

**Management and assessment of sex changing fishes**

PMAFS protogynous hermaphrodite modeling workshop

August 29-30, 2012

Mikaela M. Provost and Olaf P. Jensen

Institute of Marine & Coastal Sciences

Rutgers University

71 Dudley Rd. – New Brunswick, NJ

[provost@marine.rutgers.edu](mailto:provost@marine.rutgers.edu)

## **Abstract**

Sex changing fish 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 a sex changing fish. For very few hermaphroditic species the effects of fishing on population characteristics is well known, but for the majority of hermaphroditic fishes there are large gaps in knowledge in the scientific literature. Inconsistent strategies for management and lack of information with respect to the effects of fishing, has made it difficult for stock assessments to adequately account for sex change in population models. A review of stock assessments for sex changing species shows that this life history has been addressed in many stock assessments, ranging from verbal acknowledgement that sex change could present a problem to fishery managers to the establishment of marine protected areas. Most assessments ignore sex change entirely in population models, a few evaluate trends in sex ratio or size and age at sex change, and only a handful explicitly model the dynamics of both sexes. Data gaps (e.g., time series of the sex ratio of landings) and limited understanding of the social and environmental cues involved with sex change hinder efforts to account for sex change in stock assessment and management.

## **Introduction**

The phenomenon of sex change is found in a wide variety of animal species and has been the subject of numerous studies addressing its implications for fitness (Smith 1975, Warner 1975, Ghiselin 1969). In contrast, the implication of sex change in fisheries management is much less well known. For economically important species it is especially important to understand the ecological triggers of sex change since harvesting individuals may strongly influence sex change rates and the sex ratio. Fluctuating rates of sex reversal has been predicted to have large impacts on important population parameters; i.e. population growth rate and fertilization rates (Alonzo and Mangel 2004). Ignoring this unique life history is to falsely assume that the response of hermaphroditic fish

to fishing pressure is equivalent to that of gonochordistic (non-sex changing) species, something which has not yet been thoroughly tested and observed in wild populations. Understanding the ways in which harvest impacts sex reversal will help illustrate the current status of exploited fish populations under recent and historical exploitation rates.

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, 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. In ecosystems with patchy resource distribution (e.g. tropical coral reefs), the sex ratio in subpopulations may fluctuate due to isolation and migration between subgroups, changing sex may be favored if the sex ratio is heavily skewed in one direction (e.g. Labridae) (Ross 1990). 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 females 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 broad 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 family, 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 implications of sex change for fisheries stock assessment and management.

Here, we review sex change and its implications for stock assessment and management. In some cases, specific actions have been adopted to compensate for the effects of fishing on sex changing populations; we have reviewed these actions in stock assessments and created general categories to describe how sex change is handled in stock assessments. Previous studies that measured the sex ratio through time show that harvest can impact sex change rates and sex ratios in hermaphroditic populations (Alonzo and Mangel 2004, Hamilton et al. 2007). We hypothesize that heavy exploitation will result in either:

- (a) Strongly skewed sex ratios in favor of females in protogynous populations (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.

We expect either outcome to occur since size limits result in disproportionately high fishing mortality on the 'second sex', i.e. males in protogynous populations and females in protandrous

populations. Although the triggers of sex change have not been entirely disentangled, there is evidence that point to social factors as important variables involved with the triggering of sex change (Benton and Berlinsky 2006, Cole and Shapiro 1995, Warner and Swearer 1991) and so we review these as well. Social dynamics may shift considerably in exploited populations as individuals who escaped the fishery adjust to new size and sex ratios. We also compile literature that shows sex-specific reproductive behavior and sex selectivity are critical components for understanding the effects of fishing on hermaphroditic populations. Fishing gear that preferentially selects males or females will have strong impacts on sex ratios may be more likely to alter social dynamics.

### **Section 1: Ecological aspects of sex changing fishes**

#### Taxonomy 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 broad 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). Broadly distributed across a diverse range of lineages, sex change is particularly common in fishes.

In teleosts sex change is not only common, but is diverse in strategy, having been confirmed in 48 families from thirteen orders, (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 fishes, fertilization is external and the energy required to undergo sex change may be relatively low. 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) (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 in fish: a number of species in Sparidae (porgies) and Pomacentridae (damsel-fishes) 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) (Allsop and West 2004, Blaber et al. 1999). In fishes, sex change is relatively common and diverse.

