

UNDERSTANDING SEX CHANGE IN EXPLOITED FISH POPULATIONS: A REVIEW OF EAST
COAST FISH STOCKS AND ASSESSMENT OF SELECTIVITY AND SEX CHANGE IN BLACK SEA
BASS (*CENTROPRISTIS STRIATA*) IN NEW JERSEY

by

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ABSTRACT OF THE THESIS

Understanding sex change in exploited fish populations: A review of East Coast fish stocks and assessment of selectivity and sex change in black sea bass (*Centropristis striata*) in New Jersey

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Hermaphroditic species present unique challenges to fishery managers because the effects of fishing on hermaphroditic population dynamics are not entirely understood. In protogynous hermaphrodites (female to male sex change) the sex ratio varies with size as females change to males. It is expected that male fish have disproportionately high fishing mortality in size regulated fisheries for two reasons. First, males are predicted to be more vulnerable to fishing because they are larger than females and, second, male fish often exhibit aggressive behavior. The implications of prolonged fishing pressure on the population dynamics of protogynous hermaphrodites varies across species. More information about species' patterns of sex change is needed in order to understand the effects of fishing. This study is divided into two separate chapters: (1) review how sex change is currently handled in stock assessments along the eastern coast of the U.S. in order to identify key data gaps, and to compare hermaphroditic and gonochoristic stock status. (2) Using a tagging study, measure sex selectivity and sex change as a function of size, age, and season in black sea bass (*Centropristis striata*), an economically important protogynous hermaphrodite in New Jersey and along the East Coast.

A review of eleven hermaphroditic stock assessments revealed that sex change is handled in a variety of ways. Despite that no stock assessments assessed sex-specific

mortality; hermaphroditic stock status was not any worse off than gonochoristic stock status. In black sea bass, the vulnerability of capturing males and females varied by size and between commercial and recreational fishing gears. For commercial traps, males of intermediate size range (280–360 mm) were most likely to be captured, probability ranged 0.07–0.12. For recreational hook-and-line, male vulnerability increased with size: the largest males (440–500 mm) had the highest chance of being captured, probability ranged 0.30–0.60. Across most sizes (129–483 mm), commercial traps captured a significantly higher proportion of males at length compared to hook-and-line fishing gear. Size at 50% sex change was 365 mm and all sex changing females were 3–4 years old. Females that changed sex ranged from 290–370 mm to 342–480 mm. Complete sex change events happened over the winter between the summer spawning seasons in 2011 and 2012, it was expected that slightly less than half (47%) of female black sea bass in 2011 changed sex by the following year in 2012.

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TABLE OF CONTENTS

ABSTRACT OF THE THESIS.....	ii
ACKNOWLEDGEMENTS	iv
TABLE OF CONTENTS	v
LIST OF TABLES	vii
LIST OF FIGURES	viii
Chapter 1: General Introduction	1
Chapter 2: Assessment and management of sex changing fishes	
Abstract	4
2.1 Introduction	4
2.2 Ecological aspects of sex changing fishes	8
2.2.1 Taxonomic patterns of sex change.....	8
2.2.2 Advantages of sex change: protogyny vs. protandry	10
2.2.3 Ecological and evolutionary aspects of sex change and life history in black sea bass	12
2.3 Management and stock assessment of sex changing fishes	14
2.3.1 Reproductive behavior and vulnerability	15
2.3.2 Sexual dimorphism and vulnerability	17
2.4 Population dynamics and stock assessment	17
2.4.1 Hypothesis #1: Increasingly skewed sex ratios	18
2.4.2 Hypothesis #2: Shift in age (or size) at sex change	19
2.4.3 Effects of skewed sex ratios and shifts in age at sex change on fertilization rates	20
2.4.4 Sex change in stock assessments	22

Chapter 3: Sex, size, and age selectivity in wild black sea bass and the influence of size, age, and season on sex change

Abstract	31
3.1 Introduction	32
3.1.1 Selectivity	33
3.1.2 Sex change	35
3.1.3 Life history of black sea bass and stock status	36
3.1.4 Objectives	38
3.2 Methods	
3.2.1 Sampling location	39
3.2.2 Field sampling	40
3.2.3 Tagging protocol	41
3.2.4 Data analysis	42
3.3 Results	43
3.4 Discussion	
3.4.1 Limitations to study	46
3.4.2 Evidence of sex selectivity	46
3.4.3 Sex change as a function of size, age, and season	50
Chapter 4: General Conclusions	69
Literature cited	71

LIST OF TABLES

– Chapter 2 –

Table 2.1. Examples of exploitation changing the sex ratio of sex-changing fish

Table 2.2. Examples of exploitation changing the age or length at sex change

Table 2.3. Treatment of sex change in stock assessments

– Chapter 3 –

Table 3.1. A summary of black sea bass tagging data in southern New Jersey in 2011 and 2012

Table 3.2. Summary of black sea bass recapture rates caught by two different gear types

Table 3.3. Summary of male and female recapture rates in traps and by hook-and-line

Table 3.4. Summary of black sea bass that changed sex in 2011 and 2012

LIST OF FIGURES

– Chapter 2 –

Figure 2.1. Size at sex change as a function of reproductive value

Figure 2.2. Overfished and overfishing status of hermaphroditic and gonochoristic stocks

– Chapter 3 –

Figure 3.1. Contrasting the difference between asymptotic- and dome-shaped selectivity curves

Figure 3.2. Size distribution and frequency of black sea bass caught by traps and hook-and-line gear

Figure 3.3. The proportion of wild black sea bass males at length caught in commercial traps and by recreational hook-and-line gears

Figure 3.4. The proportion of wild black sea bass males at age caught in commercial traps and by recreational hook-and-line gear

Figure 3.5. Size distribution and frequency of male and female black sea bass caught in commercial traps

Figure 3.6. Size distribution and frequency of male and female black sea bass caught by hook and line gear

Figure 3.7. The probability of recapturing wild black sea bass by size, sex, and fishing gear

Figure 3.8. Probability of female black sea bass changing sex from 2011 to 2012

Figure 3.9. Probability of sex change at length in wild black sea bass

– Chapter 1 –

GENERAL INTRODUCTION

Sex change has been studied in evolutionary and ecological contexts throughout its record in the published literature. Sex change allows hermaphrodite species to maximize their reproductive value through time, in different habitats, and over the course of changing body size. Sex reversal is a process that occurs broadly in faunal groups ranging from Arthropods to Echinoderms (Allsop and West 2004), and is particularly common in teleost fishes (Sadovy de Mitcheson and Liu 2008). The process of changing sex reflects a similarly broad spectrum of diversity (Munday et al. 2006); hermaphroditic species can follow protogyny (female to male sex change, e.g. Benton and Berlinsky 2006) or protandry (male to female sex change, e.g. Moyer and Nakazono 1978) while others may take advantage of both strategies (Kuwamura et al. 2007). Consequently, the environmental and social triggers and controls of changing sex are complex, and for many hermaphroditic species, unknown.

The complexity of sex change ecology has led to interesting challenges for fisheries managers. In stock assessments population growth is typically estimated by tracking temporal changes in female biomass (spawning stock biomass) (Hilborn and Walters 1992). When individuals undergo sex reversal they impact population sex ratio and, without accounting for this in population dynamics models, the abundance of males and females may be over- or under-estimated (Alonzo et al. 2008). Additionally, fisheries exploitation has implications on rates of sex change (Buxton 1993) and leads to changes the sex ratio (McGovern et al. 1998) and size at sex change (Hamilton et al. 2007). The effects of fishing on hermaphroditic fish species are not entirely understood which presents managers with unique challenges for management.

The assessment of protogynous hermaphrodites varies by species and management region. In stock assessments along the East Coast of the U.S., sex change is handled in a variety of ways: some assessments report sex-at-age data and changes in the proportion male over time (e.g. red grouper, *Epinephelus morio*, South Atlantic Fishery Management Council) while others report very little sex-at-age data (e.g. gag, *Mycteroperca microlepis*, Gulf of Mexico Fishery Management Council). None of the East Coast stock assessments for protogynous hermaphrodites assess sex-specific mortality rates. This information is essential to have in order to measure the effects of fishing on population dynamics and make predictions about future abundance levels under current fishing conditions.

One protogynous hermaphrodite in the Mid-Atlantic, black sea bass (*Centropristis striata*) is facing similar questions about managing the effects of exploitation. The Mid-Atlantic stock covers U.S. waters in the western Atlantic Ocean from Cape Hatteras, North Carolina northward to the U.S. – Canadian border. Black sea bass spawn on reefs and artificial wrecks inshore May – October. In autumn when ocean water temperatures decline, black sea bass migrate offshore to areas along the continental shelf (Shepherd and Terceiro 1994). Two management entities work cooperatively to develop fishery regulations: the Atlantic States Marine Fisheries Commission and the Mid-Atlantic Fishery Management Council, these organizations work with the National Marine Fisheries Service to ensure Federal regulations are met. The black sea bass stock was under a stock rebuilding strategy and was declared rebuilt in 2009 (Shepherd and Nieland 2010). Shortly after, the Northeast Data Poor Stocks Working Group deemed the black sea bass stock as “data poor” because of the data gaps surrounding their life history as protogynous hermaphrodites.

There are clear data gaps in our knowledge of assessing protogynous hermaphrodite stocks and knowing the implications of fishing on hermaphroditic population dynamics. In Chapter 2 of this thesis, I report how sex change is currently

handled in assessments of protogynous hermaphrodites on the East Coast of the U.S. ranging from the Gulf of Mexico to the Gulf of Maine. In Chapter 3, I present analysis using data collected from a tagging experiment on black sea bass off the south-central coast of New Jersey to measure sex selectivity for two different gear types and examine sex change as a function of size, age, and season.

– Chapter 2 –

MANAGEMENT AND ASSESSMENT OF SEX CHANGING FISHES

Abstract

Sex changing species present unique challenges for stock assessment and management. In most stock assessments, fishery managers are quick to acknowledge the potential problems inherent with managing hermaphroditic fish, and yet sex change is addressed in a variety of ways in stocks along the East Coast. The majority of stock assessments do not monitor the effects of fishing on life history characteristics and population dynamics which is primarily a function of data availability. An updated review of sex change and a summary of how stock assessment reports handle sex change showed that many assessments report sex ratio at age and the age at sex change, but no stock assessments assessed sex-specific mortality rates and few have tracked overall changes in the percentage of male or female fish and the timing of sex change over time. Although hermaphroditic stock status does not drastically differ from that of gonochoristic species, sex change will need to be further incorporated into population models as exploitation rates increase.

2.1 Introduction

The phenomenon of sex change is found in a wide variety of animal species. Sex change has been the subject of numerous studies addressing its implications for fitness (Ghiselin 1969, Smith 1975, Warner 1975), but the implication of sex change in fisheries management is much less well known. For exploited species, harvest impacts the demographic structure of fish populations and such changes in hermaphroditic species alters the rate of individuals changing sex, and potentially impacts the population sex ratio. Fluctuating sex ratios and shifting rates of sex change pose unique problems for fishery

managers because there may be large and lasting impacts on population growth rate, fertilization rates, and recruitment (Alonzo and Mangel 2004). Ignoring this unique life history strategy in stock assessments is to falsely assume that the response of sex-changing fish to fishing pressure is equivalent to that of gonochoristic (non-sex changing) species. Previous studies show that for many sex-changing fish species, prolonged fishing pressure can have lasting consequences on the population that are unseen in gonochoristic species. Since sex change is a critical component of population dynamics in hermaphroditic fishes, it is especially important for fishery managers to know the ecological context of sex change in managed species.

Sex change has been described in both ecological and evolutionary terms across a wide diversity of taxonomical groups (Policansky 1982). Early reviews of hermaphroditic fishes laid the theoretical groundwork for sex change and, based on ecological factors (i.e. distribution of resources, connectivity between sub-populations, and mating structure), outlined hypotheses predicting the timing of sex change (Ghiselin 1969, Warner 1975, Warner et al. 1975). The size-advantage hypothesis, first coined by Ghiselin (1969), became the most widely accepted hypothesis and states that an individual is expected to change sex when its probability of reproduction would be higher as the opposite sex. The timing of sex change has been predicted by estimating and comparing male and female reproductive output at age (Warner 1975, Warner et al. 1975). In protogynous populations (species that change sex from female to male), female reproductive output is relatively high at younger ages compared to males and is characterized by a large proportion of females at small sizes. When male reproductive output exceeds that of female reproductive output, sex change is expected to occur. More recent studies suggest that sex change is more flexible than originally thought, individuals have been found to utilize a diverse array of sex changing

strategies, i.e. some individuals change sex early, others late, and some species change more than once within the same population (Munday et al. 2006).

Evolutionary reviews of sex change have been repeatedly updated and carried out at broad and fine phylogenetic scales. Early on, reviews primarily focused on documenting where sex change occurs in plant and animal groups (Policansky 1982 and Smith 1975). Not until the 1990's was the evolution of sex change linked to social structure in subpopulations, i.e. how group size and the rigidity of dominant hierarchies resulted in either protogynous or protandrous (male to female sex change) strategies (Ross 1990). With the advancement of molecular tools in DNA sequencing, molecular-based phylogenies have been constructed in fishes to infer the history of evolutionary transitions between hermaphroditism and gonochorism (species in which individuals do not change sex) (Mank et al. 2006, Erisman and Hastings 2011). In fishes, and especially within the Serranidae, the evolutionary path of sex change shows that hermaphrodite and gonochoristic strategies shift frequently, appearing and disappearing in lineages with hermaphroditic ancestors (Erisman and Hastings 2011). While sex change has been considered in depth from an ecological perspective through detailed investigations in social structure and distribution of individuals, as well as in an evolutionary context by tracking sex change within narrow and broad lineages, very little work has been done to investigate the implicates of sex change for fisheries stock assessment and management.

Here, I review the most recent studies of the ecological aspects of sex change and, more importantly, the implications of sex change for stock assessment and management. For some sex-changing species, specific actions have been adopted to compensate for the effects of fishing on sex changing populations; I review these actions and describe how sex change is currently handled in stock assessments. I also highlight specific ways in which sex change might be handled in stock assessments and provide suggestions for future sex

change studies that will help illuminate ways to improve the management of sex-changing fish. I hypothesize that heavy exploitation will result in either:

- (a) Strongly skewed sex ratios in favor of females in protogynous species (sex ratios in protandrous populations are expected to shift in favor of males), or
- (b) A downward shift in the age or size at which sex change occurs.

