaluation Panel, SEDAR Grouper Assessment Review Document: SEDARS1-RW01.
- Van Sant, S. B., M. R. Collins, and G. R. Sedberry. 1994. Preliminary evidence from a tagging study for a gag (*Mycteroperca microlepis*) spawning migration with notes on the use of oxytetracycline for chemical tagging. *Proc. Gulf Carib. Fish. Inst.* 43: 417-428
- Warner, R. R. 1975. The adaptive significance of sequential hermaphroditism in animals. *Amer. Natur.* 109: 61-82.

APPENDIX A: AGE-STRUCTURED MODEL CODE

! This model adapts the age-structured model described in Heppell et al (2006).

! Set up the matrices and limits:

module constants

```
INTEGER, PARAMETER:: maxage=30
INTEGER, PARAMETER:: maxyears=100
INTEGER, PARAMETER:: stagenum=4
INTEGER, PARAMETER:: maxreps=500
INTEGER:: idum,i,j,t,r
INTEGER:: iyear(maxyears)
INTEGER:: iage(maxage)
INTEGER:: stage(stagenum)
REAL:: xsum(maxyears,maxreps,4)
REAL:: f,m,rani
```

end module constants

! Known parameters:

module parameters

USE constants

```
REAL, PARAMETER:: linf=1310.           ! asymptote of vB growth equation (mm)
REAL, PARAMETER:: k=0.14              ! slope of vB growth equation
REAL, PARAMETER:: tzero=0.37          ! x-intercept of vB
INTEGER, PARAMETER:: theta=50         ! fertilization parameter
REAL, PARAMETER:: fmax=1.0           ! maximum fertilization rate
REAL, PARAMETER:: bigk=1.0e7         ! recruitment maximum
REAL, PARAMETER:: survyoy=0.3        ! larval survivorship
REAL, PARAMETER:: survegg=3.3e-6     ! egg mortality
REAL, PARAMETER:: rmat=8.41          ! slope of maturation probability
REAL, PARAMETER:: qmat=2.946         ! intercept of maturation probability
REAL, PARAMETER:: rtrans=0.0597     ! slope of transition probability
REAL, PARAMETER:: qtrans=5.745      ! intercept of transition probability
REAL, PARAMETER:: a=1e-8            ! multiplier of L-W function
REAL, PARAMETER:: b=2.99            ! exponent of L-W function
REAL, PARAMETER:: c=0.00338         ! density transition (a)
REAL, PARAMETER:: d=3.13            ! density transition (b)
REAL, PARAMETER:: qprime=5.0        ! density transition (q')
```

end module parameters

! Variables solved by model

module var

USE constants

```
REAL:: N(maxyears,stagenum,maxage+1) ! number of fish in population by year, sex,
! age
INTEGER:: bystage(stagenum)
INTEGER:: byage(maxage)
REAL:: abund(maxage,stagenum)
```

```

REAL::ansurv(stagenum)
REAL::fishmort(stagenum)
REAL::probmat(maxage)
REAL::probsex(maxage)
REAL::newmats(maxage)
REAL::newfems(maxage)
REAL::newmales(maxage)
REAL::males(maxage)
REAL::females(maxage)
REAL::imms(maxage)
REAL::juvs(maxage)
REAL::totmales,totfems,yieldbio,totyield!,totjuvs,totage
REAL::totpop
REAL::avgpop(maxyears,maxreps)
REAL::pmales,toteggs,trident
REAL::recruits
REAL::eggs(maxage)
REAL::length(maxage)
REAL::weight(maxage)
REAL::yield(maxage)
INTEGER::InputStatus,OpenStatus
INTEGER::fswitch,bigf
INTEGER::sswitch,scen
INTEGER::fertswitch,mparun,dens,dist
REAL::mpa,mpamult,redist,sel
end module var

program age
  USE constants
  USE parameters
  USE var
  implicit none

  open(UNIT=8,FILE='yield_up.csv',STATUS='unknown')
  open(UNIT=9,FILE='avgpop_up.csv',STATUS='unknown')
  open(UNIT=10,FILE='avgsex_up.csv',STATUS='unknown')
  open(UNIT=11,FILE='recruits.csv',STATUS='unknown')
  open(UNIT=12,FILE='summary.csv',STATUS='unknown')
  open(UNIT=13,FILE='agetot.csv',STATUS='unknown')

  print *, 'Enter: 1=change F (Heppell) 2=change MPAs'
  read (*,1000)fertswitch
  print *, 'Density? 1=no 2=yes'
  read (*,1000)dens
  if(fertswitch.eq.1) then
    print *, 'Enter 0=No fishing, 1=Fishing'
    read (*,1000)fswitch
    if(fswitch.eq.0)bigf=1