Hermaphroditism among extant teleosts is buried within clades characterized by gonochronism, and 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 fishes (Scaridae) and deep-water fishes (order Inioi) typically have a patchy distribution and at times, low local population density making it difficult to find suitable mates (Ghiselin 1969, Smith 1975). These factors may promote selection pressures in favor of hermaphroditic sex strategies to ensure individuals are able to produce 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 (*Chlorophthalmus* and *Bathypterois*) and Stomiiformes (*Cyclothone* and *Gonostoma*) are deep-water hermaphroditic species, but within the same order 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).

#### Advantages of sex change: protogyny vs. protandry

The advantage of either protogyny or protandry 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 reproductive value of male and female fish increases at different rates. 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 (Fig 1). The curves, which model reproductive value over the lifespan of a fish, cross at a certain age or length in a 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.

Many factors may influence the slope and curvature of reproductive value or fitness curves. Reproductive behavior, sexual dimorphism, and sex-specific predation impact fitness over time which can change the reproductive ability of males and females at different ages. The shape and form of a reproductive value curve is likely to vary among individuals of a population and clearly varies among species and, therefore, hard to measure and thus rarely estimated directly (Munday

et al 2006). There is a large body of theoretical work detailing the expected timing of sex reversal, sex allocation in hermaphroditic species, and the expected breeding ratios in sex changing populations (Charnov 1982, Warner 1988, Policansky 1987, Leigh et al. 1976), and there is comparatively few field-based or laboratory studies that measure the timing of sex change when exposed to different social conditions.

Ecological conditions that favor sex change depend on a complex system of physical and social factors interacting together. The primary determinants of sex-change strategies (protogynous vs. protandrous) are social organization (hierarchies, aggregations) and mating system (harems, polygamy) which are in turn dependent on resource distribution through space and time (Ross 1990). Social factors are also associated with different mechanisms of sex change, i.e. whether or not sex change is facilitated by suppression, where sex change is triggered when certain individuals are absent, or induction mechanisms, when sex change is triggered by the presence of certain individuals. The most common and well-studied social factors include: whether or not individuals form large or small groups during spawning, if individual fish have the ability to control mating opportunities of other individuals within the group, whether there is opportunity for migration between population patches, and whether groups form rigid social hierarchies. For example, in protandrous suppression, males are only able to reverse their sex in the absence of a dominant female, this type of sex change strategy is characteristic of populations with patchy resource distribution and when migration between patches is limited (e.g. *Amphiprio*) (Ghiselin 1969, Ross 1990). Other combinations of social factors (group size, dominance, hierarchies, migration) and sex change mechanisms (suppression or induction) are associated with either protogynous and protandrous sex change.

The advantage of protogyny versus protandry also depends on the number of mating partners per individual fish. For example, polygamy is expected to occur in protogynous populations where one dominant 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 if the larger fish is female, which is the case in protandrous species. In groups with polygamous mating strategies (i.e. protogynous populations), more zygotes are produced if the largest individual in the spawning group is a male (Ross 1990). Anemonefishes (*Amphiprion pomacentrids*) and the Nassau grouper (*Epinephelus striatus*) 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 Nassau grouper is protogynous and individuals form large spawning aggregations of up to 100,000 (Smith 1972) and have a much higher potential for multiple spawning mates. Large, dominant male Nassau grouper will control the mating opportunities of smaller female grouper. Small male Nassau grouper have relatively low reproductive value compared to similar sized females, and at larger sizes females will undergo sex change in order to maximize their reproductive output as males (Ross 1990). 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 groups: endogenous and exogenous. Endogenous triggers are age- or size- mediated and are said to be 'fixed'. At some 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 or induced by the presence/absence 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). Munday et al. (2006) found that 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 know relatively very little about the intersection of external and internal controls for sex change in most species.

#### 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*), and species in the genera *Anthiinae* and *Cheilodoperca* 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 Mexico to the Gulf of Maine (Shepherd and Nieland 2010). 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). During the spring, black sea bass

north of Cape Hatteras migrate from the continental shelf edge toward their spawning grounds on wrecks and reefs (depths of 50-110 meters) relatively close to shore (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 later 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 change in black sea bass has been studied through a series of 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 likely triggered by the absence of large, dominate male black sea bass. This study was particularly useful because it documented sex change in individual fish. Studies that look at sex change in black sea bass *in situ* identify sex-changing individuals based on tissues in their gonads (Wenner et al. 1986, Cochran and Grier 1991, Hood et al. 1994). In all three of these studies, black sea bass were captured and gonads were prepared for histology. Sex changing fish were defined as those whose gonads had a “proliferation of male tissue into neighboring female lamellae” (Cochran and Grier 1991). Through this method, black sea bass were found to transition at 2-4 years old (Hood et al. 1994) and most individuals

made the transition sometime 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. The experiment by Benton and Berlinsky (2006) followed the succession of sex change by tracking individual fish, but this study was not designed to observe when sex change wild populations. Field studies in which black sea bass are tracked by recapturing tagged individuals will document sex change in wild populations, identify when sex change occurs, and determine how common sex change is in wild populations.