In the first hypothesis I expect that sex ratios will become increasingly skewed because fishing mortality is disproportionately higher on one sex than the other. Since sex ratio changes with size, size selective fisheries indirectly target the 'second' sex more so than the 'first' sex. In the second hypothesis I predict that the removal of large fish, specifically males in protogynous species (change is female to male) and females in protandrous species (change is male to female), will result in individuals changing sex at earlier ages and smaller sizes. Although the triggers of sex change have not been entirely disentangled, there is evidence that points to social factors as important variables of the sex change process (Warner and Swearer 1991, Cole and Shapiro 1995, Benton and Berlinsky 2006).

In this literature review I compile and organize published studies and assessments into three categories. I review recent developments in the ecological aspects of sex-changing fish (2.2 *Ecological aspects of sex changing fishes*). In this section I discuss sex change across taxonomical groups, advantages of protogyny and protandry, and the ecological and evolutionary aspects of sex change in black sea bass (*Centropristis striata*). Next I outline the current management and stock assessment of sex-changing fishes (2.3 *Management and stock assessment of sex changing fishes*). Here we describe the reproductive behavior and sexual dimorphism as it relates to fishing vulnerability. And last, we cover the population dynamics and stock assessment of sex-changing fish (2.4 *Population dynamics and stock assessment*). It is in this last section we compile the evidence for the two aforementioned hypotheses and discuss the effects of fishing on population

dynamics. For the sake of brevity, we restricted our review of sex-changing fish in stock assessments to those species managed on the eastern coast of the United States of America from the Gulf of Maine to the Gulf of Mexico.

2.2 Ecological aspects of sex changing fishes

2.2.1 Taxonomic patterns of sex change

The evolutionary history of sex change in extinct and extant species is diverse, disjunct, and non-linear. Sex change appears in a wide spectrum of taxonomical lineages ranging from worms with simple reproductive organs to fishes with relatively complex reproductive systems (Polikansky 1982, Charnov 1982, Allsop and West 2003). In total, sex change is documented in over 120 species from five phyla. In Arthropods five families exhibit sex-change with most sex changing species concentrated in Decapoda. Echinoderms include four species; Mollusks include 10 species; and Annelid worms, three species (Allsop and West 2004). Hermaphroditic species appear to be rare in elasmobranchs, but sex change has been documented in some deep-sea species (Iglesias et al. 2005). In teleost fish, however, sex change is broadly distributed across a diverse range of lineages and is particularly common.

In teleosts sex change is not only common, but is diverse in strategy, having been confirmed in 48 families from thirteen orders, (Sadovy de Mitcheson and Liu 2008). In an effort to explain the prevalence of sex change among teleosts, Warner et al. (1975) and Mank et al. (2006) hypothesized that the cost of sex change in species with internal fertilization (e.g. mammals, birds), and in species whose females are viviparous or bear large eggs may be enormous compared to species that fertilize externally. In most fishes, fertilization is external and the energy required to undergo sex change may be relatively low compared to other phyla. In addition to its prevalence, sex change has taken on several

different forms including protogyny (female-to-male), protandry (male-to-female), simultaneous hermaphroditism (individual possess both male and female organs), and bi-directional sex change (individual can change sex multiple times) (Sadovy de Mitcheson and Liu 2008). Among all sex changing animals, protandry primarily occurs in invertebrates and protogyny in vertebrates (Allsop and West 2004). There are, however, exceptions to this especially among fishes: a number of species in Sparidae (porgies) and Pomacentridae (damselfishes) are protandrous. In some species of Gobiidae (gobies), Cirrhitidae (hawkfishes), and Labridae (wrasses) individuals are capable of switching back and forth between sexes (bi-directional sex change). Protandry has been documented in Clupeidae (*Tenualosa macrura*, a tropical shad) (Allosp and West 2004, Blaber et al. 1999). Thus, sex change a trait that is traced across many families of fishes; it is common and takes on many different forms.

Hermaphroditism among extant teleosts is buried within clades characterized by gonochronism. No single lineage of hermaphroditism has been found to be evolutionary ancient; i.e. sex-changing fishes are polyphyletic (Erisman and Hasting 2011). For this reason, the presence of sex-change has been predicted on the basis of ecological context rather than evolutionary history (Ghiselin 1969). For example, reef dwelling parrot fishes (Scaridae) and deep-water fishes of the order Iniomi typically have a patchy distribution and at times, low local population density making it difficult to find suitable mates (Ghiselin 1969, Smith 1975). These ecological selection pressures favor species that are able to change sex because they are able to ensure the production of future zygotes. There are, however, ecological patterns that are expected to favor hermaphroditic life history traits in some species, but sex change does not appear. Aulopiformes (*Choloropthalmus* and *Bathypterois*) and Stomiiformes (*Cyclothone* and *Gonostoma*) are deep-water hermaphroditic species, but within these same orders there are other deep-water relatives

that inhabit a similar ecological niche and are not hermaphroditic. Similar diversity in reproductive strategy is found in the Cypriniformes where some genera are hermaphroditic and others are gonochoristic (Mank et al. 2006). Although ecological patterns may explain the appearance of sex change in most species, there is still much to learn about why some species are hermaphroditic and others not.

2.2.2 Advantages of sex change: protogyny vs. protandry

The advantage of protogyny (female to male) or protandry (male to female) depends on the reproductive value of males and females at young and old ages. According to the size-advantage hypothesis first put forth by Ghiselin (1969), hermaphroditic fish undergo sex change in order to maximize their reproductive output over time. With changing length, the rate of increase in reproductive value is sex-specific. In the case of protogyny, females at small sizes have higher reproductive value than males of similar length, but at large sizes males have greater reproductive value than females (Ghiselin 1969). The timing of sex reversal, according to Warner (1975), Warner et al. (1975), and Leigh et al. (1976) is most favored when one sex gains relatively more reproductive ability with size or age. This idea was expanded by Charnov (1982), Policansky (1982), and Iwasa (1991) to include the sex-differential advantage in mortality and growth with size or age in order to construct sex-specific reproductive value curves (Figure 2.1). The curves, which model reproductive value over the lifespan of a fish and include sex-specific mortality and growth rates, cross at a certain age or size in sex-changing species due to sex-specific characteristics (growth, mortality, etc.). The intersection of male and female reproductive value curves is the age or length at which sex change is expected to occur.

One ecological aspect of protogyny versus protandry is the number of mating partners per individual fish. Polygamy, where one fish mates with multiple partners, is expected to occur primarily in protogynous species where one dominate male will control

mating opportunities of multiple females (see Warner 1975 for theoretical explanation). In species where multiple mates are not simultaneously available (e.g. individuals tend to be isolated and do not form aggregations) then protandry is more common (Ross 1990). This is because the members of a monogamous pair produce more zygotes. In protandrous species females tend to be larger and large females produce more eggs. Alternatively, in protogynous species with polygamous mating strategies more zygotes are produced if the largest individual in the spawning group is a male (Ross 1990). Anemonefishes (*Amphiprion pomacentrids*) and the Spanish hogfish (*Bodianus rufus*) are good examples to contrast the differences between protogyny and protandry with respect to the number of mating partners. Anemonefishes, which are obligate commensals of sea anemones on Indo-Pacific coral reefs, are protandrous (Fautin 1991). One pair of anemonefish will occupy an individual sea anemone; cross-over from other anemones is rare and highly dependent on the proximity of neighboring colonized sea anemones. The Spanish hogfish is protogynous and individuals form spawning aggregations on coral reefs in the Caribbean island archipelagos (Hoffman 1985). Large, dominant male Spanish hogfish will control the mating opportunities of smaller females. At larger sizes females will undergo sex change in order to maximize their reproductive output if dominant males leave the population (Hoffman 1985). Ross (1990) provides a thorough list of other sex-changing fish species and their sex reversal patterns.

The controls and triggers of sex change can be categorized into two broad classes: endogenous and exogenous. Endogenous triggers are age- or size- mediated and are said to be 'fixed'. At a genetically predetermined point in a fish's life history the individual will undergo sex change regardless of ambient conditions or the presence of other members in the population. The timing of fixed sex change is likely the product of evolutionary fine-tuning and is inelastic in response to environmental conditions or population dynamic

pressures (Allsop and West 2003, for example, see McGovern et al. 1998). Exogenous sex-change is triggered by stimuli from other individuals or environmental conditions and can be either suppressed (Benton or Berlinsky 2006) or induced (Kuwamura et al. 2002) by the presence of dominant individuals. Most laboratory sex change experiments or field-based observations strongly suggest exogenous triggers are at play in hermaphroditic species, and these studies point to controls that involve social factors such as sex or size ratios, aggressive behavior, or possibly fish coloration (Ross et al. 1983, for example, see Benton and Berlinsky 2006). Alternatively, in a review by Munday et al. (2006) the timing of sex change in some species appeared to be fixed despite significant changes in life history parameters (growth, mortality). The authors suggested that changes in age or size at sex change may not occur until the sex ratio exceeds a particular threshold, which might explain the potential disparity between predicted and observed patterns of the timing of sex change. We do not know enough about the intersection of external and internal controls for sex change in most hermaphrodite species to predict the timing of sex change across a spectrum of environmental conditions.

2.2.3 Ecological & evolutionary aspects of sex change and life history in black sea bass

From an evolutionary perspective, black sea bass (*Centropristis striata*) have retained their ancestral mating strategy as protogynous hermaphrodites. Within the Serranidae family, protogyny was the earliest mating strategy from which other sexual mating patterns evolved. In addition to *C. striata*, and the other species in *Centropristis* (*C. philadelphica* and *C. ocyurus*), species in the genera *Anthiinae* and *Cheilidoperca* retained protogynous hermaphroditism. Simultaneous hermaphroditism evolved once (*Serranus* clade) in the Serranidae lineage and gonochorism evolved once within the genus *Paralabrax* (Erisman and Hastings 2011).

Black sea bass are found in estuaries and continental shelf waters of the Northwest Atlantic from the Gulf of Maine to the Gulf of Mexico (Shepherd and Terceiro 1994). They are managed as two stocks separated at Cape Hatteras, North Carolina (Bowen and Avise 1990). Although the northern stock is considered to be uniformly one stock, there are geographic differences in meristics and some variation in morphology (Shepherd 1991). Every spring, black sea bass north of Cape Hatteras migrate inshore from the continental shelf edge toward their spawning grounds on wrecks and reefs (depths of 50-110 meters) (Lavenda 1949, Frame and Pearce 1973, Musick and Mercer 1977). The spawning season lasts roughly from May through November at which point the larger individuals lead the migration back to the continental shelf. It is believed small black sea bass embark on their migration after the larger individuals have left (Musick and Mercer 1977).

The hatch success of black sea bass larvae occurs when water temperature is between 15 and 27 C and salinity is no greater than 15 parts per thousand (Berlinsky et al. 2004). Until black sea bass larvae reach 10-16 millimeters, they will remain buoyant and pelagic and then move into estuaries and settle on the benthos for protection. For their first summer and fall (July through October) black sea bass young-of-the-year will remain in the estuary before moving off toward the continental shelf in the winter when water temperature begin to drop (Able et al. 1995). Some proportion of juvenile black sea bass have remained as residents in the estuary for more than the initial two seasons, however the significance of this proportion is unknown and is likely small (Able and Hales 1997).

Sex reversal in black sea bass has been studied through laboratory experiments and field observations. Benton and Berlinsky (2006) verified sex change in black sea bass by holding fish in tanks and found strong evidence that sex reversal is triggered by the absence of large, dominate male black sea bass. Wenner et al. 1986, Cochran and Grier 1991, Hood et al. 1994 looked at sex change in black sea bass *in situ* identify sex-changing individuals

based on tissues in their gonads. In all three studies, black sea bass were captured and gonads were examined for signs of sex change; i.e. “proliferation of male tissue into neighboring female lamellae” (Cochran and Grier 1991). Through this method, black sea bass were in transition at 2-4 years old (Hood et al. 1994) and most individuals transitioned between early fall and December (Cochran and Grier 1991) in the Gulf of Mexico. Although these studies examined sex change in wild populations, they were unable to determine when sex change occurs and its prevalence. Field studies, which track individual black sea bass throughout the spawning season, will document the timing and prevalence of sex change in wild populations.

2.3 Management and stock assessment of sex changing fishes

Sex changing fish species present unique challenges to fisheries managers. In stock assessments of gonochoristic fishes (non-sex changing species) sex ratio is often not assessed and spawning stock biomass is a calculation of mature female biomass. This is a reasonable simplification if the fishery impacts both sexes equally or if male abundance does not limit fertilization or reproductive output. In sex changing species, however, there is reason to suspect that fishing mortality does not impact males and females equally. Size selectivity, either inherent to the fishing gear or a result of management actions such as size limits, translates into sex-based differences in fishing mortality rate for fish species where the sex ratio changes with size. Change in sex ratio with size is a common feature of hermaphroditic fish species and also occurs in gonochoristic species with sexually dimorphic growth (e.g., summer flounder, Morse 1981 and Morson et al. 2012). Though gear selectivity on size and age is either known or measured in stock assessments, gear selectivity on sex is relatively unknown. If fishing differentially selects males and females, and ultimately results in higher mortality rates on the ‘second’ sex in hermaphroditic

species, the sex ratio is expected to shift in favor of the first sex. Shifting sex ratios in a sex changing species has serious consequences on population growth, fertilization, and stability over time (Alonzo et al. 2008).

2.3.1 Reproductive behavior and vulnerability

Although the exact mechanism is unknown, there is evidence that heavily exploited hermaphroditic species that form spawning aggregations tend to have increasingly skewed sex ratios (Sadovy 1994, Carter et al. 1994, Coleman et al. 1996). Aggregating species are more susceptible to overfishing since fishermen are better able to target high-density pockets of fish (Olsen and LaPlace 1979). Gag (*Mycteroperca microlepis*) and scamp (*Mycteroperca phenax*), which are both protogynous hermaphrodites and form large aggregations, suffered a drop in the proportion male from 17% to 1% and from 36% to 18%, respectively, over a span of 25 years (Coleman et al. 1996). Red grouper (*Epinephelus morio*), a non-aggregating protogynous hermaphrodite however, showed little change in sex ratio over the same time period and under similar fishing conditions. Many reasons may explain why aggregating species experience increasingly skewed sex ratios. Sex-specific behavior of individuals in the aggregation may affect probability of capture, or aggregations may be sex-specific and males and females separate spatially. Knowing more about hermaphroditic life history will help explain the mechanism behind this phenomenon.