```

```

        if(fswitch.eq.1)bigf=2
        end if
if(fswitch.gt.0) then
    print *, 'Enter F regime: 1=SQ 2=SC 3=SR 4=SRD 5=NC 6=CutF'
    read (*,1000)sswitch
        if(sswitch.eq.1)scen=1
        if(sswitch.eq.2)scen=2
        if(sswitch.eq.3)scen=3
        if(sswitch.eq.4)scen=4
        if(sswitch.eq.5)scen=5
        if(sswitch.eq.6)scen=6
end if

if(fertswitch.eq.2) then
    print *, 'Enter redist secenario: 1=alter F; 2=redist; 3=Edges:'
    read (*,1000)dist
        if(dist.eq.1)mparun=1
        if(dist.eq.2)mparun=2
        if(dist.eq.3)mparun=3
end if
print *, 'Enter F-value:'
read (*,10)sel
if(mparun.lt.3)then
    print *, 'Enter % reserves (0.0 - 1.0):'
    read (*,10)mpamult
        if(mpamult.lt.1)mpa=(1-mpamult)
        if(mpamult.eq.0)mpa=1
        if(mpamult.eq.1)mpa=0
end if
redist=(1+mpamult)

print *, 'MPA=',mpa
print *, 'redist',redist
print *, 'F-mult',sel

```

10 FORMAT(F4.3)

1000 FORMAT(i3)

```

do r=1,maxreps                ! Loop over replications
    call init                  ! set up initial population
        pmales=0.0345
do t=1,maxyears-1            ! Loop over years
    totyield=0.0;yieldbio=0.0
do i=1,maxage                ! Loop over ages
    yield(i)=0
do j=1,stagenum              ! Loop over stages
    call mortality            ! Call mortality function
end do

```

```

call sexchange          ! Call sex change operation subroutine
call sumstat           ! Call pre-breeding census
    length(i)=linf*(1-EXP(-k*((i)+tzero)))
    weight(i)=(a*((length(i)**b))
    totyield=totyield+yield(i)
    yieldbio=yieldbio+(yield(i)*weight(i))
end do
call spawning          ! Call spawning, get # of eggs, # fertilized
call sr                ! Call the stock-recruit function

write(8,*)t,yieldbio
call output
call ageing
write(9,*)t,totpop
write(10,*)t,pmales
write(11,*)t,recruits
write(12,*)t,totpop,pmales,yieldbio
write(13,*)t,totage
end do
end do
end program

```

!*****

```

subroutine init          ! Set up the initial distribution
    USE constants
    USE parameters
    USE var
    implicit none

```

```

N(1,1,1)=2344190;N(1,2,1)=0;N(1,3,1)=0;N(1,4,1)=0
N(1,1,2)=0;N(1,2,2)=1747014;N(1,3,2)=140846;N(1,4,2)=0
N(1,1,3)=0;N(1,2,3)=622977;N(1,3,3)=955763;N(1,4,3)=0
N(1,1,4)=0;N(1,2,4)=43604;N(1,3,4)=1273026;N(1,4,4)=0
N(1,1,5)=0;N(1,2,5)=2160;N(1,3,5)=1200070;N(1,4,5)=0
N(1,1,6)=0;N(1,2,6)=0;N(1,3,6)=271566;N(1,4,6)=4166
N(1,1,7)=0;N(1,2,7)=0;N(1,3,7)=269744;N(1,4,7)=20987
N(1,1,8)=0;N(1,2,8)=0;N(1,3,8)=307074;N(1,4,8)=44251
N(1,1,9)=0;N(1,2,9)=0;N(1,3,9)=67911;N(1,4,9)=14566
N(1,1,10)=0;N(1,2,10)=0;N(1,3,10)=59599;N(1,4,10)=17236
N(1,1,11)=0;N(1,2,11)=0;N(1,3,11)=72061;N(1,4,11)=26555
N(1,1,12)=0;N(1,2,12)=0;N(1,3,12)=30091;N(1,4,12)=13622
N(1,1,13)=0;N(1,2,13)=0;N(1,3,13)=17008;N(1,4,13)=9220
N(1,1,14)=0;N(1,2,14)=0;N(1,3,14)=9614;N(1,4,14)=6123
N(1,1,15)=0;N(1,2,15)=0;N(1,3,15)=5434;N(1,4,15)=4008
N(1,1,16)=0;N(1,2,16)=0;N(1,3,16)=3071;N(1,4,16)=2594
N(1,1,17)=0;N(1,2,17)=0;N(1,3,17)=1736;N(1,4,17)=1663
N(1,1,18)=0;N(1,2,18)=0;N(1,3,18)=981;N(1,4,18)=1058
N(1,1,19)=0;N(1,2,19)=0;N(1,3,19)=554;N(1,4,19)=669