## **Section 2: Management and stock assessment of sex changing fishes**

Management of sex changing fishes presents unique challenges to fisheries managers. In stock assessments for gonochoristic species, the sex ratio is often not measured and spawning stock biomass is based on biomass of mature female fish. 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). 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).

### Reproductive behavior and vulnerability

Although the exact mechanism is unknown, there is evidence that hermaphroditic species that form spawning aggregations tend to have increasingly skewed sex ratios when heavily exploited (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*), both of which are protogynous hermaphrodites and form large aggregations suffered a drop in the proportion of males from 17% to 1% and from 36% to 18%, respectively, over a span of 25 years (Coleman et al. 1996). Whereas red grouper (*Epinephelus morio*), a non-aggregating protogynous hermaphrodite, showed little change in sex ratio over the same time period and under similar fishing pressure. There still remains, much to be learned of gear selectivity on sex in spawning aggregations. Data is scarce when it comes to tracking sex ratios in hermaphroditic species over long periods of time, making it difficult to quantify the effects of fishing on aggregating and non-aggregating hermaphroditic species.

Aggressive behavior, a common feature of reproductively active fishes, may increase vulnerability to the fishery and explain differences in gear selectivity between males and females. In protogynous species, male fish are known to exert aggressive behavior while defending territories (Warner et al. 1975) 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 at a similar length. Videos show that males positioned themselves higher in the water column and Gilmore and Jones (1992) hypothesized that behavior-related selectivity would result in higher fishing mortality on male scamp.

Evidence for behavior-related selectivity has been mostly observational and anecdotal, and very few experiments have been done to test this hypothesis directly. DeVries (2007) tested whether male red porgy (*Pagrus pagrus*), a protogynous hermaphrodite co-occurring in areas with scamp, were more likely to be caught by hook-and line gear before females since, similar to scamp, male red porgy tended to be larger in size and more aggressive than female scamp. In the Gulf of Mexico, DeVries (2007) concluded that hook and line gear was not more selective of males than females, noting that the order in which individual red porgy were caught at all the sampling sites was random with respect to sex and size. Consensus on aggressive behavior and gear selectivity has not been reached and could be remedied by future studies that take into account the existing sex ratio in wild populations. Comparing the sex ratios caught by various fishing gears to the sex ratio in wild populations or looking at recapture rates of tagged fish will illuminate biases in gear selectivity on sex.

Spawning harems and mate choice are inherent aspects of reproductive behavior in sex changing fish and, if interrupted may result in decreased fertilization rates. Harems, defined as groups of females for which mating opportunities are controlled by one dominant male, have been observed in many sex changing species (McCormick et al. 2010, Nemtsov 1985, Moyer and Nakazono 1978), and are likely to be found in other sex changing species whose reproductive behavior is less well understood. Red hind (*Epinephelus guttatus*), for example, form small groups made of a single male with many females during their two week spawning period (Sadovy et al. 1994). Removal of the dominant male has the potential to disrupt the group's social dynamics and may or may not influence fertilization rates within the harem. Although many studies suggest that the selective removal of dominant male individuals will trigger sex reversal in by larger females (Platten et al. 2002, Hawkins and Roberts 2004, Benton and Berlinsky 2006, Nemtsov 1985), the impact of sustained selective removal is unclear. If dominant individuals within the harem are removed at high frequency, as might be expected in heavily exploited populations, is the turnover

time for new females to replace the dominant male fast enough to maintain optimal sex ratios and fertilization rates? Spawning harems are difficult to observe in wild populations especially for deep water species, the effects of selective removal on social dynamics remains unclear.