Aggressive behavior, a common feature of reproductively active fishes, may increase catchability and explain differences in sex selectivity between males and females. In many protogynous species, male fish exert aggressive behavior while defending territories (Warner et al. 1975, Hoffman 1985) or guarding female mates (Frickle and Frickle 1977, Moyer and Nakazono 1978). Observations from Gilmore and Jones (1992) found that male scamp (*Mycteroperca phenax*) had greater overall movement, displayed more aggressive behavior (lunging, attacking), and (anecdotally) had a higher propensity to bite hooks

compared to females of a similar length. Gilmore and Jones (1992) hypothesized that male scamp were more likely to have higher fishing mortality because of their aggressive behavior observed through underwater videos. Aggressive behavior, however, may not be universal to all sex changing species. In red porgy, a protogynous hermaphrodite also located in the Gulf of Mexico and South Atlantic, there was no appreciable difference in the selectivity of males and females since the order of red porgy caught was random with respect to sex and size (DeVires 2007). Consensus on aggressive behavior and gear selectivity has not been reached and could be remedied by future studies that measure sex selectivity and observe behavior in the wild.

Spawning harems and the process of choosing a mate are inherent aspects of reproductive behavior in sex changing species and may increase species' vulnerability to fishing. Harems, defined as a group of females for which mating opportunities are controlled by one dominant male, have been observed in many sex changing species (McCormick et al. 2010, Nemtzov 1985, Moyer and Nakazono 1978) and are expected to be found in other hermaphroditic species whose reproductive behavior is less well understood. Through fishing, selective removal of aggressive, dominant males in harems may change group dynamics during reproduction. Some studies suggest that removing dominant males will trigger sex reversal in the largest females (Platten et al. 2002, Hawkins and Roberts 2004, Benton and Berlinsky 2006, Nemtzov 1985). If there is sustained, frequent removal of males, however, the outcome is unclear. In red hind (*Epinephelus guttatus*), for example, small groups consisting of a single male with many females are formed during a two week spawning period (Sadovy et al. 1994). If dominant males were lost to the fishery during the short reproductive season, a turn-over period may be required for females to reverse their sex and harems or spawning groups to be re-established. Fishing may have unintended consequences on the ability of sex changing fish to mate and

produce fertilized zygotes, a more thorough understanding of reproductive behavior will help reveal the effects of selectively removing males from a population.

2.3.2 Sexual dimorphism and vulnerability

Fish that undergo sex change experience an increase in growth rate which increases their vulnerability in a size-selective fishery. As individuals transition from female to male, fish experience a burst of somatic growth to ensure their dominance amidst competing males or females of similar size who could fulfill the male role as well. For protogynous species, growth rates in recently transitioned males are greater than their female counterparts, e.g. parrotfishes (Munday et al. 2004) and tropical wrasse (McCormick et al. 2010). Species with faster growth rates are known to be more susceptible to fishing capture (Sinclair et al. 2002). Individuals with faster growth rates, and presumably more aggressive behavior in sex changing fish, also require a greater intake of energy. Other species with similar high energy requirements are more likely to bite baited hooks and, as a consequence, are more vulnerable to this kind of fishing pressure (Sutter et al. 2012).

2.4 Population dynamics and stock assessment

The effect of fishing on population dynamics of hermaphroditic species is rarely random. Observing and predicting the effects fishing has on sex changing species is an important component of stock assessments. In some stocks, changes in population structure have been noticed only after decades of data collection and assessment (Coleman et al. 1996), while others revealed the influence of fishing on hermaphroditic species through comparisons of fished and unfished populations (Götz et al. 2008). In a smaller subset of studies, changes in hermaphroditic life history that result from fishing have been shown through historical and spatial comparisons (Hamilton et al. 2007). The effect of fishing on hermaphroditic population dynamics is traced back to a species' reproductive behavior and

the sex change as a life history characteristic. Predicting the change in population structure due to fishing has been difficult because the triggers and controls of sex change and sex selectivity of the fishery are not well understood. Based on the size-advantage hypothesis (Ghiselin 1969) and observations in the field and laboratory, fishing can have two different hypothesized effects on population structure of sex changing species.

2.4.1 Hypothesis #1: Increasingly skewed sex ratios

Sex selective fishing increasingly skews sex ratios in hermaphroditic species.

Protogynous species have characteristically large proportions of female fish in small size classes, and large proportions of male fish in large size classes. Size selective fishing indirectly removes large proportions of male fish. Fishing gear (e.g. pots, seine nets, trawls, etc.) varies with mesh size and targets the largest individuals in the population. Selective removal of large fish would, indirectly, result in disproportionately high fishing mortality in males in protogynous species; increasingly skewing the sex ratio toward females. In protandrous species, where small size classes primarily comprise of males and large fish tend to be female, the effect of fishing is expected to be opposite: sex ratios will be increasingly skewed toward males with females experiencing higher fishing mortality. A collection of field studies (Table 2.1) have found clear evidence that increasingly skewed sex ratios is associated with higher levels of fishing pressure in hermaphroditic species.

Fishing effecting sex ratios has been observed in historical and spatial comparisons. In a study by Coleman et al. (1996), sex ratio was tracked in two commercially important protogynous grouper species over 25 years of heavy fishing pressure. Gag (*Mycteroperca microlepis*), and scamp (*Mycteroperca phenax*) suffered a drop in the proportion of males from 17% to 1% and 36% to 18%, respectively. Beets and Friedlander (1998) examined red hind (*Epinephelus guttatus*) in the U.S. Virgin Islands and found that during periods of high fishing mortality the sex ratio became more skewed toward females: 15 females per male

(6% male). When a no-take zone was established to protect red hind spawning grounds, fishing mortality decreased and within seven years the red hind sex ratio was restored to 4:1 (20% male). Buxton (1993), Wyanski et al. (2000), Platten et al. (2002), and Shepherd et al. (2010) compared protogynous populations on reefs open and closed to fishing and found that sex ratios were increasingly skewed in populations exposed to exploitation compared to those in protected areas. Although gear selectivity was not measured on male and female fish directly, in each of these studies the sex ratio shifted to favor the 'first' sex (i.e. female in protogynous species) during periods of heavy fishing pressure, suggesting that fishing is sex selective.

2.4.2 Hypothesis #2: Shift in age (or size) at sex change

Alternatively, hermaphroditic species preserve an optimal sex ratio when females change sex earlier in response to sex selective fishing. Heavy fishing mortality on males in protogynous species rapidly removes males compared to females. In response, females are able to increase their reproductive value by undergoing sex reversal at earlier ages and replacing lost males. The downward shift in the age (or size) at sex change is a compensatory mechanism to maintain the sex ratio that optimizes population fitness (Shapiro 1979). This phenomenon has been observed in laboratory experiments (Benton and Berlinsky 2006) and has been observed in multiple field studies (Table 2.2).

Hamilton et al. (2007) used historical comparisons to examine the effects of exploitation on sex ratios and the age at sex change in California sheephead (*Semicossyphus pulcher*), a protogynous hermaphrodite in south-central California. During a twenty year period commercial and recreational fishing rose unregulated in many sections of the California coast. In protected areas fishing remained low and was primarily limited to small-scale artisanal fisheries. Over time, average female length decreased in populations of California sheephead exposed to heavy fishing pressure (suggesting that females matured at

smaller sizes) (Hamilton et al. 2007). In exploited sheephead populations percent male in all size classes shifted so that more males were occurring at smaller sizes, further indicating that females underwent sex reversal at smaller sizes.

In comparative studies of fished and non-fished hermaphroditic populations, age at sex change was lower in exploited populations than protected populations. The venus tusk fish (*Choerodon venustus*) is a protogynous hermaphrodite and is heavily exploited on the Great Barrier Reef. In locations of high exploitation, the average size of transitioning females (as indicated by the presence of male testicular tissue in the female gonad) was smaller than transitioning females in populations protected from fishing (Platten et al. 2002). Similarly, Götz et al. (2008) conducted fishing and visual surveys of seabream (*Chrysoblephus laticeps*), a protogynous hermaphrodite, in and outside of the Goukamma Marine Protected area in South Africa. Sex ratios of populations in and outside the marine protected area were found to be the same, however, the age at sex change was smaller in populations exposed to fishing outside the marine reserve. Similar patterns were also found in multiple species of parrotfish (Scaridae), all protogynous hermaphrodites, in the Caribbean Islands (Hawkins and Roberts 2004).

2.4.3 Effects of skewed sex ratios and shifts in age at sex change on fertilization rates

Increasingly skewed sex ratios will result in reduced fertilization rates and, as a consequence, slower population growth. An example of this was seen in the Caribbean sea urchin (*Diadema antillarum*) in 1983-1984 when population density was dramatically reduced by 96% after a severe mortality event (Lessios 1988). Although female body size and egg production per female greatly increased because of low population density after 1984, the number of fertilized zygotes produced per female did not increase because female fertilization was drastically unsuccessful (Levitan 1991). Similarly, a heavily male-biased fishery for blue crab in the Chesapeake is thought to result in decreased fertilization rates as

a result of sperm limitation (Hines et al. 2003). A reduction in the male population of protogynous fish species may have a similar effect; female egg production may remain high, however, zygote production could be limited if fertilization by males is increasingly rare.

The effects of shifting sex ratios on fish recruitment have not been directly measured in field experiments, but theory and simulation studies strongly indicate recruitment will be significantly reduced (Alonzo and Mangel 2004). If all male size classes are fished in a protogynous species (and in the case of protandrous species, female size classes), population collapse is predicted to occur even if fishing pressure is moderate (Alonzo and Mangel 2004). In stock assessments, recruitment is a function of female spawning stock biomass. Brook et al. (2008) found that if the population had a strong potential for sperm limitation, biological reference points (e.g. B_{MSY}) were better predicted when recruitment was measured as a function of male spawning stock biomass. For many protogynous species, quantifying sperm limitation is difficult and likely unknown. When the potential for sperm limitation is unknown, recruitment as a function of both male and female spawning stock biomass is the best predictor of biological reference points (Brooks et al. 2008).

One potential side effect of small male populations in heavily fish protogynous species is reduced genetic diversity (Chapman et al. 1999) and subsequently a reduction in population growth, also known as the Allee effect, i.e., the phenomenon of negative population growth at low population size (Allee 1931). Even if fertilization rates remain high during times of male scarcity, the bottleneck of genetic material through a small male population will decrease the population's overall genetic diversity and may result in reduced ability to adapt to environmental variability and pathogens. These less visible genetic bottleneck effects can occur even while fertilization rates remain high (Levitan 1992).

Reductions in fishing mortality alone may not be a sufficient (or efficient) means of limiting impacts on the sex ratio. If fishing pressure is reduced without changing the sex selectivity of fishing gear, fishing mortality will be disproportionately high on males in protogynous species and females in protandrous species. To reverse the effects of fishing on sex ratio and age at sex change sex selectivity of all gear types must be measured. Changes in management plans would be species-specific and depend on the species' mating system (i.e. protogynous or protandrous), social interactions (e.g. harems, mating pairs), and life history patterns (e.g. sex-specific aggregations, migration). Furthermore, specific goals of the fishery must also be incorporated because different fishing restrictions will result in different outcomes. For example, in a case study on gag (*Mycteroperca microlepis*) Heppell et al. (2006) showed that population growth was highest when female fishing mortality was reduced, but the optimal sex ratio was maintained best when protected areas were implemented to preserve spawning grounds. Proactive management plans that compensate for the effects of fishing on protogynous species require careful consideration of species' life history and fishing sex selectivity.

2.4.4 Sex change in stock assessments

In stock assessments sex change is handled in a variety of ways. This is not unexpected since data of sex reversal is scarce and the effects of exploitation are not well established, no standard method has been developed and adopted by the stock assessment process. Some hermaphroditic species are well-studied and in these stocks the effects of fishing on sex change are monitored through changes in the sex ratio and shifts in the size at sex change. In a summary of hermaphroditic stocks on the east coast of the United States from the Gulf of Maine to the Gulf of Mexico, only some stocks monitor the effects of fishing (Table 2.3). Stock assessments in the Mid-Atlantic include black sea bass, and in the South Atlantic hermaphroditic stocks include black sea bass, hogfish, red porgy, gag, and black,

red, and snowy grouper. In the Gulf of Mexico, hermaphroditic stocks include gag, red grouper, and yellowedge grouper.

Most hermaphroditic stock assessments have made some adjustments to accommodate sex change, but the majority of assessments do not monitor the effects of fishing. Of the 11 stocks summarized, nine stocks calculate spawning stock biomass on a combined biomass of males and females. Most assessments, 10 of 11, report sex ratio and size or age at sex change. However, the sex ratio and age at sex change data was not used to gauge the impacts of fishing on males and the timing of sex change. Only four of 11 stocks report if age at sex change has shifted over time and only two of 11 stocks report if the percentage of males in the population has dropped.

Despite that most assessments do not report fluctuations in the sex ratio or age at sex change; hermaphroditic stock status is not any worse off than stock status of gonochoristic stocks (Figure 2.2). Five of the 11 stocks are overfished even though their population cannot support high exploitation rates. Three stocks are underfished, while another 3 have relatively low biomass and low exploitation rates. Even though stock status of sex changing fish is not greatly different from gonochoristic stocks, it is unclear how increasing rates of fishing mortality will effect populations because sex selectivity is not measured for any stock (Table 2.3).

In summary, sex change presents unique challenges to fishery managers. Fishing, either directly or indirectly, imposes sex selectivity on the population which results in disproportionate mortality rates on males and females. In stock assessments, sex change is not uniformly handled and sex selectivity is not estimated or measured. In many cases, assessment surveys are not collecting all the data needed to monitor changes in the age at sex change or shifts in sex ratios. So far this has not resulted in sex changing species being

dramatically different in stock status compared to gonochoristic species. But as fishing pressure increases, models will need to be used to recognize this unique life history.

LIST OF TABLES

Table 2.1. Examples of exploitation changing the sex ratio of sex-changing fish

Species	Location	Δ proportion male	Citation
Gag (<i>Mycteroperca microlepis</i>)	Gulf of Mexico	17% to 1%	Coleman et al. (1996)
Scamp (<i>Mycteroperca phenax</i>)	Gulf of Mexico	36% to 18%	Coleman et al. (1996)
California sheephead (<i>Semicossyphus pulcher</i>)	California	25% to 20%	Hamilton et al. (2007)
Blue-throated wrasse (<i>Notolabrus tetricus</i>)	South Australia	10% to 5%	Shepherd et al. (2010)
Snowy grouper (<i>Epinephelus niveatus</i>)	North and South Carolina, US	7-23% to 1%	Wyanski et al. (2000)

Table 2.2. Examples of exploitation changing the age or length at sex change.