```

```

N(1,1,20)=0;N(1,2,20)=0;N(1,3,20)=313;N(1,4,20)=420
N(1,1,21)=0;N(1,2,21)=0;N(1,3,21)=177;N(1,4,21)=263
N(1,1,22)=0;N(1,2,22)=0;N(1,3,22)=100;N(1,4,22)=164
N(1,1,23)=0;N(1,2,23)=0;N(1,3,23)=57;N(1,4,23)=102
N(1,1,24)=0;N(1,2,24)=0;N(1,3,24)=32;N(1,4,24)=63
N(1,1,25)=0;N(1,2,25)=0;N(1,3,25)=18;N(1,4,25)=39
N(1,1,26)=0;N(1,2,26)=0;N(1,3,26)=10;N(1,4,26)=24
N(1,1,27)=0;N(1,2,27)=0;N(1,3,27)=6;N(1,4,27)=15
N(1,1,28)=0;N(1,2,28)=0;N(1,3,28)=3;N(1,4,28)=9
N(1,1,29)=0;N(1,2,29)=0;N(1,3,29)=2;N(1,4,29)=6
N(1,1,30)=0;N(1,2,30)=0;N(1,3,30)=1;N(1,4,30)=3

```

```

idum=-814                ! random number seed
  if (r.gt.1) then
    idum=idum+r
  end if
end subroutine

```

```

end subroutine
!*****

```

```

subroutine mortality
  USE constants
  USE parameters
  USE var
  implicit none

  if (bigf.eq.2.AND.scen.eq.1) then
    if (j.eq.1) then
      m=0.4;f=0.0
    else if (j.eq.2) then
      m=0.25;f=0.4
    else if (j.eq.3) then
      m=0.15;f=0.4
    else if (j.eq.4) then
      m=0.125;f=0.3
    end if
  else if (bigf.eq.2.AND.scen.eq.2) then
    if (j.eq.1) then
      m=0.4;f=0.0
    else if (j.eq.2) then
      m=0.25;f=0.3
    else if (j.eq.3) then
      m=0.15;f=0.3
    else if (j.eq.4) then
      m=0.125;f=0.225
    end if
  else if (bigf.eq.2.AND.scen.eq.3) then
    if (j.eq.1) then
      m=0.4;f=0.0
    end if
  end if

```

```

    else if (j.eq.2) then
        m=0.25;f=0.4
    else if (j.eq.3) then
        m=0.15;f=0.3
    else if (j.eq.4) then
        m=0.125;f=0.0
end if
else if (bigf.eq.2.AND.scen.eq.4) then
    if (j.eq.1) then
        m=0.4;f=0.0
    else if (j.eq.2) then
        m=0.25;f=0.4
    else if (j.eq.3) then
        m=0.15;f=0.375
    else if (j.eq.4) then
        m=0.125;f=0.0
end if
else if (bigf.eq.2.AND.scen.eq.5) then
    if (j.eq.1) then
        m=0.4;f=0.0
    else if (j.eq.2) then
        m=0.25;f=0.0
    else if (j.eq.3) then
        m=0.15;f=0.1
    else if (j.eq.4) then
        m=0.125;f=0.3
end if
else if (bigf.eq.2.AND.scen.eq.6) then
    if (j.eq.1) then
        m=0.4;f=0.0
    else if (j.eq.2) then
        m=0.25;f=0.2
    else if (j.eq.3) then
        m=0.15;f=0.2
    else if (j.eq.4) then
        m=0.125;f=0.15
end if
else if (bigf.eq.1) then
    if (j.eq.1) then
        m=0.4;f=0.0
    else if (j.eq.2) then
        m=0.25;f=0.0
    else if (j.eq.3) then
        m=0.15;f=0.0
    else if (j.eq.4) then
        m=0.125;f=0.0
end if
end if

```

```

if (mparun.eq.1) then
  if (j.eq.1) then
    m=0.4;f=0.0
  else if (j.eq.2) then
    m=0.25;f=(0.267*sel)
  else if (j.eq.3) then
    m=0.15;f=(0.348*sel*(0.25*mpa+0.75))
  else if (j.eq.4) then
    m=0.125;f=(0.299*sel*mpa)
  end if
else if (mparun.eq.2) then ! redistribute
  if (j.eq.1) then
    m=0.4;f=0.0
  else if (j.eq.2) then
    m=0.25;f=(0.267*redist)
  else if (j.eq.3) then
    m=0.15;f=(0.348*(0.25*mpa+0.75)*redist)
  else if (j.eq.4) then
    m=0.125;f=(0.299*mpa*redist)
  end if

  annsurv(j) = EXP(-m-f)
  fishmort(j)=1-EXP(-f)
  yield(i)=yield(i)+f*((N(t,j,i)*(1-annsurv(j))/(m+f)))

  N(t,j,i)=annsurv(j)*N(t,j,i)
end subroutine
!*****

subroutine sexchange
  USE constants
  USE parameters
  USE var
  implicit none

  newmats(i)=0.0;newfems(i)=0.0;newmales(i)=0.0

  probmat(i)=1.0/(1.0+(EXP(rmat-(qmat*(i))))))
  if (probmat(i).gt.0.9) then
    probmat(i)=1.0
  end if

  if (dens.eq.1) then
    probsex(i)=(1-EXP(-rtrans*((i)-qtrans)))
  end if
  if (dens.eq.2) then
    probsex(i)=(1-EXP(-((c/pm ales)*((i)-(qprime+d*pm ales**0.5))))))