### Sexual dimorphism and vulnerability

Fish that undergo sex change are more vulnerable to fishing mortality because they exhibit sexual dimorphic growth rates. As an individual undergoes the female-to-male transition, the fish experiences a burst of somatic growth. For protogynous species, growth rates in recently transitioned males are greater than their female counterparts, e.g. parrotfishes (Munday et al. 2004), tropical wrasse (McCormick et al. 2010), and black sea bass (Colburn et al. 2009). Fishing is almost always size-selective and the combination of gear selectivity and size limits results in higher fishing mortality rates on larger individuals. As a consequence, faster growing individuals will enter the fishery more quickly than slow growing individuals (Sinclair et al. 2002). However, fishing gear that has an upper bound size limit (e.g. commercial pots) may not result in biased selectivity toward sex changing fish if sex change occurs in large individuals who have grown beyond the upper bound size limit.

### **Section 3: Population dynamics and stock assessment**

The effects of fishing on hermaphroditic species are rarely random. In exploited populations, gear selectivity on male and female fish is expected to differ if the species is sexually dimorphic and exhibit sex-specific reproductive behavior, characteristics common to protogynous species (Warner et al. 1975, Frickle and Frickle 1977). If the vulnerability of male and female fish is not proportional to the existing sex ratio, then heavy exploitation is expected to alter the sex ratio over time. Since population growth, recruitment, and overall viability of the population are linked to the sex ratio, knowing the sex selectivity of a fishery is important. Specifically, what effect does size and sex selective fishing have on hermaphroditic populations? From predications made in

ecological theory related to fitness and observations in previous studies, hermaphroditic species may respond to fishing pressure in one of two ways. First, will sex changing species have increasingly skewed sex ratios after prolonged exploitation? Or, secondly, will individuals change sex at earlier ages to compensate for lost members that were caught in the fishery? In either scenario: whether a population experiences increasingly skewed sex ratios, or the population maintain an optimal sex ratio by having individuals change sex earlier, the response has serious consequences for hermaphroditic species and their population dynamics.

#### Hypothesis #1: Skewed sex ratios

Sex-selective fishing pressure on hermaphroditic species may result in an increasingly skewed sex ratio. Protogynous populations are characterized by large proportions of female fish at small size classes, and larger fish tend to be male. Fishing gear (e.g. pots, seine, trawl, etc.) is undoubtedly size-selective and targets the largest individuals in the population. Indirectly, selective fishing on large fish results in disproportionately high fishing mortality in male fish in protogynous populations. Not only is the male population expected to experience a greater reduction in abundance compared to female fish, the sex ratio will become increasingly skewed toward females. In protandrous populations, where small size classes are primarily comprised of males, 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 1) have found clear evidence that increasingly skewed sex ratios is associated with high fishing pressure in hermaphroditic species.

In a study by Coleman et al. (1996), the 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, as a result of sustained size-selective fishing mortality. Beets



and Friedlander (1998) looked at red hind (*Epinephelus guttatus*) in the U.S. Virgin Islands and found that when fishing mortality increased, mean length decreased (suggesting a female-dominated population since females are smaller than males) and the sex ratio became more skewed toward females: 15 females for every one male (6% male). When a no-take zone was established to protect spawning grounds fishing mortality decreased, and within seven years the red hind sex ratio was restored to 4:1 (20% male). Platten et al. (2002), Buxton (1993), Wyanski et al. (2000), and Shepherd et al. (2010) also 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 cases the sex ratio shifted to favor the 'first' sex (i.e. female in protogynous species) during periods of heavy fishing pressure.

Pushed to the extreme, overly skewed sex ratios will have negative impacts on the population's overall fitness. How much of a skew in the number of males and females is necessary to negatively affect population growth? What are the warning signs of such consequences? Will fertilization rates drop as one sex becomes scarcer? Most answers to these questions are still unknown for hermaphroditic species.

#### Hypothesis #2: Shift in age at sex change

Alternatively, in response to heavy fishing pressure, hermaphroditic species may preserve an optimal sex ratio by undergoing sex change at earlier ages. Heavy fishing mortality on the 'second sex' (i.e. males in protogynous populations) results in relatively rapid removal of males compared to females. In response, females may undergo sex change at earlier ages to replace males lost to the fishery. The downward shift in the age at which sex change occurs serves as 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). Females that change sex earlier will spend less time producing eggs, which may negatively impact production of zygotes in the long-term.

Hamilton et al. (2007) used historical comparisons to examine the effects of exploitation on sex ratios and the age at which sex change occurs in California sheephead (*Semicossyphus pulcher*), a protogynous hermaphrodite, in south-central California. During the twenty years for which data were collected, commercial and recreational fishing on California sheephead rose unregulated in many sections of the California coast. In other areas of southern California 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). Also, in the exploited populations the percent male in all size classes shifted so that there were more male fish occurring at smaller sizes, further indicating that female California sheephead underwent sex reversal at smaller sizes.