Species	Location	<u>Δ in age or size</u>	Citation
California sheephead (<i>Semicossyphus pulcher</i>)	California	-240 mm	Hamilton et al. (2007)
Venus tusk fish (<i>Choerodon venustus</i>)	Great Barrier Reef, Australia	-409 mm	Platten et al. (2002)
Roman (<i>Chrysoblephus laticeps</i>)	South Africa	-2 years, 4 months	Götz et al. (2008)
Parrotfish (<i>Sparisoma viride</i>) (<i>Sparisoma rubripinne</i>) (<i>Scarus taeniopterus</i>) (<i>Sparisoma aurofrenatum</i>) (<i>Scarus iserti</i>)	Caribbean Islands	-7 mm -8 mm -6 mm -5 mm -4 mm	Hawkins and Roberts (2004)
Shrimp (<i>Pandalus borealis</i>)	Alaska	-2 mm	Charnov and Anderson (1989)

Table 2.3. Treatment of sex change in stock assessments. All species are protogynous and managed by the Gulf of Mexico, South Atlantic, and Mid-Atlantic Fisheries Management Councils. Scamp (*Mycteroperca phenax*) and red hind (*Epinephelus guttatus*) were omitted from the table because data is scarce and stock assessments have not been done.

Family	Stock	Spawning stock biomass (SSB)	Reports sex ratio at age (or size)	Reports change in proportion male	Change in the age (or size) at sex change	Measures or estimates sex selectivity	Citation
Serranidae	Black sea bass <i>Centropristis striata</i> South Atlantic	Male + female	Yes	Not reported	Not reported	Not reported	SAFMC (2011)
	Black sea bass <i>Centropristis striata</i> Mid-Atlantic	Male + female	Yes	Not reported	Not reported	Not reported	NEFSC (2012)
	Black grouper <i>Mycteroperca bonaci</i> S. Atlantic, Gulf of Mexico	Male + female	Yes	Not reported	Not reported	Not reported	SAFMC, GMFMC (2010)
	Gag grouper <i>Mycteroperca microlepis</i> Gulf of Mexico	Female	Not reported	Not reported	Yes (no decrease reported)	Not reported	GMFMC (2009)
	Gag grouper <i>Mycteroperca microlepis</i> South Atlantic	Male + female	Yes	Not reported	Yes (no decrease reported)	Not reported	SAFMC (2006)
	Red grouper <i>Epinephelus morio</i> South Atlantic	Male + female	Yes	Yes	Yes (no decrease reported)	Not reported	SAFMC (2010)
	Red grouper <i>Epinephelus morio</i> Gulf of Mexico	Female	Yes	Not reported	Yes (no decrease reported)	Not reported	GMFMC (2009)
	Snowy grouper <i>Epinephelus niveatus</i> South Atlantic	Male + female	Yes	Not reported	Not reported	Not reported	SAFMC (2004)
	Yellowedge grouper <i>Epinephelus flavolimbatus</i> Gulf of Mexico	Male + female	Yes	Not reported	Not reported	Not reported	GMFMC (2011)
	Hogfish <i>Lachnocheilus maximus</i> S. Atlantic, Gulf of Mexico	Male + female	Yes	Not reported	Not reported	Not reported	SAFMC, GMFMC (2004)
Labridae							
Spanidae	Red porgy <i>Pagrus pagrus</i> South Atlantic	Male + female	Yes	Yes	Not reported	Not reported	SAFMC (2012)

FIGURE CAPTIONS

Figure 2.1. Size at sex change as a function of reproductive value. Reproductive value of male (bold line) and female fish (dashed line) with increasing age (or size) for a protogynous species; curves are based on Charnov (1982). Females are expected to change sex at the point of intersection when reproductive value of male fish is higher than females.

Figure 2.2. Overfished and overfishing status of hermaphroditic and gonochoristic stocks. Current biomass and exploitation rates scaled to levels that would maintain maximum sustainable yield (B_{MSY} and U_{MSY}) for 178 stocks world wide. Hermaphroditic stocks are black and gonochrositic stocks are open circles.

Figure 2.1

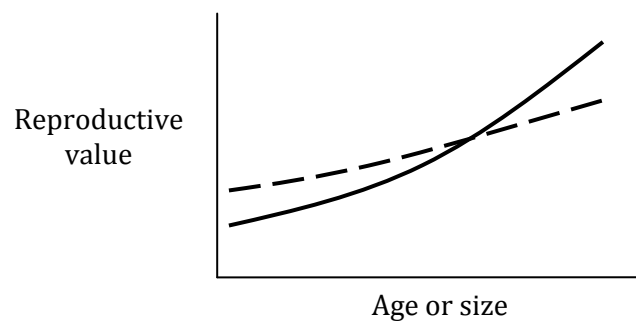
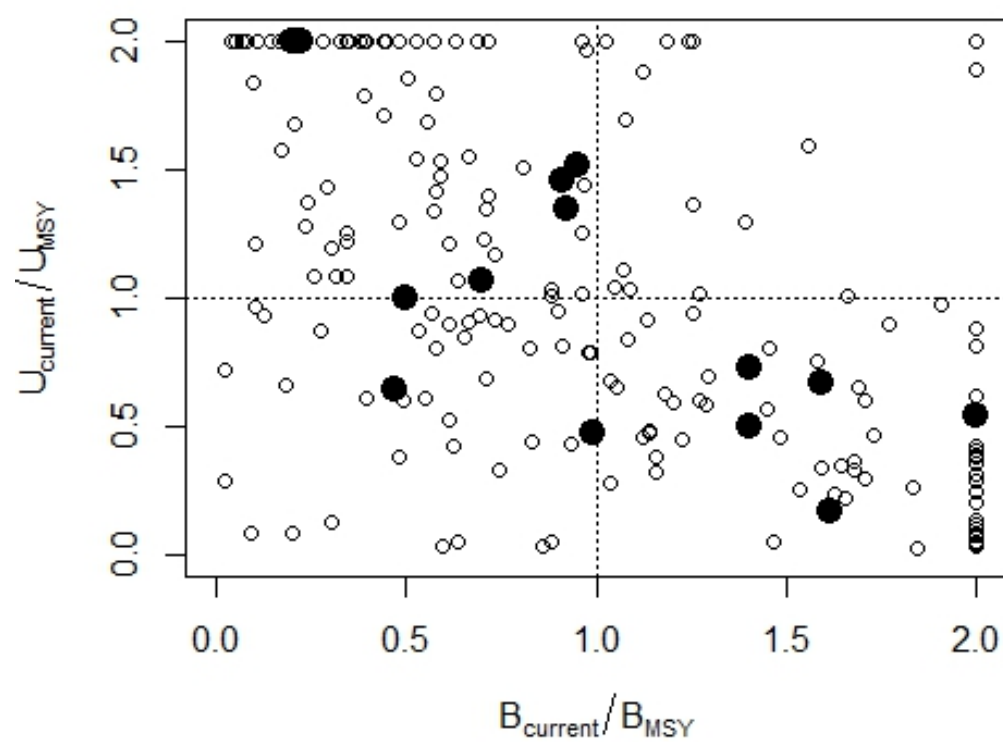


Figure 2.2



– CHAPTER 3 –

SEX-, SIZE-, AND AGE-SELECTIVITY IN A BLACK SEA BASS FISHERY AND THE INFLUENCE OF SIZE, AGE AND SEASON ON SEX CHANGE

Abstract

Fishing operations are often biased toward certain individuals in the population, resulting in fishing mortality that varies by size and age. In protogynous hermaphrodite species (female to male sex change), the sex ratio varies with size and, consequently, indirectly causes fishing gear to be sex selective. Protogyny is also associated with complex social structures and patterns of sex-specific behavior that may directly result in sex selectivity. A tagging experiment was carried out in 2011 and 2012 in south central New Jersey on black sea bass (*Centropristis striata*), an economically important protogynous hermaphrodite. Tagging data were used to measure sex selectivity curves for commercial and recreational fishing gears, and to measure sex change as a function of size, age, and season to further understand black sea bass life history. Sex selectivity curves varied by sex and gear. Male black sea bass experienced increasing selectivity with greater body size, producing an asymptotic selectivity curve. Alternatively, males experienced dome-shaped selectivity by commercial traps, indicating traps were biased toward intermediate size males. Male black sea bass also experienced greater selectivity over a wider range of body sizes compared to female selectivity for both fishing gears. Commercial traps captured a higher proportion of males at length compared to hook-and-line fishing gear, especially at small to intermediate body sizes. Sex change was found in eight females, size at sex change was 365 mm and all sex changing females were 3-4 years old. In 2011 15 females were tagged and recaptured in 2012 to verify sex change, seven of these changed sex, giving an

annual sex change rate of 0.47. Fifty percent of females were expected to change sex at 365 mm and 3-4 years.

3.1 Introduction

The process of fishing, whether by net, trap, or hook, is rarely effective at capturing individuals across all sizes and ages in wild fish populations (Lewin et al. 2006). As a consequence, fishing mortality rates vary by size and age, a phenomenon described as size selectivity (Beverton and Holt 1957, Quinn and Deriso 1999). Similarly, when the process of fishing does not effectively capture males and females in proportion to their natural abundances fishing mortality varies by sex and is a process known as sex selectivity.

The size selectivity of a fishery is influenced by many factors. Outside factors, such as management regulations (McClanahan and Mangi 2004), market value of fish species (Zimmermann et al. 2011), and cultural preferences (Aswani and Hamilton 2004) determine which fish species of what body sizes experience the highest mortality rate. The fish most 'at risk' of being captured is also a function of the interaction between fish and fishing gear, including factors such as gear placement in aquatic environments, gear design, and species' feeding ecology (see Løkkeborg and Bjordal 1992 for examples). Variation in fish behavior (Williams et al. 2013), body size (Løkkeborg and Bjordal 1992), and movement throughout aquatic habitats and in the vicinity of fishing gear can influence the vulnerability of being captured (Parrish 1999). It is, therefore, imperative that life history be accounted for when assessing fishery selectivity.

Life history is especially important in sex selectivity for protogynous hermaphrodite fish species. A common life history characteristic of all protogynous hermaphrodites is that male fish tend to be larger and females are generally smaller in size (Charnov 1982). Since the sex ratio varies by size, it is expected that size-limited fishing gears will indirectly result

in disproportionately high fishing mortality on male fish. There are other common protogynous life history characteristics that may directly increase the selectivity of males; these include, for example, sex-specific behavior (Black et al. 2011), sexual dimorphism (Munday et al. 2004), and sex-specific migratory patterns (Shapiro et al. 1993). Not only are males larger and, therefore, more vulnerable to size selectivity, male fish tend to be more aggressive (Warner and Swearer 1991) and have faster growth rates (Munday et al. 2004) which is expected to increase their susceptibility to fishing gear (Sutter et al. 2012). The potential sampling bias of fishing gear toward males, either through indirect or direct processes, causes protogynous species to be especially vulnerable to the consequences of sex selective fishing pressure.

3.1.1 Selectivity

In stock assessments, size selectivity curves are necessary for interpreting catch-at-age data. Size selectivity curves indicate the probability of capture at age or size, and describe which size classes are most vulnerable to being captured. Size selectivity curves can be sex and gear specific. Catch-at-age data cannot show which fish are most vulnerable to capture because catch data is an incomplete snapshot of the wild population's size and age structure. Catch data alone does not provide rates of capture by size across the size spectrum of body sizes. The process of calculating capture rates involves a comparison of size distributions between the wild population and catch, a process that is nearly impossible to do with populations in marine environments. Without knowing the complete size distribution in the wild, little can be inferred about a fish's vulnerability from catch distributions alone. Size selectivity curves, in conjunction with catch-at-age data, are used to infer the sampling bias of fishing gear and make assumptions about the variation of fishing mortality across size for males and females.

Catch-at-age data can be interpreted in multiple ways. Catch data is usually dome-shaped over a range of sizes (Figure 3.1a), with relatively few small and very large fish in catch. There are many reasons to explain why small fish are not captured: small fish are avoided in fisheries with minimum size regulations, undersized individuals escape capture due to gear design (e.g. escape vents in traps, see Harada et al. 2007), or small fish do not occur in areas where intensive fishing practices occur. Even though small fish are rare in the catch, small fish remain relatively more abundant in the wild population than older and larger fish since older year classes have been reduced to smaller abundances because of annual natural mortality rates. Relatively low abundance of large fish in the catch; however, could indicate one of two possible scenarios. First, large fish may no longer be abundant in the population, and that few large fish in the catch is an accurate reflection of their relatively low abundance in the population. Or, large fish experience low capture rates because they avoid capture by fishing gear. In either case, the capture rate, or selectivity, of large individuals in the population varies.

The shape of size selectivity curves helps determine which of the two aforementioned scenarios explains why large fish are rare in the catch. Asymptotic size selectivity curves (Figure 3.1b) assume that selectivity increases with size and that fishing is mostly biased toward the largest sizes classes. Therefore, the relative abundance of large fish in the catch is greater than the relative abundance of large fish in wild populations. Dome-shaped size selectivity curves (Figure 3.1c), alternatively, assume that the largest size classes are not fully selected by fishing gear. Capture rates are highest for intermediate size classes since both small and large fish avoid capture and, consequently, experience the lowest fishing mortality.

Each selectivity curve, asymptotic or dome-shaped, can lead to very different management advice for fisheries because of their different assumptions about large fish.

The perception that either absence or presence of large size classes in wild populations is important for assessing factors related to population growth (i.e. fertilization rates, recruitment, and mortality). In one case, the population is assumed to have relatively high abundance of large fish (dome-shaped, Figure 3.1c) whereas asymptotic selectivity assumes a relatively low proportion of large fish (Figure 3.1b). Such assumptions may have consequences for fishery managers and setting catch limits, minimum size regulations, and allowable fishing gear.

Knowing the size selectivity of different fishing gears is important for interpreting catch data and making assumptions about size structure in wild populations. For protogynous hermaphrodite fishes, estimating sex selectivity is particularly important because it can cause different mortality rates for males and females. Persistent sex selectivity may lead to unanticipated changes in the sex ratio and rate of sex change which can have lasting consequences on hermaphroditic fish population dynamics.

3.1.2 Sex change

The process of sex change plays an important role in hermaphroditic population dynamics. Population dynamics, defined as the study of how and why there are short- and long-term changes in size and age composition of a population (Quinn and Deriso 1999), present unique challenges to managers of hermaphroditic fish species. The process of changing sex inherently alters the number of males and females at size and age. Changes in the rate of sex change may affect size and age distributions of males and females which, in turn, can affect fertilization rates (Levitan 1992), egg production (Alonzo and Mangel 2004), and potentially recruitment (Brooks et al. 2008). It is expected that fishing pressure will alter the rate of sex change (see Hamilton et al. 2007 and Hawkins and Roberts 2004 for examples); however, the effect of fishing on sex change rates varies among hermaphroditic species (see Coleman et al. 1996 for examples).