```

```

end if
  if (probsex(i).lt.0.0) then
    probsex(i)=0.0
  end if

newmats(i)=probmat(i)*N(t,1,i)
  if ((i).gt.1) then
    newmats(i)=0.0
  end if
newfems(i)=probmat(i)*N(t,2,i)
  if ((i).gt.5) then
    newfems(i)=0.0
  end if
newmales(i)=probsex(i)*N(t,3,i)
  if ((i).lt.6) then
    newmales(i)=0.0
  end if
end subroutine
!*****

subroutine sumstat
  USE constants
  USE parameters
  USE var
  implicit none

  N(t,4,i)=N(t,4,i)+newmales(i)
  N(t,3,i)=N(t,3,i)+newfems(i)-newmales(i)
  N(t,2,i)=N(t,2,i)-newfems(i)
  N(t,1,i)=N(t,1,i)-newmats(i)
  if (N(t,1,i).lt.0.0) then
    N(t,1,i)=0.0
  end if
  if (N(t,2,i).lt.0.0) then
    N(t,2,i)=0.0
  end if
  if (N(t,3,i).lt.0.0) then
    N(t,3,i)=0.0
  end if
end subroutine
!*****

subroutine spawning
  USE constants
  USE parameters
  USE var
  implicit none

```

```

totmales=0.0;totfems=0.0;toteggs=0.0;totpop=0.0!;totjuvs=0;totage=0

do i=1,maxage
  totmales=totmales+N(t,4,i)
  totfems=totfems+N(t,3,i)

  eggs(i)=(2e6*(i))-4e6
  if(eggs(i).lt.0.0)then
    eggs(i)=0.0
  end if
  toteggs=toteggs+eggs(i)*N(t,3,i)

end do

  totpop=totmales+totfems
end subroutine
!*****

subroutine sr
  USE constants
  USE parameters
  USE var
  implicit none
  REAL::logdev,rc

  pmales=totmales/(totmales+totfems)
  trident=fmax*(1-EXP(-theta*pmales))
  recruits=toteggs*trident*survegg*survyoy*logdev(idum)
  rc=toteggs*trident*survegg
  if (rc.gt.bigk) then
    recruits=bigk*survyoy*logdev(idum)
  end if
end subroutine
!*****

subroutine ageing
  USE constants
  USE parameters
  USE var
  implicit none

  N(t+1,1,1)=recruits
  N(t+1,2,1)=0
  N(t+1,3,1)=0
  N(t+1,4,1)=0

  do i=1,maxage
    N(t+1,4,i+1)=N(t,4,i)

```

```

        N(t+1,3,i+1)=N(t,3,i)
        N(t+1,2,i+1)=N(t,2,i)+N(t,1,i)
    end do
end subroutine
!*****
!*****

! Code from Press et al. (2007); generates a uniform 0 to 1 random number

REAL(4) FUNCTION RAN1(IDUM)
INTEGER idum
DIMENSION R(97)
INTEGER, SAVE:: IX1, IX2, IX3  !KPE added declaration and SAVE
INTEGER:: J
PARAMETER (M1=259200,IA1=7141,IC1=54773,RM1=3.8580247E-6)
PARAMETER (M2=134456,IA2=8121,IC2=28411,RM2=7.4373773E-6)
PARAMETER (M3=243000,IA3=4561,IC3=51349)
DATA IFF /0/
SAVE R

IF (IDUM.LT.0.OR.IFF.EQ.0) THEN
    IFF=1
    IX1=MOD(IC1-IDUM,M1)
    IX1=MOD(IA1*IX1+IC1,M1)
    IX2=MOD(IX1,M2)
    IX1=MOD(IA1*IX1+IC1,M1)
    IX3=MOD(IX1,M3)
    DO 11 J=1,97
        IX1=MOD(IA1*IX1+IC1,M1)
        IX2=MOD(IA2*IX2+IC2,M2)
        R(J)=(FLOAT(IX1)+FLOAT(IX2)*RM2)*RM1
11 CONTINUE
    IDUM=1
ENDIF

IX1=MOD(IA1*IX1+IC1,M1)
IX2=MOD(IA2*IX2+IC2,M2)
IX3=MOD(IA3*IX3+IC3,M3)
J=1+(97*IX3)/M3
IF(J.GT.97.OR.J.LT.1)THEN
    print *, 'problem in ran1, J=',J
    ! PAUSE
ENDIF

RAN1=R(J)
R(J)=(FLOAT(IX1)+FLOAT(IX2)*RM2)*RM1
RETURN
END