In similar comparative studies of fished and non-fished hermaphroditic populations, age at sex change was lower in exploited populations. The venus tusk fish (*Choerodon venustus*), a protogynous hermaphrodite, is heavily exploited on the Great Barrier Reef. In areas 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 located outside of 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).

### 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, reduced 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 per capita zygote production 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 relatively rare.

The effects of shifting sex ratios on fish recruitment has not been directly measured in field experiments, but theory and simulation studies strongly indicate recruitment will be reduced greatly when the sex ratio increasingly favors one sex (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). Alonzo and Mangel also found that measures of spawners-per-recruit were particularly poor predictors of the effect of fishing on sex changing populations if fertilization rates were not included. In stock assessments, recruitment is usually measured as a function of female spawning stock biomass. Brook et al. (2008) found that if the potential for sperm limitation was strong, biological reference points (e.g.  $B_{MSY}$ ) were better predicted when recruitment was measured as a function of male spawning stock biomass. In most cases, however, the ability to quantify the potential for sperm limitation is difficult and may be unknown for most species. In this

case, recruitment as a function of both male and female spawning stock biomass was 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 few male individuals will decrease the population's 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 size and sex selectivity of fishing gear, there is still expected to be a disproportionate impact of fishing on the terminal sex, i.e. males in protogynous species and females in protandrous species. To increase population fitness and reverse the effects of fishing on the sex ratio and the age at sex change, the type of management plan implemented would be species-specific and depend on mating system (i.e. protogynous or protandrous), social interactions (e.g. harems), and life history patterns (e.g. aggregations, migration). 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. Characteristics of the species and goals of the fishery will influence the type of regulations and management plans.

### Sex change in stock assessments

In stock assessments sex change is handled in a variety of ways. Given that data on sex changing fish is relatively low and the effects of exploitation is unknown, no standard method has been developed and adopted by stock assessment scientists. Some hermaphroditic species are well-studied in comparison to others; the knowledge differential is apparent in stock assessments by the degree to which fishery managers address this unique life history trait in data reports and models.

In this paper we review stock assessments for all sex-changing fish managed on the east coast of the United States from the Gulf of Maine to the Gulf of Mexico and one California stock (California sheephead) for the ways in which sex change was handled. Stock assessments in the North and Mid-Atlantic include black sea bass and northern shrimp, and in the South Atlantic and Gulf of Mexico, stock assessments include: red grouper, black sea bass, red porgy, hogfish, and two stocks of gag (Table 3). All stock assessments were produced by the Mid-Atlantic Fishery Council and South Atlantic Fishery Management Council for the northern and southern species, respectively. The California Department of Fish and Game sponsored the stock assessment for California sheephead.

In general, stock assessments for sex-changing species differed from those for gonochoristic species in one or more of four ways (Table 3).

- (1) Some assessments calculated spawning stock biomass (SSB) from the combined mature biomass of males and females rather than from females alone. Vaughan et al. (1992) suggested that male biomass contributed to the production of recruits and should be incorporated in SSB for hermaphroditic species. Similarly, Brooks et al. (2008) tested this assertion with simulation models and found that when the potential for male contribution to fertilization is unknown, reference points were estimated more closely to the true reference points if SSB combined male and female biomass.

- (2) Some assessments reported the age and length at which 50% of individuals transitioned sex. For a select few of these assessments, historical data on sex ratios were available and comparisons in age at sex change could be made over time as exploitation rates either increased, decreased, or stayed the same.
- (3) A few assessments used population models that explicitly differentiate between males and females, however, most do not.
- (4) For some fisheries, management has been modified to account for the effects of fishing on sex-changing fish. This may include changing the selectivity on sex for certain gear types or establishing protected areas to preserve spawning grounds or spawning aggregations.

Figure 1. 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.