In hermaphroditic fish species the process of sex change is diverse (Munday et al. 2006) and may explain why the effect of fishing on sex change rates varies among protogynous species. Sex change has many forms, it can be protogynous (e.g. Benton and Berlinsky 2006) or protandrous (e.g. Moyer and Nakazono 1978); sex reversal may be triggered by shifts in local sex ratios (see Munday et al. 2006 for examples), population density (Lutnesky 1994), and size ratio (Buston 2003). For some species, sex change is a process that occurs throughout the entire year (e.g. red hind, Shapiro et al. 1993) or is restricted to one season (McGovern et al. 1998). The effects of fishing on rates of sex change have been far from uniform in hermaphrodite species. For example, female tusk fish (*Choerodon venustus*) underwent sex change earlier when fishing pressure increased (Platten et al. 2002), but had no effect on rates of male sex change in a protandrous shrimp (*Pandalus borealis*, Bergström 1997). Knowing when sex change occurs as a function of size, age, and season will help disentangle the relationship between fishing pressure and sex change rates.

3.1.3 Life history of black sea bass and stock status

Black sea bass (*Centropristas striata*) is an economically and culturally important protogynous hermaphrodite in the Middle Atlantic Bight. Their life history differs from black sea bass in the South Atlantic because they make an annual migration between the reefs located 5-10 miles off shore to the continental shelf (Musick and Mercer 1977). Every spring black sea bass return to reefs and artificial wrecks for the spawning season (May – October). In the Fall black sea bass will return to the continental shelf for the winter until the following Spring. Black sea bass hatch on reefs and wrecks and, as larvae, will spend their first winter on the inner continental shelf of New Jersey (Kendall 1972, Able et al. 1995) as well as in estuaries (Able et al. 1995). There is not enough information yet in support of sex-specific migratory patterns in black sea bass.

Sex change in black sea bass has been studied through laboratory experiments and field observations. In the South Atlantic Bight, gonad histology shows males are present in every age and size class. Black sea bass in transition were most frequent 160-259 mm, and immediately following spawning events (March-May and September-October) 14% of black sea bass were transitioning (Wenner et al. 1986). A similar bimodal breeding pattern exists in the Gulf of Mexico (Cochran and Grier 1991). Black sea bass in the Middle Atlantic Bight, however, have one spawning event that occurs in May through October (Shepherd and Nieland 2010) and less is known about the percentage of transitioning individuals. Removal experiments in laboratory tanks show that sex change in black sea bass is controlled by social or visual cues; females will undergo sex change in the absence of large, dominant males (Benton and Berlinsky 2006).

Along the East Coast of the United States, black sea bass are divided into two separate stocks: there is a northern stock, Mid-Atlantic stock, located from the Gulf of Maine to Cape Hatteras, North Carolina and the southern stock, South Atlantic stock, from Cape Hatteras to southern end of Florida. The Mid-Atlantic and South Atlantic stocks are considered two separate populations of the same species. There is a third black sea bass management unit, Gulf of Mexico stock; fish from this stock represent a separate subspecies, *Centropristis striata melana*. The Mid-Atlantic stock is currently in good health: overfishing is not occurring and the population is not overfished, but questions still remain about the effect fishing has on sex change. For approximately three decades from 1975 to 2003 black sea bass were overfished (Shepherd and Nieland 2010). As part of the Northeast Data Poor Stocks Working Group in 2008, black sea bass were identified as a 'data poor species' because of their hermaphroditic life history, and inadequate fishery-independent survey methods. The working group concluded that additional field evaluation of black sea bass

spawning behavior is needed to understand the implication of exploitation on black sea bass.

3.1.4 Objectives

This study addresses fundamental questions about sex selectivity and investigates the process of sex change in black sea bass along the coast of New Jersey. We focus on two objectives:

- (1) Quantify size selectivity curves for male and female black sea bass caught by two different gear types: commercial traps and recreational hook-and-line, and
- (2) Examine sex change among female black sea bass as a function of size, age, and season

To measure sex selectivity, the size distribution of a tagged group of males and females will be compared with the size distribution of recaptured males and females with respect to each fishing gear. Selectivity curves will be modeled across size and age for each sex. This method has been used in previous studies to measure selectivity and is the most direct method for estimating selectivity in wild populations (Hamley and Regier 1973, Miller and Fryer 1999).

This study differs from previous studies of sex change in hermaphrodite species because we track the sex of individual fish to verify the occurrence or absence of sex change. In previous sex change studies, fish were sampled one or more instances throughout the year in order to examine gonads and identify the percentage of transitional individuals (Wenner et al. 1986, Shapiro et al. 1993, Coleman et al. 1996). This method is useful to measure the prevalence of sex change at the time of sampling, but is less useful if estimating the overall proportion of fish that change sex over a period of time. It is likely that sex change varies temporally throughout the year (see Coleman et al. 1996 and Shapiro et al.

1993 for examples) and that the duration of an individual undergoing sex reversal can occur within days or weeks (see Warner and Swearer 1991, Benton and Berlinsky 2006). The prevalence of sex change may be severely under-estimated if individual sex is not tracked over time through a tagging study.

This study also differs from previous sex change studies because here we track actual sex change events. In previously published literature it is conventional to assume that individuals identified as in 'sexual transition' based on gonad histology (Wenner et al. 1986) or by intermediate morphology (Hamilton et al. 2007) will complete the process without reverting back to their first sex (i.e. females transitioning to males would never stop their transition process and return to female in protogynous species). Removal studies conducted in laboratory tanks (Benton and Berlinsky 2006) and wild populations (Warner and Swearer 1991) suggest that the process of sex change, once started, is not interrupted; however, the triggers of sex change in the wild may be less clear-cut compared to removal experiments. By tagging individual fish and tracking their sex through time we can determine when actual sex change events occur.

The aim of this study is to measure sex selectivity in black sea bass and compare selectivity curves for commercial and recreational fishing gears. This study will also measure sex change as a function of size and age, and track when females are most likely to change sex throughout the summer and fall over a two year period.

3.2 Methods

3.2.1 Sampling location

Black sea bass were sampled from May to October in 2011 and 2012 on the coast of south-central New Jersey. Sampling was primarily based out of the Rutgers Marine Field Station in Tuckerton, New Jersey on Rutgers owned vessels. Black sea bass were also

captured from two charter boats, *R/V Karen Ann II* (10.7 meters, Capt. Adam Nowalsky) and *R/V Evelyn Ann* (10.7 meters, Capt. Joel Mick), one party boat, *R/V Miss Beach Haven* (24.4 meters, Capt. Frank Camarda and Brant Whittaker), and one commercial fishing vessel, *F/V Rachel Marie* (13.1 meters, Capt. Eric Burcaw). Fishing sites ranged from 6 to 20 kilometers from shore in waters 15 to 30 meters depth.

Sampling sites were primarily chosen based on fish availability. Black sea bass are structure-oriented during the summer spawning season and are a popular sport-fish on artificial wrecks and reefs just offshore from the New Jersey coastline. Tug boats, subway cars, reef balls, tires, etc. have been purchased by local fishing clubs to provide excellent habitat for black sea bass. Based on advice from charter and commercial boat captains, we were able to identify highly productive reefs and wrecks for sampling black sea bass in 2011 and 2012.

3.2.2 Field sampling

Two methods were used to capture black sea bass: hook-and-line and commercial traps. Baited circle hooks were used between 8 AM and 5 PM on hook-and-line sampling days. Commercial traps were standard size, 106.7 cm long, 53.3 cm wide, and 34.3 cm tall. Each trap was outfitted with a standard size escape vent, cement anchor runners, and wire webbing on the outside of the trap. Both hook-and-line and trapping efforts to capture black sea bass were carried out in overlapping locations so that both types of fishing gear sampled from the same black sea bass population. After a soaking period of 5-14 days, traps were retrieved, black sea bass were measured, sexed, tagged, and traps were reset.

Males were identified by expressing milt with abdominal massage (DeGraaf et al. 2004). Females were identified by ovarian biopsy using a polypropylene cannula tube (1.49 mm outer diameter, 1.19 mm internal diameter) following the methods of Shehadeh et al. (1973) and Benton and Berlinsky (2006). In cases when sex could not be determined *in situ*,

unidentified black sea bass were dissected in the laboratory to confirm sex. In order to determine age, five to ten scales were removed behind the pectoral fin and were pressed into acetate slides. Concentric annuli were counted on an Eyecom 3000 Com Fiche Reader. All black sea bass ages were validated by Josh Dayton, black sea bass expert ager, at the NOAA Aging Laboratory in Woods Hole, MA.

3.2.3 Tagging protocol

A mark-recapture study was done to estimate sex selectivity between recreational (hook-and-line) and commercial (traps) gears. The size and sex distribution of marked individuals was compared to the size and sex distribution of recaptured individuals caught in traps and by hook-and-line. Relative recapture rates of male and female tagged black sea bass for hook-and-line and commercial traps showed the sampling bias of each fishing gear.

In 2011 and 2012, 1,500 black sea bass >280 mm were tagged with Floy internal anchor tags (FM-84). This tag type was chosen because it has had long term retention rates in previous black sea bass studies (Moser and Shepherd 2009) and in other marine species (Waldman et al. 1991). Catch and release procedures involved with capturing, tagging, and releasing black sea bass has contributed very little to fishing mortality (Bugley and Shepherd 1991).

All Floy tags had a unique identification number, telephone contact number, and “Rutgers Reward” printed on both sides in opposite directions such that the identification number was visible from the base and the top of the tag. Tags were color-coded by reward value in orange (n=1,299), earning a baseball cap if recaptured, and red (n=200) which generated a \$100 reward if recaptured. To encourage the return black sea bass carcasses with tag returns from local fishermen, fishermen were entered into an annual \$1,000 lottery for every tagged black sea bass carcass that was returned with the tag.

The tagging procedure followed the methods of Moser and Shepherd (2009). A 5 mm incision was made in the abdominal cavity at the midpoint of the pectoral fin on the left side of the fish. In total, handling time lasted no longer than 2 minutes. Black sea bass were released immediately if they were in good condition; fish that appeared weaker were monitored in live wells on board to monitor their recovery for 2-5 minutes. Black sea bass pulled up from deep sampling sites often had extended swim bladders; pressure was released when the incision was made into the abdominal cavity for tagging. Tagged fish that appeared weakened, especially after holding them for >15 minutes were not released. Tag retention rates were determined by holding tagged black sea bass in tanks in multiple studies at the NEFSC Woods Hole and J. J. Howard Labs, Rhode Island Department of Marine Fisheries facility in Jamestown, and Rutgers University Marine Field Station in Tuckerton, New Jersey.

Black sea bass recaptured by local fishermen were reported by telephone and email. Latitude and longitude of where the fishermen caught the fish were recorded when possible; points of reference and artificial reef name were used if exact location was unavailable. In cases when the fish carcass was available, black sea bass were picked up from fishermen along with the tag. All recaptured fish were checked for signs of sex change by comparing the sex at time of recapture to the fish's sex when originally tagged and released. If black sea bass carcasses were unavailable, tags were sent via postal service to the Rutgers Marine Field Station.

3.2.4 Data analysis

Since size is related to sex in protogynous hermaphrodites (larger fish tend to be male), analyses of sex selectivity and sex change all account for fish length. Sex selectivity curves were calculated for males and females captured by hook-and-line and trap gear types. Each curve measured the probability that a tagged male or female will be recaptured

in either traps or by hook-and-line fishing gear at a given length. For male black sea bass, the total number of tagged males recaptured by hook-and-line and the total number of tagged males recaptured in traps was divided by the total number of tagged males. Similarly, total number of females recaptured by hook-and-line and the total number of females recaptured in traps were divided by the total number of tagged females. Recapture probabilities for males caught by hook-and-line and in traps, and females caught by hook-and-line and in traps were calculated based on recapture rates within truncated size bins to account for the confounding effects of fish length.

To model (1) the estimated size of when 50% of females change sex and (2) the proportion of male black sea bass captured by both gear types at length involved fitting a generalized linear model using a logit-link function and a binomial error distribution (commonly referred to as logistic regression). When calculating the size at 50% sex change, the response variable was the presence of sex change, $p(\text{sex change}) = 1$, or not changing sex, $p(\text{sex change}) = 0$. When calculating the proportion of male black sea bass captured at a given length, the response variable was sex (male = 1, female = 0) and gear type was included as a covariate (hook-and-line or trap).

3.3 Results

Overall, 3,994 black sea bass were sampled in 2011 and 2012 (Table 3.1, Figure 3.2). Of these, 2,430 were caught by hook-and-line methods and 1,517 were caught in commercial traps. Total sample sizes for males and females were 1,762 and 1,931, respectively. In 2011, 973 tags and in 2012, 526 tags were deployed across all sampling sites for a total of 1,499 deployed tags. Of all tagged fish, 723 were male and 757 were female. The overall recapture rate was 0.31 (461/1,499), but black sea bass carcasses were turned in for only 308 fish of the 461 tags returned. During sampling we deployed 1,299

orange tags (low reward) and 200 red tags (high reward tags). Recapture rate for orange tags was 0.29 (378/1,298) and for red tags 0.37 (75/200). Based on the difference between high and low reward tags, we expect approximately 20 tagged black sea bass were captured by fishermen but never reported and turned in.

A total of 2,430 black sea bass were caught by hook-and-line gear and 1,517 black sea bass caught in commercial traps (Table 3.2). Of these, 91 tagged females and 66 males were recaptured by hook-and-line gear. In commercial pots, 34 tagged females and 66 tagged males were recaptured. Overall recapture rates by sex and gear were as follows: females recaptured by hook-and-line 0.12 (91/757), males recaptured by hook-and-line 0.09 (66/723), females recaptured in traps 0.04 (34/757), and males recaptured in traps 0.09 (66/723).

Commercial traps captured a significantly higher proportion of male black sea bass at length and age than the proportion of males captured by hook-and-line gear ($P < 0.0001$) (Figure 3.3 and Figure 3.4). The size range of fish caught by each capture method differed. In traps, male fish length ranged from 129 mm to 483 mm, and female body size in traps ranged from 129 – 425 mm (Figure 3.5). Hook-and-line gear captured a wider size range, males captured by hook-and-line ranged 173 – 533 mm and females ranged 94 mm to 458 mm (Figure 3.6).