```

```
!*****
```

```
! Normal distribution generator
```

```
FUNCTION gasdev(idum)
  REAL::gasdev
  INTEGER::iset
  REAL::fac,gset,rsq,v1,v2,r1,r2
  save iset,gset
  data iset/0/

  if(idum.lt.0) iset=0
  if(iset.eq.0) then
1      v1=2.*ran1(idum)-1.
      v2=2.*ran1(idum)-1.
      rsq=v1**2+v2**2
      if(rsq.ge.1..or.rsq.eq.0) goto 1
      fac=sqrt(-2.*log(rsq)/rsq)
      gset=v1*fac
      gasdev=v2*fac
      iset=1
  else
      gasdev=gset
      iset=0
  endif
  return
end
```

```
!*****
```

```
! Lognormal distribution generator
```

```
FUNCTION logdev(idum)
  REAL::logdev

  logdev=(EXP(0.46*gasdev(idum)))
  return
end
```

```
!*****
```

APPENDIX B: INDIVIDUAL BASED MODEL CODE

! This model adapts the individual based model described in Alonzo and Mangel (2004).

! Set up global matrices and limits

module constants

```
INTEGER, PARAMETER:: numage=50
INTEGER, PARAMETER:: numsites=100
INTEGER, PARAMETER:: maxage=30
INTEGER, PARAMETER:: maxyears=100
INTEGER, PARAMETER:: maxreps=20
INTEGER, PARAMETER:: totfish=numage*maxage
INTEGER:: idum
INTEGER:: iyear
INTEGER:: ifish
INTEGER:: idavail
INTEGER:: idfree(totfish)
INTEGER:: rep
```

end module constants

!*****

module parameters

```
REAL(8):: alpha=9185.0           ! spawner-recruit function
REAL(8):: beta=0.0006072         ! spawner-recruit function
REAL(8):: r=1.0                  ! steepness of selectivity curve
REAL(8):: f                      ! fishing mortality multiplier
REAL(8):: k=0.14                 ! growth coefficient
REAL(8):: linf=1310.             ! von Bertalanffy growth function linf
REAL(8):: tzero=0.37            ! vB growth function x-intercept
REAL(8):: a=1.669               ! constant in egg production
REAL(8):: b=1024.               ! constant in egg production
REAL(8):: c=2500.               ! multiplier in egg production
REAL(8):: q=0.0241              ! maturity shape parameter
REAL(8):: lm=592.               ! length at 50% maturity
REAL(8):: rho=0.0206            ! sex change shape parameter
REAL(8):: lc=1072.              ! length at 50% sex change
REAL(8):: fa=-0.01109           ! fishing selectivity constant
REAL(8):: fb=0.1366             ! fishing selectivity multiplier
REAL(8):: fc=-0.02481           ! fishing selectivity power
REAL(8):: nata=0.4298           ! multiplier in natural mortality
REAL(8):: natb=-0.488           ! power in natural mortality
REAL(8):: kappa=1.              ! fertilization maximum
REAL(8):: chi=50.               ! fertilization parameter
REAL(8):: nmax=1500.            ! maximum recruitment
REAL(8):: ya=1e-8
```

end module parameters

!*****

```

module var
  USE constants
  REAL(8):: xlength(totfish)
  REAL(8):: xworth(totfish)
  INTEGER:: xsex(totfish)
  INTEGER:: xsite(totfish)
  REAL(8):: xeggs(totfish)
  INTEGER:: xmatur(totfish)
  INTEGER:: xage(totfish)
  REAL(8):: popsize=1500
  REAL(8):: numberage(maxage)
  REAL(8):: lenage(maxage)
  REAL(8):: mlenage(maxage)
  REAL(8):: females(maxage)
  REAL(8):: males(maxage)
  REAL(8):: imms(maxage)
  REAL(8):: eggs(numsites)
  !REAL(8):: sperm(numsites)
  REAL(8):: totfeggs,toteggs
  REAL(8):: spermratio
  REAL(8):: ferteggs(numsites)
  REAL(8):: pf(numsites)
  REAL(8):: recruits
  REAL(8):: totmales,pmale
  REAL(8):: totfemales
  REAL(8):: totimms
  REAL(8):: yield
  REAL(8):: yieldbio
  INTEGER:: numntmr
  INTEGER:: idntmr(numsites)
  INTEGER:: swntmr
  INTEGER:: swf
  INTEGER:: swfish,dens
  REAL(8):: xfish
  REAL(8):: totpop,totalfish,totadults!,probsex
  REAL(8):: nummales(numsites)
  REAL(8):: numfemales(numsites)
  REAL(8):: ratio(numsites)
end module var
!*****