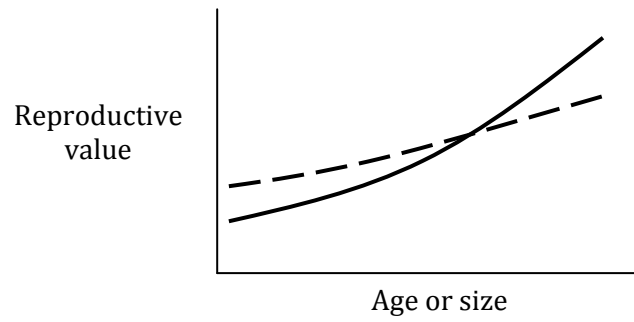


Table 1. Examples of exploitation changing the sex ratio of sex-changing fish

Species	Location	$\Delta$ 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. 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 3. Treatment of sex change within stock assessment models and management

Family name	Species, stock location	Mating system	Is spawning stock biomass estimated for females only or both sexes?	Reports sex ratio at age or length?	Population model differentiates males and females?	Management has been modified to account for sex change?	Citation
Serranidae	Black sea bass <i>Centropristis striata</i> Mid-Atlantic	protogynous	Female + male	No	No	None implemented	Shepherd and Neiland (2010)
	Black sea bass <i>Centropristis striata</i> South Atlantic		Female + male	No	No	None implemented	SAFMC (2005)
	Gag grouper <i>Mycteroperca microlepis</i> Gulf of Mexico		Female (total biomass was also calculated)	Yes -- No change in size and age at transition in 1977-2006. In 2006, length at 50% transition=1100mm, and age at 50% transition=10.8 yrs	No	Increased minimum length (allows more males to escape fishery). Established two marine reserves on spawning aggregation sites.	SAFMC (2006)
	Gag grouper <i>Mycteroperca microlepis</i> South Atlantic		Female + male	Yes -- In 1977, 20% of mature gag were male or transitional; in 2004 only 8% were male or transitional. In 2006, length at 50% transition=1025mm, and age at 50% transition=10.5 yrs	Yes	None implemented	SAFMC (2006)
	Red grouper <i>Epinephelus morio</i> Gulf of Mexico		Female only	No	No	None implemented	SAFMC (2009)
Pandalidae	Northern shrimp <i>Pandalus borealis</i> Gulf of Maine	protandrous	Female + male	No	No	None implemented	Idoine (2006)
Sparidae	Red porgy <i>Pagrus pagrus</i> South Atlantic	protogynous	Female + male	Yes, but no current age or length at 50% transition was given	No	None implemented	SAFMC (2002)
Labridae	Hogfish <i>Lachnoaimus maximus</i> Florida		Female + male	Yes, but no current age or length at 50% transition was given	Yes	None implemented	SAFMC (2004)
	California sheephead <i>Semicossyphus ulcher</i> California		Female + male	Yes, but no current age or length at 50% transition was given	Yes	None implemented	Alonzo et al. (2004)