The probability of recapturing male and female black sea bass varied by size, age, and fishing gear (Figure 3.7 and Table 3.3). In general, males were more likely to be recaptured over a larger size range compared to females; recaptured males ranged from 270 mm to 461 mm whereas recaptured females ranged from 250 mm to 383 mm. The probability of recapturing males by size in traps was dome-shaped (Figure 3. 7a) and reached a maximum probability of 0.12 at an intermediate size of 340-360 mm. Alternatively, the recapture selectivity curve for males caught by hook-and-line was

asymptotic-shaped and reached a maximum probability of 0.60 when males were 460-480 mm (Figure 3.7c). Female black sea bass selectivity curves differed from male black sea bass (Figure 3.7b and 3.7d) The highest probability of recapturing females in traps was 0.12 when females were 380-400 mm; female fish with a body size of 380-400 mm experience a recapture rate of 0.12, this rate is likely artificially inflated because sample sizes were low in this size class. Females caught by hook-and-line gear were most likely to be 260 – 280 mm; females in this size class experienced a recapture rate of 0.21. Recapture probabilities also varied by age, but sample sizes of recaptured individuals were much lower since many scales collected for age determination were not readable (Table 3.3).

We observed sex change in eight female black sea bass (Table 3.4). All sex change events occurred in females 290 – 370 mm, at the time of recapture newly formed males were 342 – 480 mm. Sex change occurred from 2011 to 2012, except for one female which was tagged in June, 2011 and recaptured as a male in December, 2011. Of the eight fish that changed sex, five individuals were four years old when they were tagged in 2011 and all of them verified as age five in 2012. One individual was three years old in 2011 and verified as age four in 2012. Scales from the remaining two individuals were unreadable in both 2011 and 2012.

From 2011 to 2012, the overall sex change rate was 47% (+/- 1%) (Figure 3.7). Sex change rate was calculated using the beta distribution which is continuous and bounded from 0 to 1 and makes it ideal for modeling the probability density of success in binomial data (Bolker 2007). In 2011, 430 females were tagged and of these, 15 were recaptured in 2012 to verify if sex change happened ('success') or if females remained female ('failure'). Of the 15 females tagged in 2011 and recaptured in 2012, 7 were successes and 8 were failures.

Length at 50% sex change occurred at 366 mm (Figure 3.9) based on a logistic regression model of the probability of sex change at length. A total of 114 females were tagged and recaptured throughout 2011 and 2012, 106 remained female and 8 had changed their sex.

3.4 Discussion

3.4.1 Limitations to study

Natural mortality was not accounted for in this study, but it could have an impact on interpretation of recapture rates. The shapes of selectivity curves for female black sea bass caught in traps and by hook-and-line were slightly difficult to interpret because the curves did not follow a smooth pattern. Based on the distribution of female recapture rates, it is difficult to ascertain if the probability of recapture by either commercial traps (Figure 3.6b) or hook-and-line gear (Figure 3.6d) generally increases or decreases with female size. The probability of recapturing females could follow more of a uniform distribution than either asymptotic or dome-shaped, suggesting that females within a certain size range are equally likely to be captured by traps and anglers. Between the two gear types, female black sea bass are slightly more vulnerable to recapture by anglers compared to traps; however, larger sample sizes in select size classes will likely reveal a more continuous selectivity curve that more effectively shows the relationship between female size and catchability for commercial and recreational fishing gears.

3.4.2 Evidence of sex selectivity

This study shows clear evidence of sex selectivity in the black sea bass population for commercial and recreational fishing gears. For all size classes, commercial traps captured a significantly higher proportion of male black sea bass compared to the proportion of males captured by hook-and-line fishing gear. The size selectivity curves for

male and female black sea bass varied by fishing gear, indicating that commercial and recreational fishing methods are sex selective. For males caught by anglers, the probability of being recaptured increased with size resulting in an asymptotic selectivity curve. Alternatively, male fish caught by commercial traps experienced dome-shaped selectivity, males of an intermediate size range were recaptured the most (260 – 380 mm) compared to hook-and-line gear which was biased toward males 260 – 533 mm. Both gears, traps and hook-and-line, targeted female black sea bass of a narrower size range and gear bias followed different selectivity curves compared to male black sea bass.

This is the first time sex selectivity has been directly measured in black sea bass or any other exploited protogynous grouper. The occurrence of sex selectivity, however, is not a new phenomenon and has been documented in other fisheries around the world. For example, in Japan protandrous pandalid shrimps (Pandalidae, *Pandalus*) (male to female sex change) the sex ratio is increasingly biased toward males throughout the commercial fishing season (Chiba et al. 2013). Harvested shrimp, however, were found to be 98% female because fishing methods were heavily selective of females. In the United Kingdom, sex ratios in perch (*Perca fluviatilis*) shifted dramatically in favor of females over six decades in response to strong selectivity of mature males (Langangen et al. 2011). In pandalid shrimps, perch, and others (Goni et al. 2001, Kendall and Quinn 2013), males and females experience differences in catchability that is often mediated by size selectivity in species that are drastically sexually dimorphic.

In exploited black sea bass populations, however, and potentially other protogynous groupers with similar life histories, sex-specific behavior patterns may play an important part of sex selective fishing patterns. For passive fishing methods, such as traps and hooks, behavior becomes even more important because individual fish must choose to enter the trap or lunge, attack, and bite a hook; a decision that could be influenced by the presence of

nearby individuals (Jivoff and Hines 1998, Smith et al. 2004). Protogynous fish species are known to develop complex social structures during the reproductive season (Robertson 1972, Myoer and Nakazono 1978, Hoffman 1985, Kline et al. 2011). Large males are particularly aggressive because they are actively courting, defending, and competing for female mates (Myoer and Nakazono 1978, Warner and Swearer 1991, Mumby and Wabnitz 2002, Kline et al. 2011). Since black sea bass are hermaphrodites (Benton and Berlinsky 2006), large males are expected to display similar patterns of aggressive behavior throughout the spawning season. Aggressive fish are particularly vulnerable to passive fishing gears (Sutter et al. 2012, Biro and Post 2008), and it is likely that behavior of fish, more so than body size, determines a fish's vulnerability to capture in passively operated fishing gears (Uusi-Heikkilä et al. 2008). Aggressive behavior among large male black sea bass could explain why selectivity of males was not only higher than females, but also covered a wider range of body sizes, especially for hook-and-line fishing gear.

Large male black sea bass were more likely to be recaptured by hook-and-line than by traps; this observation has two possible explanations. From the design of traps employed in our study and our observation that, it is apparent that very large black sea bass may be less likely to enter the trap than medium and small individuals, an observation seen in other species (Hepper 1977). Hook-and-line gear does not impose obvious size limits on capturing fish, so long as a fish's gape can accommodate the hook passing into the mouth. The difference in gear design suggests that it is expected the sampling bias of each gear will follow different selectivity curves (Miller and Fryer 1999). The second explanation is one related to sex-specific behavior rather than size. Differences in sex-specific behavior could make it more or less likely that individuals will enter traps. This was observed in crabs (*Callinectes sapidus* and *Portunus pelagicus*) when immature females would be likely to avoid entering traps with mature males (Jivoff and Hines 1998, Smith et al. 2004). Social

interactions between males and females of protogynous species can be constructed through complicated hierarchal networks (Sakai et al. 2003); where depending on rank within the social structure males engage in interaction (Kroon et al. 2000). Not enough information is known about male- and female-specific roles within black sea bass social structure to be certain that behavior, rather than size, is the reason for why large males are not as likely to be recaptured by traps as they are by hook-and-line.

Hook-and-line fishing gear was biased toward catching large male black sea bass, an observation that may be explained by high energetic demands of large, aggressive fish. Individuals that expend more energy through aggressive swimming, defending territories, competing for reproductive opportunities and have fast growth rates require a high intake of energy to sustain such behavior. Hook-and-line fishing gear depends on the willingness of a fish to lunge at a hook and the fish's effectiveness at 'catching' the baited hook; aggressive and fast growing individuals have higher energy demands and will attack baited hooks more frequently than less aggressive individuals (Sutter et al. 2012, Biro and Post 2008). Aggression is associated with fish of larger body size in protogynous hermaphrodites (Moyer and Nakazono 1978, Warner and Swearer 1991, Kline et al. 2011), which could explain why large males were most likely to be recaptured by hook-and-line. There is evidence that protogynous hermaphrodites follow sex-specific growth rates and that recently sex-changed males in protogynous fish species undergo a spurt of growth to ensure their dominance among competing males and large females (Garrett et al. 1993, Munday et al. 2004). If sex-changing black sea bass grow particularly fast, then it would be expected their energetic demands would out-weigh females, suggesting large males may be more likely to attack baited hooks.

Sex-specific migratory patterns have led to sex selective fishing in some fisheries (Goñi et al. 2001, Gerritsen et al. 2010), but is not likely the reason for sex selectivity in black sea bass. Trap efficiency of Mediterranean spiny lobster (*Palinurus elephas*), for example, differed for males and females throughout the fishing season because females would move to deeper depths throughout the season which is coordinated with male moulting behavior (Goñi et al. 2001). Observations of protogynous species suggest sex-specific migrations; in *E. guttatus* (Sadovy et al. 1994) and *M. microlepis* (Coleman et al. 1996) in the Gulf of Mexico and U.S. Virgin Islands, males and females co-occur only during the spawning season which is January through February. During other parts of the year, *E. guttatus* and *M. microlepis* females remain in shallow warm waters near shore and males dwell in deep, colder waters offshore. If male and female black sea bass separate spatially, similar to other protogynous groupers (Sadovy et al. 1994, Coleman et al. 1996), and if commercial fishing traps are more often placed in male-dominated habitats, then we would expect traps to capture higher proportions of male fish because females would not be in the vicinity. In black sea bass, however, sex-specific migratory patterns probably do not explain the sex-selectivity observed by commercial and recreational fishing methods. In this study, hook-and-line sampling and the deployment of traps were conducted at the same sites in order to sample from the same population. Large scale migrations just before and after the reproductive season may be sex-specific, but throughout our sampling period which corresponded with the reproductive season sex-specific habitats seem unlikely.

3.4.3 Sex change as a function of size, age, and season

Sex change occurred in female black sea bass ages 3 – 4 years (290 – 370 mm) turning 4 – 5 years (342 – 480 mm). Fifty percent of female black sea bass were expected to change sex when body size was 365 mm. Male black sea bass were present in all age classes from one through eight. Sex change among females, as a function of season, occurred

between annual spawning seasons, and slightly less than half (47%) of female black sea bass in 2011 were expected to change sex by 2012.

Previous studies of protogynous hermaphrodites show that the periodicity of sex change throughout the year is highly variable among species (Wenner et al. 1986, Shapiro et al. 1993, Burgos et al. 2007). Transition individuals were found year-round in red hind (Shapiro et al. 1993), whereas in South Atlantic black sea bass transitioning individuals were only observed during a 2-3 month window immediately following the spawning season (Wenner et al. 1986). Transitioning individuals are thought to be not reproductively functional, which explains why fish actively reversing their sex are found outside of the spawning season (Wenner et al. 1986, Shapiro et al. 1993, Burgos et al. 2007). In California sheephead (*Semicossyphus pulcher*) however, this pattern does not follow since 21% of fish sampled during the spawning season were in sexual transition (Loke-Smith et al. 2011). The timing of sexual transition in relation to spawning season, a relationship which might be able to predict when fish are expected to change sex, is also variable among fish species. Black sea bass in the South Atlantic in transition were found within a 2-3 month period after the major and minor spawning seasons (Wenner et al. 1986), but red hind in transition were found throughout the year even though spawning occurs within a narrow, one month window in early February (Shapiro et al. 1993). The periodicity of individuals in transition clearly varies among species, these studies, however, were not able to predict the prevalence of sex change; i.e. how many females are expected to change sex in population over a specific time.

Knowing the prevalence of sex change within a population has implications on stock assessment (Alonzo et al. 2008). By incorporating the overall rate of sex change in population dynamics models, the loss of female spawning biomass and addition of mature

male biomass can be accounted for annually. Failing to track the amount of biomass shifting from female to male can lead to an overestimation of spawning biomass (Alonzo et al. 2008). Given the biological and ecological complexity of sex change, the rate of sex reversal is most likely species- and possibly population-specific. In black sea bass in central New Jersey, approximately 47% of females were expected to become male by 2012. To estimate sex change rate in other hermaphroditic species, mark-recapture experiments will need to be implemented to track which individuals change and do not change sex.

In conclusion, black sea bass in the Mid-Atlantic Bight are currently exposed to sex selective fishing pressures. Males and females of similar sizes experience different rates of catchability, sex selectivity could be caused by a combination of sex-specific behavior and size selectivity on sexually dimorphic individuals. Selectivity also varied by fishing method, suggesting that different commercial and recreational fishing gears impose unique sampling biases on the black sea bass population. Since black sea bass are protogynous hermaphrodites, it is important to quantify the annual rate of sex change in population for stock assessment purposes. In our study slightly less than half (47%) of females in 2011 were expected to change sex by 2012. These results have implications for stock assessment, as well as highlight the importance of learning more about the social structure and patterns of sexual transition in black sea bass in order to better understand the effect fishing has on sex changing species.

LIST OF TABLES

Table 3.1. A summary of black sea bass tagging data in southern New Jersey in 2011 and 2012. Total recapture rate includes individuals that have been recaptured more than once; of the 461 recaptures, 29 of these were recaptured more than once. Male and female recapture rates do not include recaptured fish submitted through the tag-return program for which only a tag was returned (153 tags were submitted without the black sea bass carcass). In these cases, either the carcass was disposed by the fishermen or the tag was cut and the fish released back into the ocean.

	Tagged BSB	Recapture rates	
Total BSB caught = 3,994 (1,499 tagged)	Male= 723	Male = 18.1% (n=133)	Red tag = 37.5% (n=75/200)
Total recapture rate = 30.7% (n = 461)	Female= 757	Female = 16.4% (n=124)	Orange tag = 29.1% (n=378/1298)

Table 3.2. Summary of black sea bass recapture rates caught by two different gear types. Black sea bass were sampled in May-October of 2011 and 2012.

Gear type	Total captured	Recapture by sex (number tagged)	Recapture rate
Traps	1,517	Male = 66 (723) Female = 34 (757)	0.09 0.04
Angling	2,430	Male = 66 (723) Female = 91 (757)	0.09 0.12

Table 3.3. Summary of male and female recapture rate in traps and by hook-and-line. Sample sizes include: 4 tagged females recaptured by traps, 7 tagged males recaptured by traps, 13 tagged females recaptured by hook-and-line, and 5 tagged males recaptured by hook-and-line. Samples were lower than sample sizes for recapture rates of males and females by length because a portion of scales pressed for age determination were not readable.