```

```

program ibmupdate
  USE constants
  USE parameters
  USE var
  implicit none
  INTEGER:: i

```

```

open(UNIT=8,FILE='totpop.csv',STATUS='unknown')
open(UNIT=9,FILE='ratio.csv',STATUS='unknown')
open(UNIT=10,FILE='fert.csv',STATUS='unknown')
open(UNIT=11,FILE='sexratio.csv',STATUS='unknown')
open(UNIT=12,FILE='sumstats.csv',STATUS='unknown')

idntmr=0; numntmr=0; xfish=1.0

PRINT *, 'Enter: 0=No MPA 1=MPA'
READ(*,1000)swntmr

IF(swntmr.eq.1)then
  PRINT *, 'Enter percentage MPA (0-100):'
  READ(*,1000)numntmr
  do i=1,numsites
    IF((i).le.numntmr)then
      idntmr(i)=1
    endif
  end do
  PRINT *, 'Effort: 0=fixed 1=redistribute'
  READ(*,1000)swfish
  IF(swfish.eq.0)xfish=1.0
  IF(swfish.eq.1)xfish=(float(numsites)+float(numntmr))/(float(numsites))

endif

PRINT *, 'Enter F value:'
READ (*,1001)f

PRINT *, 'Density: 1=no 2=yes'
READ (*,1000)dens

1000 FORMAT(i3)
1001 FORMAT(F4.3)

call init
do iyear=1,maxyears
eggs=0.0
idavail=0; idfree=0
yield=0.0; yieldbio=0.0
  call sexratio
  call mortality
  call spawning
end do
call annualout
call recruitment
call ageing
call newind

```

```

        end do
end program
!*****

subroutine init
    USE constants
    USE parameters
    USE var
    implicit none
    INTEGER i,ix,ii,j
    REAL(8) ran1,initlen(maxage)

    do j=1,maxage
        initlen(j) = linf*(1.0-EXP(-k*(j+tzero)))
    end do

    idum=-1212

    do j=1,maxage
        do i=1,numage
            ii=(j-1)*numage + i
            xlength(ii)=initlen(j)
            xworth(ii)=popsize/totfish
            xsex(ii)=1
            xage(ii)=j
            ix=INT(ran1(idum)*numsites) + 1
            xsite(ii)=ix
            xeggs(ii)=0.0
            xmatur(ii) = 0
        end do
    end do
end subroutine
!*****

subroutine growth
    USE constants
    USE parameters
    USE var
    implicit none
    REAL(8) deltal
    deltal= -linf*EXP(-k*xage(ifish))*(EXP(-k)-1)
    xlength(ifish) = xlength(ifish) + deltal  ! update new length
end subroutine
!*****

subroutine mortality
    USE constants
    USE parameters

```

```

USE var
implicit none
REAL(8) selec, annsurv, natmort, sel
INTEGER j

do ifish=1,totfish ! loop over individual fish
  if(xage(ifish).eq.1)then
    sel=0.0
  else if(xage(ifish).gt.1.AND.(xage(ifish)).lt.10) then
    sel=fa*(xage(ifish)**2.0)+fb*(xage(ifish))+fc ! selectivity function
  else if(xage(ifish).ge.10)then
    sel=0.3
  end if

  if(idntmr(xsite(ifish)).eq.0.AND.(xsex(ifish)).eq.1)selec=sel
  if(idntmr(xsite(ifish)).eq.1.AND.(xsex(ifish)).eq.1)selec=0.75*sel
  if(idntmr(xsite(ifish)).eq.0.AND.(xsex(ifish)).eq.2)selec=sel
  if(idntmr(xsite(ifish)).eq.1.AND.(xsex(ifish)).eq.2)selec=0.0

  natmort=nata*(xage(ifish)**natb
  annsurv = EXP(-natmort - f*selec*xfish)

  yield = yield + (f*selec)/(f*selec+natmort)*(1.0-annsurv)*xworth(ifish)
  yieldbio = yieldbio + (f*selec)/(f*selec+natmort)*(1.0 &
  & -annsurv)*xworth(ifish)*(ya*xlength(ifish)**2.99)
  xworth(ifish)=xworth(ifish)*annsurv
end do
end subroutine
!*****

subroutine sexratio
  USE constants
  USE parameters
  USE var
  implicit none

  nummales=0.0;numfemales=0.0;ratio=0.0

  do ifish=1,totfish
    if(xmatur(ifish).eq.1.AND.(xsex(ifish)).eq.1) then
      numfemales(xsite(ifish))=numfemales(xsite(ifish))+xworth(ifish)
    end if
    if(xsex(ifish).eq.2) then
      nummales(xsite(ifish))=nummales(xsite(ifish))+xworth(ifish)
    end if

    ratio(xsite(ifish))=(nummales(xsite(ifish)))/((nummales(xsite(ifish)))+&
    &(numfemales(xsite(ifish))))
  end do