## References

- Able, K. W., M. P. Fahay, and G. R. Shepherd. 1995. Early life history of black sea bass, *Centropristis striata*, in the Mid-Atlantic Bight and a New Jersey estuary. *Fishery Bulletin* **93**.
- Able, K. W. and L. S. Hales. 1997. Movements of juvenile black sea bass *Centropristis striata* (Linnaeus) in a southern New Jersey estuary. *Journal of Experimental Marine Biology and Ecology* **213**:153-167.
- Allee, W. C. 1931. *Animal aggregations, a study in general sociology*. Univ. of Chicago Press, Chicago.
- Allsop, D. J. and S. A. West. 2003. Constant relative age and size at sex change for sequentially hermaphroditic fish. *Journal of Evolutionary Biology* **16**:921-929.
- Allsop, D. J. and S. A. West. 2004. Sex-ratio evolution in sex changing animals. *Evolution* **58**:1019-1027.
- Alonzo, S. H., T. Ish, M. Key, A. D. MacCall, and M. Mangel. 2008. The importance of incorporating protogynous sex change into stock assessments. *Bulletin of Marine Science* **83**:163-179.
- Alonzo, S. H., M. Key, T. Ish, and A. D. MacCall. 2004. Status of the California Sheephead (*Semicossyphus pulcher*) stock. *California Fish and Game* **1-118**.
- Alonzo, S. H. and M. Mangel. 2004. The effects of size-selective fisheries on the stock dynamics of and sperm limitation in sex-changing fish. *Fishery Bulletin* **102**:1-13.
- Beets, J. and A. Friedlander. 1998. Evaluation of a conservation strategy: a spawning aggregation closure for red hind, *Epinephelus guttatus*, in the US Virgin Islands. *Environmental Biology of Fishes* **55**:91-98.
- Benton, C. B. and D. L. Berlinsky. 2006. Induced sex change in black sea bass *Journal of Fish Biology* **69**:1491-1503.
- Berlinsky, D., J. C. Taylor, R. A. Howell, and T. M. Bradley. 2004. The effects of temperature and salinity on early life stages of black sea bass *Centropristis striata*. *Journal of the World Aquaculture Society* **35**:335-344.
- Blaber, S. J. M., D. T. Brewer, D. A. Milton, Gede Sedana Merta, D. Efizon, G. Fry, and T. van der Velde. 1999. The Life History of the Protandrous Tropical Shad *Tenualosa macrura* (Alosinae: Clupeidae): Fishery Implications. *Estuarine, Coastal and Shelf Science* **49**:689-701.
- Bowen, B. W. and J. C. Avise. 1990. Genetic structure of Atlantic and Gulf of Mexico populations of sea bass, menhaden, and sturgeon: influence of zoogeographic factors and life-history patterns. *Marine Biology* **107**:371-381.
- Brooks, E. N., K. W. Shertzer, T. Gedamke, and D. S. Vaughan. 2008. Stock assessment of protogynous fish: evaluating measures of spawning biomass used to estimate biological reference points. *Fisheries Bulletin* **106**:12-23.
- Buxton, C. D. 1993. Life history changes in exploited reef fishes on the east coast of South Africa. *Environmental Biology of Fishes* **36**:47-63.
- Carter, J., F. J. Marrow, and V. Pryor. 1994. Aspects of the ecology and reproduction of Nassau grouper, *Epinephelus striatus*, off the coast of Belize, Central America. *Proc. Gulf of Caribbean Fisheries Institute* **43**:64-110.
- Chapman, R. W., G. R. Sedberry, C. C. Koenig, and B. M. Eleby. 1999. Stock identification of gag, *Mycteroperca microlepis*, along the southeast coast of the United States. *Marine Biotechnology* **1**:137-146.
- Charnov, E. L. 1982. *The Theory of Sex Allocation*. University Press, Princeton.
- Charnov, E. L. and P. J. Anderson. 1989. Sex change and population fluctuations in Pandalid Shrimp. *The American Naturalist* **134**:824-827.
- Cochran, R. C. and H. J. Grier. 1991. Regulation of sexual succession in the Protogynous Black Sea Bass, *Centropristis striatus* (Osteichthyes: Serranidae). *General and Comparative Endocrinology* **82**:69-77.

- Colburn, H. R., A. B. Walker, and D. L. Berlinsky. 2009. The effects of temperature on sex differentiation and growth of black sea bass (*Centropristis striata* L.). *Aquaculture Research* **40**:729-736.
- Cole, K. S. and D. Y. Shapiro. 1995. Social facilitation and sensory mediation of adult sex change in a cryptic, benthic marine goby *Journal of Experimental Marine Biology and Ecology* **186**:65-75.
- Coleman, F. C., C. C. Koenig, and L. A. Collins. 1996. Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Environmental Biology of Fishes* **47**:129-141.
- Colin, P. L. 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces, Serranidae) and its relationship to environmental conditions. *Environmental Biology of Fishes* **34**:357-377.
- de Mitcheson, Y. S. and M. Liu. 2008. Functional hermaphroditism in teleosts. *Fish and Fisheries* **9**:1-43.
- DeVries, D. A. 2007. No evidence of bias from fish behavior in the selectivity of size and sex of protogynous red porgy (*Pagrus pagrus*, Sparidae) by hook-and-line gear. *Fisheries Bulletin* **105**:582-587.
- Erisman, B. E. and P. A. Hastings. 2011. Evolutionary Transitions in the Sexual Patterns of Fishes: Insights from a Phylogenetic Analysis of the Seabasses (Teleostei: Serranidae). *Copeia* **2011**:357-364.
- Fautin, D. G. 1991. The Anemonefish Symbiosis: What is Known and What is Not. *Symbiosis* **10**:23-46.
- Frame, D. W. and S. A. Pearce. 1973. A survey of the sea bass fishery. *Marine Fisheries Review* **35**:19-26.
- Frickle, H. and S. Frickle. 1977. Monogamy and sex change by aggressive dominance in coral reef fish. *Nature* **266**:830-832.
- Ghiselin, M. T. 1969. The evolution of hermaphroditism among animals. *The Quarterly Review of Biology* **44**:189-208.
- Gilmore, R. G. and R. S. Jones. 1992. Color variation and associated behavior in the epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* Jordan and Swain. *Bulletin of Marine Science* **51**:83-103.
- Götz, A., S. E. Kerwath, C. G. Attwood, and W. H. H. Sauer. 2008. Effects of fishing on population structure and life history of roman *Chrysolephus laticeps* (Sparidae). *Marine Ecology Progress Series* **362**:245-259.
- Hamilton, S. L., J. E. Caselle, J. D. Standish, D. M. Schroeder, M. S. Love, J. A. Rosales-Casian, and O. Sosa-Nishizaki. 2007. Size-selective harvesting alters life histories of a temperate sex-changing fish. *Ecological Applications* **17**:2268-2280.
- Hawkins, J. P. and C. M. Roberts. 2004. Effects of fishing on sex-changing Caribbean parrotfishes. *Biological Conservation* **115**:213-226.
- Heppell, S. S., S. A. Heppell, F. C. Coleman, and C. C. Koenig. 2006. Models to compare management options for a protogynous fish. *Ecological Applications* **16**:238-249.
- Hines, A. H., P. R. Jivoff, P. J. Bushmann, J. Montfrans, S. A. Reed, D. L. Wolcott, and T. G. Wolcott. 2003. Evidence for sperm limitation in the blue crab, *Callinectes sapidus*. *Bulletin of Marine Science* **72**:287-310.
- Hood, P. B., M. F. Godcharles, and R. S. Barco. 1994. Age, growth, reproduction, and the feeding ecology of black sea bass, *Centropristis striata* (Pisces, Serranidae), in the eastern Gulf of Mexico. *Bulletin of Marine Science* **54**:24-37.
- Idoine, J. S. 2006. Stock assessment of northern shrimp North Atlantic Fishery Management Council.
- Iglesias, S. P., D. Y. Sellos, and K. Nakaya. 2005. Discovery of a normal hermaphroditic chondrichthyan species: *Apristurus longicephalus*. *Journal of Fish Biology* **66**:417-428.
- Iwasa, Y. 1991. Sex change evolution and cost of reproduction. *Behavioral Ecology* **2**:56-68.