Age	Traps		Hook-and-line	
	Male (n=7/497)	Female (n=4/552)	Male (n=5/497)	Female (n=13/552)
2	0	0.01	0.007	0.017
3	0.023	0.004	0.01	0.03
4	0.009	0.01	0.009	0.03
5	0.063	0	0	0
6	0	0	0	0
7	0	0	0	0

Table 3.4. Summary of black sea bass that changed sex in 2011 and 2012. Wild black sea bass that were female at first captured (date when tagged) and later recaptured as male (recapture date).

Fish ID	Date when tagged	Recapture date	Days at large	Age (at tagging)	Size (at tagging)	Size (at recapture)
00280	6/15/2011	12/6/2011	174	4	340	348
00701	8/24/2011	5/27/2012	277	4	343	400
00431	7/13/2011	5/26/2012	318	4	355	342
00698	8/24/2011	8/22/2012	364	Scales omitted	317	370
01318	5/23/2011	5/23/2012	366	4	290	351
00453	7/13/2011	8/6/2012	390	Scales omitted	370	450
00161	6/3/2011	7/13/2012	406	4	308	385
01339	6/9/2011	8/12/2012	430	3	307	480

FIGURE CAPTIONS

Figure 3.1 Contrasting the difference between asymptotic and dome-shaped selectivity curves. A simulated example showing (a) age distribution in the catch, as well as two different selectivity curves: (b) a percent saturation curve with age where the oldest size classes are fully selected and (c) a dome-shaped selectivity curve where vulnerability is lowest at very young and old age classes. The assumed population structure under saturation selectivity curves (d) and dome-shaped selectivity curves (e).

Figure 3.2. Size distribution and frequency of black sea bass caught by traps and hook-and-line gear. Size distribution of black sea bass caught in commercial pots (orange bars) and caught by recreational hook and line gear (blue bars). Black sea bass caught in commercial pots ranged in size from 129 – 483 mm, black sea bass caught by hook-and-line gear ranged in size from 94 – 533 mm. Sample size for each gear was 2,430 by angling and 1,517 by potting.

Figure 3.3. The proportion of wild black sea bass males at length caught in commercial traps and by recreational hook-and-line gears. The orange line represents males caught in traps and the blue line represents males caught by recreational hook-and-line. The difference between the proportion male caught in traps and the proportion caught by angling at size was highly significant ($P < 0.0001$). Circle size is proportional to number of observations at a given integer length. Sample sizes for traps and angling was 1,517 and 2,430, respectively.

Figure 3.4. The proportion of wild black sea bass males at age caught in commercial traps and by recreational hook-and-line gears. The proportion of male black sea bass caught at age

by hook-and-line fishing gear (thin line) compared with the proportion male caught at age by commercial traps (thick line).

Figure 3.5. Size distribution and frequency of male (red bars) and female (green bars) black sea bass caught in commercial traps. Female size distribution is overlaid on top of male size distribution (male distribution is behind). Minimum size limit in the commercial fishery is 280 mm (indicated by solid black line).). Males caught in commercial trap ranged in size from 129 – 483 mm, female black sea bass caught in pots ranged in size from 129 – 425 mm.

Figure 3.6. Size distribution and frequency of male (red bars) and female (green bars) black sea bass caught by hook and line gear. Male size distribution is overlaid on top of female distribution (female distribution is behind). The minimum size limit in the recreational fishery is 317 mm (indicated by solid black line). Males caught by hook and line gear ranged in size from 173 – 533 mm, female black sea bass caught in pots ranged in size from 94 – 458 mm.

Figure 3.7. The probability of recapturing wild black sea bass by size, sex, and fishing gear. The probability of recapturing (a) males in traps, (b) females in traps, (c) males by hook-and-line, and (d) females-by-hook and line. Dashed lines indicate the fishery's minimum size limit. A total of 723 and 757 male and female black sea bass were tagged in 2011 and 2012, respectively. Sample sizes of recaptured black sea bass included: 66 males were recaptured in traps, 66 males were recaptured by hook-and-line; 34 females were recaptured in traps; and 91 females were recaptured by hook-and-line. *Low sample sizes. In (c), starred bar on left had 3 of 5 (60%) tagged BSB recaptured and starred bar on right had 1 of 1 (100%) tagged BSB recaptured. In (d) starred bar had 1 of 1 (100%) tagged BSB recaptured.

Figure 3.8. Probability of female black sea bass changing sex from 2011 to 2012. Probability density function for the probability of sex change (female to male) for individuals released in one year (2011) and recaptured the following year (2012). A total of 430 females were tagged in 2011; of these, 15 individuals were recaptured in 2012. Seven of the 15 recaptures had changed sex to male since 2011 and the remaining 8 were still female when recaptured.

Figure 3.9. Probability of sex change at length in wild black sea bass. Length at 50% sex change is 366 mm. Sample size includes all black sea bass that were female when first tagged and recaptured later to verify sex change. Of these, 114 females remained female when recaptured and 8 females were recaptured as males.