```

```

        if(ratio(xsite(ifish)).lt.0.01) then
            ratio(xsite(ifish))=0.01
        end if
        if(ratio(xsite(ifish)).gt.0.25) then
            ratio(xsite(ifish))=0.25
        end if
    end do
end subroutine
!*****

subroutine spawning
    USE constants
    USE parameters
    USE var
    implicit none
    REAL(8) t1,t2,t3,probmatur,probsex,ran1

    do ifish=1,totfish ! loop over individual fish
        t1=EXP(-q*(xlength(ifish)-lm))
        probmatur = 1.0/(1.0+t1)
        if(xmatur(ifish).eq.0.and.ran1(idum).le.probmatur)then
            xmatur(ifish)=1 ! mature
        endif

        if(xmatur(ifish).eq.1. and. xsex(ifish).eq.1)then
            if(dens.eq.1) then
                t2=EXP((-rho)*(xlength(ifish)-lc))
                probsex = 1.0/(1.0+t2)
            end if

            if(dens.eq.2) then
                t3=EXP((-0.0847*(ratio(xsite(ifish))**0.5))*(xlength(ifish)-lc))
                probsex = 1.0/(1.0+t3)
            end if
            if(ran1(idum).le.probsex)then
                xsex(ifish)=2 ! male
            endif
        endif

        if(xmatur(ifish).eq.1.and.xsex(ifish).eq.1)then
            xeggs(ifish)=(a*xlength(ifish)-b)*c
            if(xeggs(ifish).lt.0.0)xeggs(ifish)=0.0
        endif

        eggs(xsite(ifish)) = eggs(xsite(ifish)) + xeggs(ifish)*xworth(ifish)
    end do
end subroutine
!*****

```

```

subroutine annualout
  USE constants
  USE parameters
  USE var
  implicit none
  INTEGER i,j
  REAL(8) fracmales(maxage),fracfemales(maxage)

  numberage=0.0; lenage=0.0; mlenage=0.0; totpop=0.0; females=0.0; males=0.0
  fracfemales=0.0; fracmales=0.0; totalfish=0.0
  totfemales=0.0; totmales=0.0; pmale=0.0; totimms=0.0; imms=0.0; totadults=0.0

  do i=1,totfish
    numberage(xage(i))=numberage(xage(i))+xworth(i)
    lenage(xage(i))=lenage(xage(i))+xlength(i)*xworth(i)
    totpop=totpop + xworth(i)

    if(xmatur(i).eq.1.and.xsex(i).eq.2)then
      males(xage(i)) = males(xage(i)) + xworth(i)
      totmales=totmales + xworth(i)
    end if

    if(xmatur(i).eq.1.and.xsex(i).eq.1)then
      females(xage(i)) = females(xage(i)) + xworth(i)
      totfemales=totfemales + xworth(i)
    end if

    if(xmatur(i).eq.0) then
      imms(xage(i)) = imms(xage(i)) + xworth(i)
      totimms=totimms + xworth(i)
    end if
  end do

  totalfish = totalfish + totmales + totfemales + totimms
  totadults=totaladults + totmales+totfemales
  pmale = pmale + (totmales/(totmales+totfemales))

  do j=1,maxage
    if(numberage(j).gt.0.0)then
      mlenage(j)=lenage(j)/numberage(j)
    else
      mlenage(j)=0.0
    end if
    if(males(j).gt.0.0)then
      fracmales(j)=males(j)/(males(j)+females(j))
    else
      fracmales(j)=0.0

```

```

        end if
        if(females(j).gt.0.0)then
            fracfemales(j)=females(j)/(females(j)+males(j))
        else
            fracfemales(j)=0.0
        end if

    end do
end subroutine
!*****

subroutine recruitment
    USE constants
    USE parameters
    USE var
    implicit none
    REAL(8) nzero,naught
    INTEGER j

    totfeggs=0.0;toteeggs=0.0

    do j=1,numsites
        pf(j)=kappa*(1-EXP(-chi*ratio(j)))
        if(pf(j).gt.1.0)pf(j)=1.0
        ferteggs(j) = eggs(j)*pf(j)
        totfeggs = totfeggs + ferteggs(j)
        toteeggs = toteeggs + eggs(j)
    end do

    nzero = ((totfeggs)/(alpha + beta*totfeggs))
!    if(naught.le.nmax)then
        recruits = nzero
WRITE(8,*)iyear,totadults,totpop,totimms,totfemales,totmales,recruits,(j,numberage(j),j=1,maxage)
WRITE(9,*)iyear,totmales,totfemales,pmale,(nummales(j),j=1,numsites),(numfemales(j),j=1,numsites),(ratio(j),j=1,numsites)
WRITE(10,*)iyear,toteeggs,pmale,(pf(j),j=1,numsites),totfeggs,recruits
WRITE(11,*)iyear,totadults,pmale,(pf(j),j=1,numsites)
WRITE(12,*)iyear,totadults,pmale,totalfish,totpop,recruits,yieldbio

end subroutine
!*****

subroutine ageing
    USE constants
    USE parameters
    USE var
    implicit none