Figure 3.1

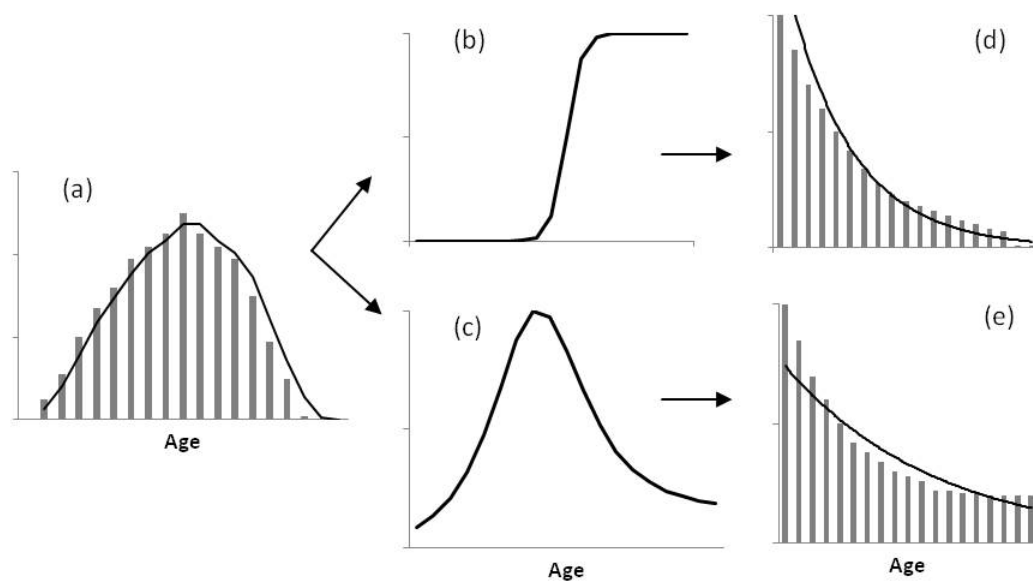


Figure 3.2

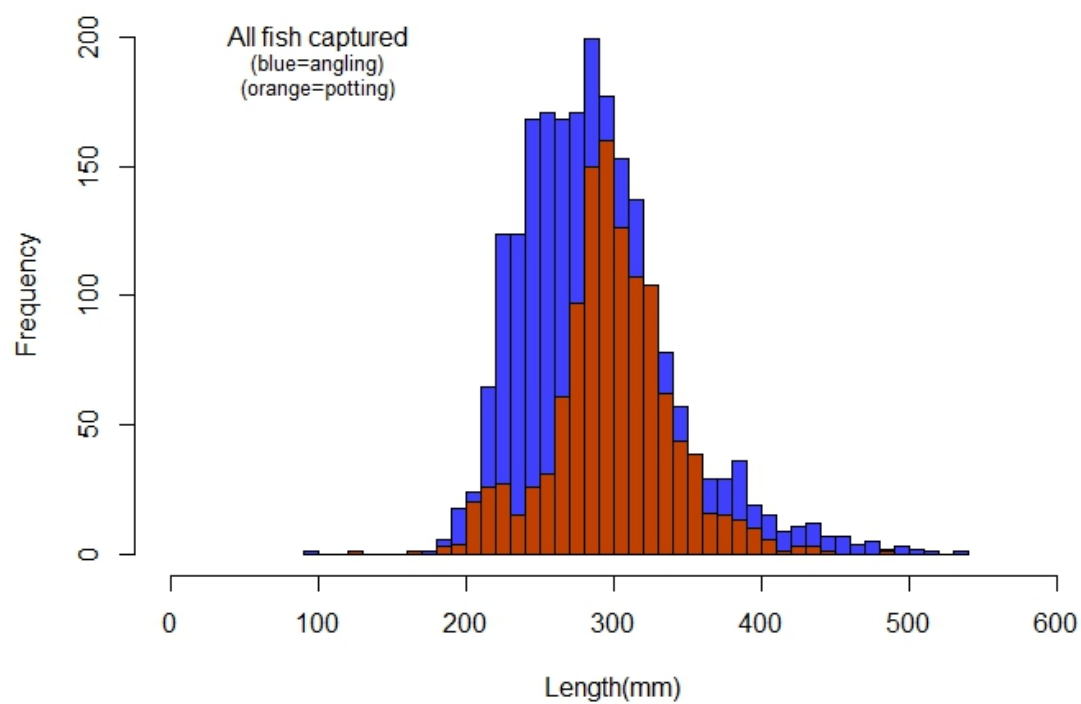


Figure 3.3

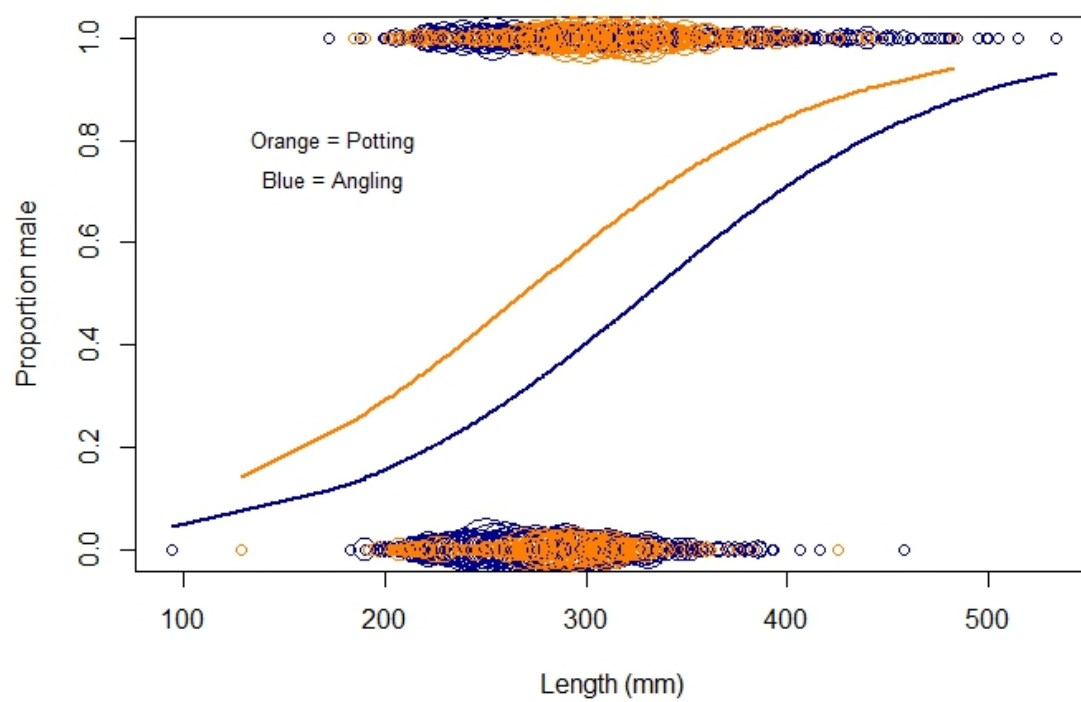


Figure 3.4

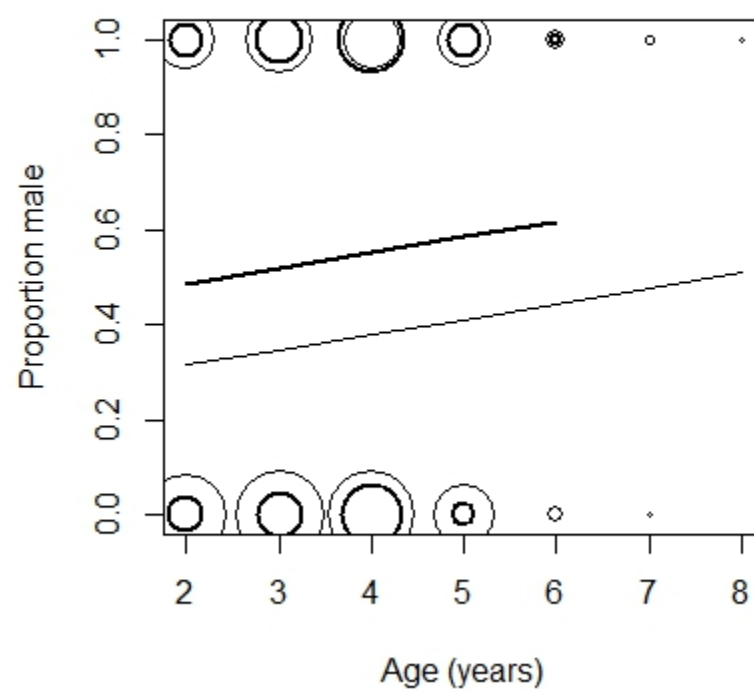


Figure 3.5

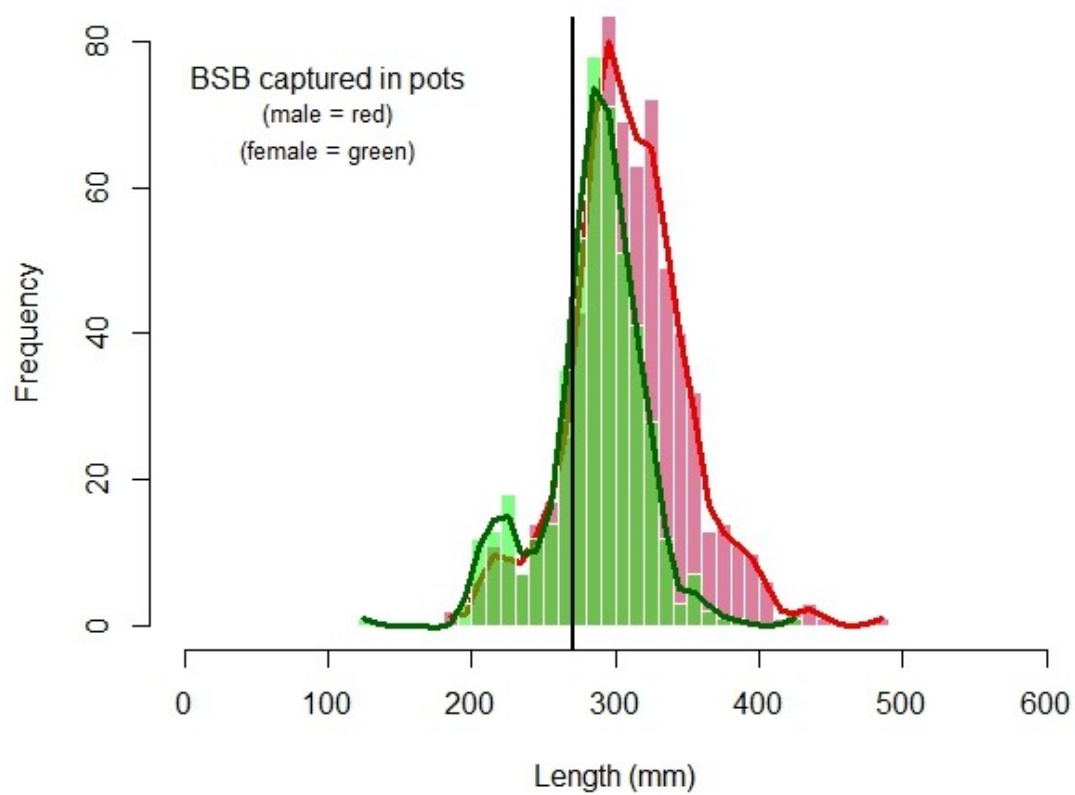


Figure 3.6

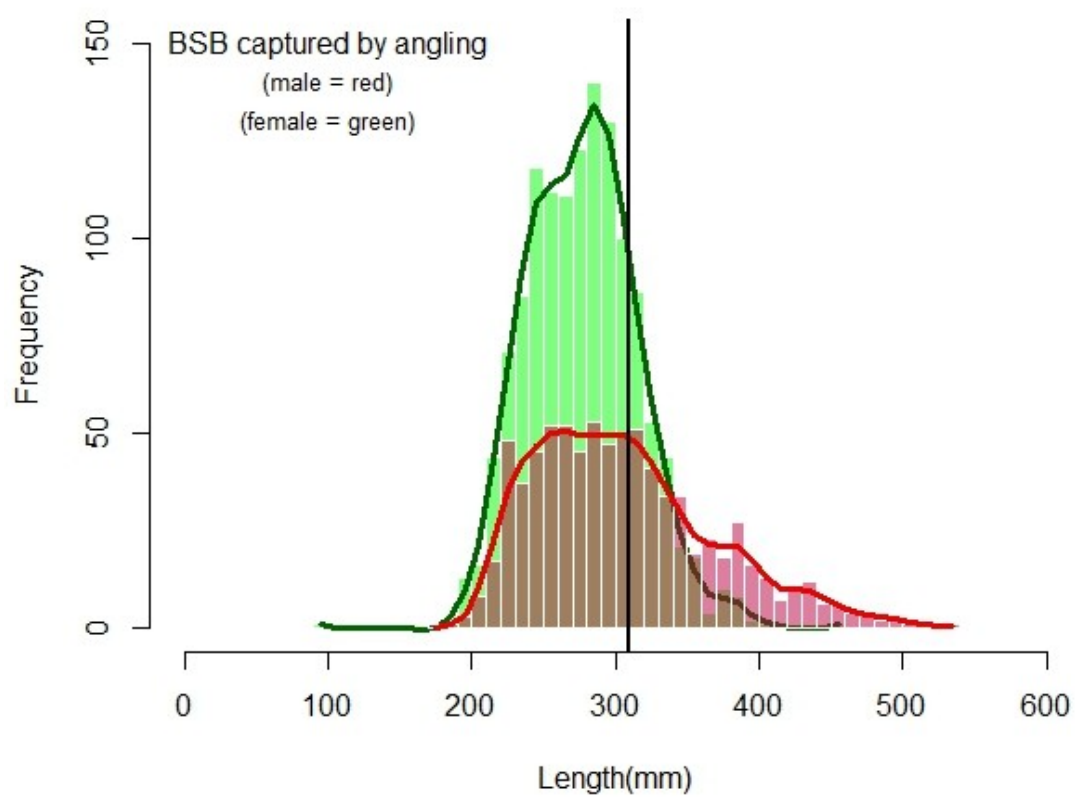


Figure 3.7

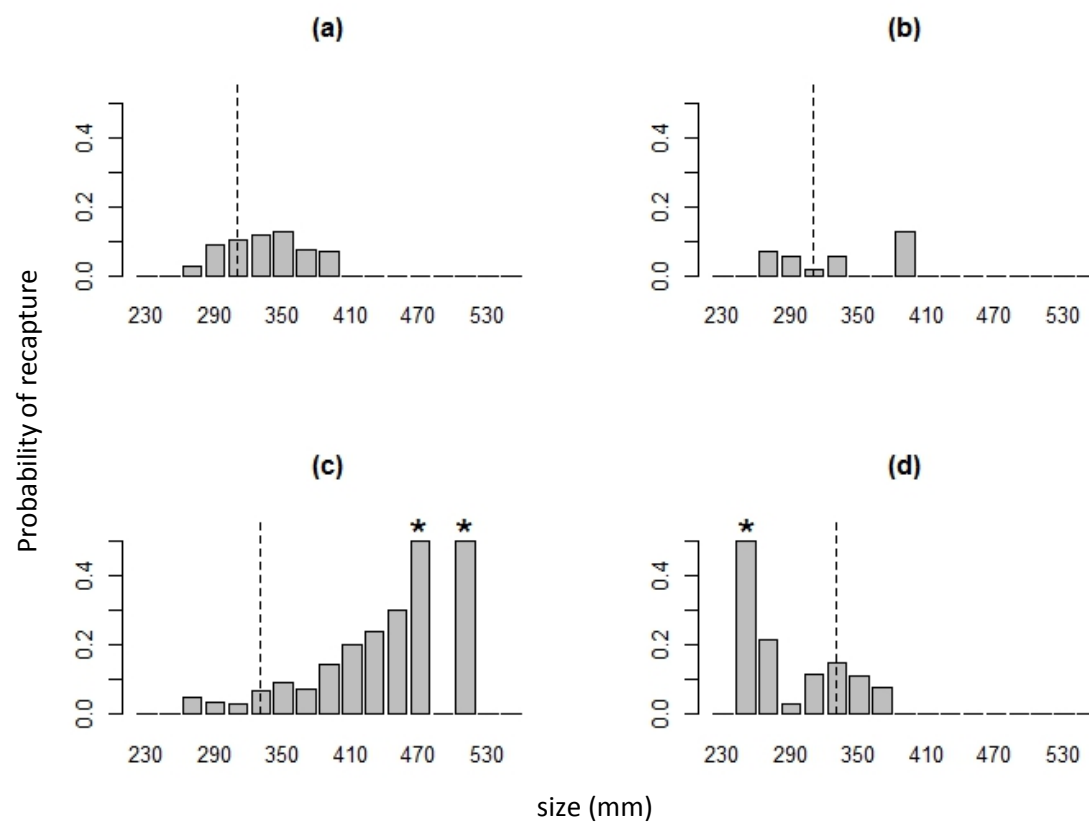


Figure 3.8

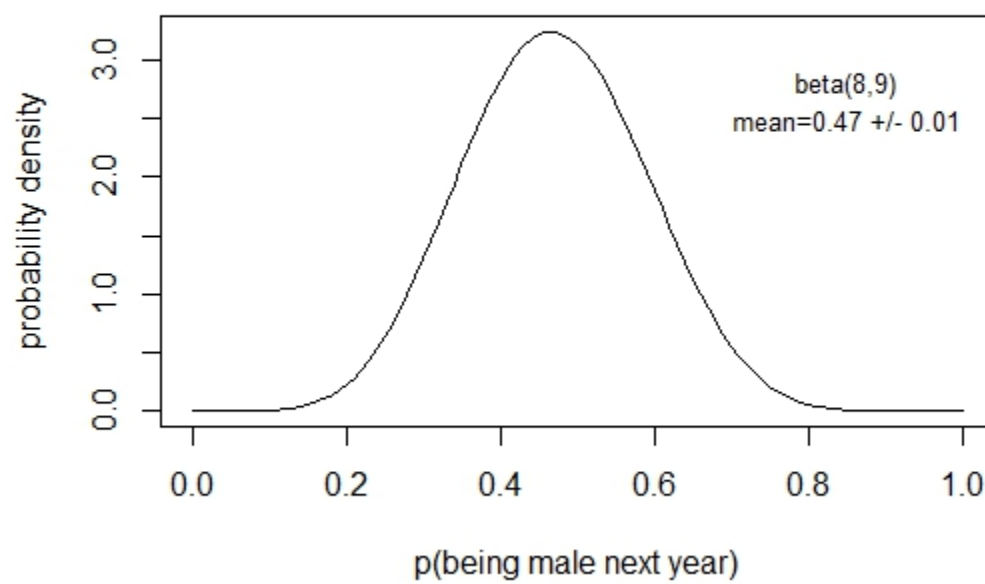
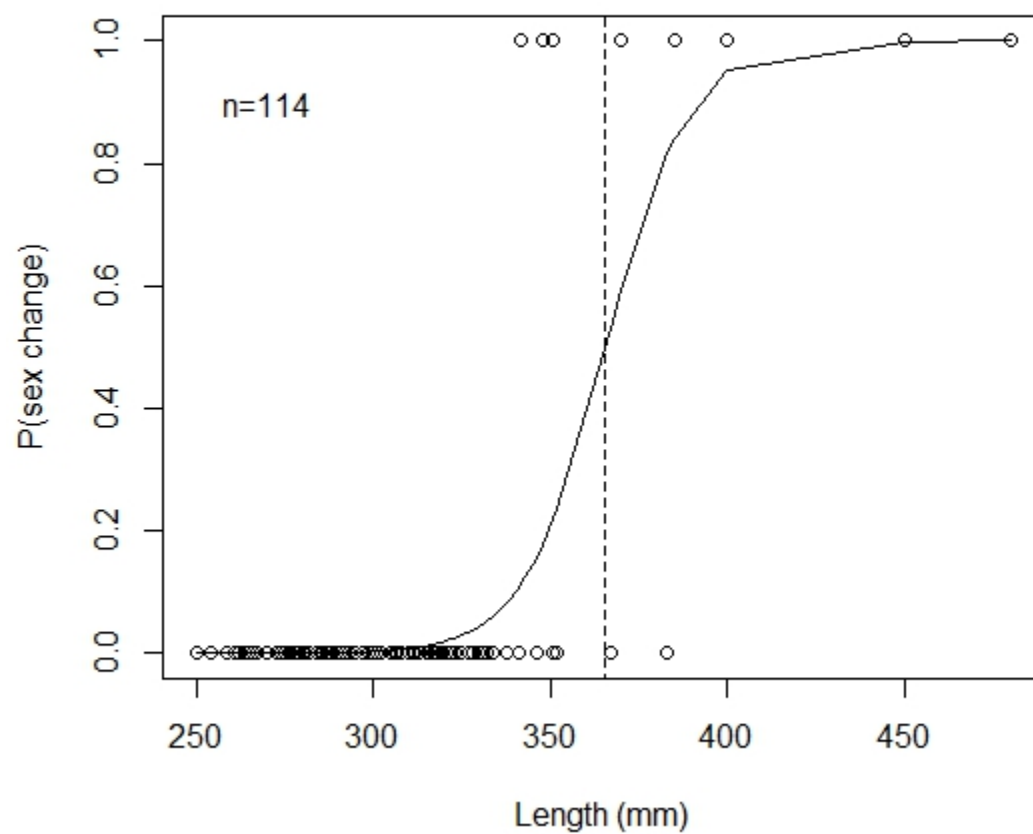


Figure 3.9



– CHAPTER 3 –

GENERAL CONCLUSIONS

The findings from this study showed how sex change is currently handled in stock assessments and provided insight into the effects of fishing on black sea bass in New Jersey. Specifically this study (1) reviewed protogynous hermaphrodite stock assessments on the east coast of the U.S. to assess how sex change is currently addressed in assessment reports, (2) quantified size selectivity curves for males and females caught by hook-and-line and trap fishing gears, and (3) measured sex change in the New Jersey black sea bass population as a function size, age, and season in 2011 and 2012.

Of the 11 stocks summarized, nine stocks calculated spawning stock biomass based on the combined biomass of males and females, a recommendation for exploited hermaphrodite stocks (Brooks et al. 2008). Most assessments, 10 of 11, reported the population sex ratio and size or age at sex change. However, population sex ratio and size or age at sex change data was not always used to gauge the impacts of fishing on the proportion male and the timing of sex change; i.e. only four of 11 stocks reported if the size or age at sex change decreased, and only two of 11 stocks reported any change in the percentage of males with increasing harvest rates. None of the stock assessments measured or estimated sex selectivity of different fishing gears; and yet the stock status of hermaphroditic species was not any worse off than the stock status of gonochoristic species.

Among black sea bass in New Jersey, clear evidence was found of sex selectivity for two gear types. Commercial traps captured a significantly higher proportion of male black sea bass at a given size compared to the proportion of males captured by hook-and-line fishing gear. Overall, male black sea bass were more vulnerable to being recaptured over a wider size range compared to female black sea bass for both types of fishing gear. For recreational hook-and-line fishing gear, the male selectivity curve was asymptotic shaped

which meant the probability of recapture increased with size. For commercial trap fishing gear, however, the male selectivity curve was dome-shaped, indicating that traps were biased toward males of an intermediate size range.

As a function of size, half of female black sea bass expected to change sex did so at 365 mm. All instances of sex change in this study occurred in females 3 – 4 years old. There were no females that completed the sex reversal process during the spawning season; however, eight females did complete the sex change process over the winter season between 2011 and 2012 spawning seasons. Based on the number of tagged females in 2011 that were examined for sex reversal in 2012, it was expected that slightly less than half (47%) of females in 2011 changed sex by the following year.

Currently, no stock assessments measure sex selectivity even though protogynous hermaphrodites probably experience sex-specific capture rates based on the findings from this study. As exploitation rates increase it is likely that the effects of fishing on population dynamics will become more pronounced and hermaphroditic stocks will be at a disadvantage compared to gonochoristic stocks. More tagging studies will be required to assess sex selectivity in other exploited hermaphrodites and additional field observations will help reveal the complex social structure and sex-specific behavior that occurs in sex changing species during the spawning season. The combination of these field efforts will increase our understanding about the effects of fishing on sex changing species.

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