```

```

INTEGER i, icount
real(8) deltal

do i=1,totfish
    deltal= -lnf*EXP(-k*xage(i))*(EXP(-k)-1)
    xlength(i) = xlength(i) + deltal

    xage(i)=xage(i) + 1
    if (xage(i).gt.maxage)then
        idavail=idavail+1
        idfree(idavail)=i
    end if
end do
end subroutine
!*****

subroutine newind
    USE constants
    USE parameters
    USE var
    implicit none
    REAL(8) ran1

    icount=idavail
    do i=1,numage
        if(icount.le.0)then
            PRINT *,'error - tried to add more new fish than spaces available'
            pause
        endif
        ii=idfree(icount)
        xlength(ii)=228.6
        xworth(ii)=recruits/float(numage)
        xsex(ii)=1
        xage(ii)=1
        ix=INT(ran1(idum)*numsites) + 1
        xsite(ii)=ix
        xeggs(ii)=0.0
        xmatur(ii) = 0
    end do
    count=icount-1
end do

end subroutine
!*****
! Code from Press et al. (2007); generates a uniform 0 to 1 random number

REAL(8) FUNCTION RAN1(IDUM)
INTEGER idum
DIMENSION R(97)

```

```

INTEGER, SAVE:: IX1, IX2, IX3  !KPE added declaration and SAVE
INTEGER:: J
PARAMETER (M1=259200,IA1=7141,IC1=54773,RM1=3.8580247E-6)
PARAMETER (M2=134456,IA2=8121,IC2=28411,RM2=7.4373773E-6)
PARAMETER (M3=243000,IA3=4561,IC3=51349)
DATA IFF /0/
SAVE R

```

```

IF (IDUM.LT.0.OR.IFF.EQ.0) THEN
  IFF=1
  IX1=MOD(IC1-IDUM,M1)
  IX1=MOD(IA1*IX1+IC1,M1)
  IX2=MOD(IX1,M2)
  IX1=MOD(IA1*IX1+IC1,M1)
  IX3=MOD(IX1,M3)
  DO 11 J=1,97
    IX1=MOD(IA1*IX1+IC1,M1)
    IX2=MOD(IA2*IX2+IC2,M2)
    R(J)=(FLOAT(IX1)+FLOAT(IX2)*RM2)*RM1
  11 CONTINUE
  IDUM=1
ENDIF

```

```

IX1=MOD(IA1*IX1+IC1,M1)
IX2=MOD(IA2*IX2+IC2,M2)
IX3=MOD(IA3*IX3+IC3,M3)
J=1+(97*IX3)/M3
IF(J.GT.97.OR.J.LT.1)THEN
  PRINT *, 'problem in ran1, J=',J
ENDIF

```

```

RAN1=R(J)
R(J)=(FLOAT(IX1)+FLOAT(IX2)*RM2)*RM1
RETURN
END

```

!*****

! Normal distribution generator

```

FUNCTION gasdev(idum)
  real::gasdev
  integer::iset
  real::fac,gset,rsq,v1,v2,r1,r2
  save iset,gset
  data iset/0/

  if(idum.lt.0) iset=0
  if(iset.eq.0) then

```

```

1      v1=2.*ran1(idum)-1.
      v2=2.*ran1(idum)-1.
      rsq=v1**2+v2**2
if(rsq.ge.1..or.rsq.eq.0) goto 1
      fac=sqrt(-2.*log(rsq)/rsq)
      gset=v1*fac
      gasdev=v2*fac
      iset=1
      else
      gasdev=gset
      iset=0
      endif
      return
end
!*****

! Lognormal distribution generator
FUNCTION logdev(idum)
  real::logdev
  logdev=(EXP(0.46*gasdev(idum)))
  return
end

```

VITA

Robert Dodge Ellis was born in Honolulu, Hawaii, in April 1981. He was raised in Long Beach, California, and graduated from Long Beach Polytechnic High School's PACE magnet program in June 1999. He attended the University of California Santa Barbara from 1999 to 2003, spending his final year as an Education Abroad Program participant at the University of Western Australia in Perth, Australia. In March 2004 he received the degree of Bachelor of Science in aquatic biology. After three years working in various capacities in education, he entered the Louisiana State University in August 2007. Following his anticipated graduation with the degree of Master of Science in oceanography in August 2009 he will attend the Florida State University as a candidate for the Doctor of Philosophy Degree in biology.