- Lavenda, N. 1949. Sexual difference and normal protogynous hermaphroditism in the Atlantic sea bass, *Centropristes striatus*. *Copeia* **3**:185-194.
- Leigh, E. G., E. L. Charnov, and R. R. Warner. 1976. Sex ratio, sex change, and natural selection. *Proceedings of the National Academy of Sciences* **73**:3656-3660.
- Lessios, H. A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean - what have we learned. *Annual Review of Ecology and Systematics* **19**:371-393.
- Levitan, D. R. 1992. Community structure in times past - influence of human fishing pressure on algal urchin interactions *Ecology* **73**:1597-1605.
- Mank, J. E., D. E. L. Promislow, and J. C. Avise. 2006. Evolution of alternative sex-determining mechanisms in teleost fishes. *Biological Journal of the Linnean Society* **87**:83-93.
- McCormick, M. I., C. A. Ryan, P. L. Munday, and S. P. W. Walker. 2010. Differing Mechanisms Underlie Sexual Size-Dimorphism in Two Populations of a Sex-Changing Fish. *Plos One* **5**.
- McGovern, J. C., D. M. Wyanski, and O. Pashuk. 1998. Changes in the sex ratio and size at maturity of gag, *Mycteroperca microlepis*, from the Atlantic coast of the southeastern United States during 1976-1995. *Fisheries Bulletin* **96**:797-807.
- Morse, W. W. 1981. Reproduction of the summer flounder, *Paralichthys dentatus* (L.). *Journal of Fish Biology* **19**:189-203.
- Moyer, J. T. and A. Nakazono. 1978. Protandrous Hermaphroditism in six species of the Anemonefish Genus *Amphiprion* in Japan. *Japanese Journal of Ichthyology* **25**:101-106.
- Munday, P. L., P. M. Buston, and R. R. Warner. 2006. Diversity and flexibility of sex-change strategies in animals. *Trends Ecol Evol* **21**:89-95.
- Munday, P. L., A. L. Hodges, J. H. Choat, and N. Gust. 2004. Sex-specific growth effects in protogynous hermaphrodites. *Canadian Journal of Fisheries and Aquatic Sciences* **61**:323-327.
- Musick, J. A. and L. P. Mercer. 1977. Seasonal distribution of black sea bass, *Centropristis striata*, in the Mid-Atlantic Bight with comments on the ecology and fisheries of the species. *Transactions of the American Fisheries Society* **106**:12-25.
- Nemtsov, S. C. 1985. Social control of sex change in the Red Sea razorfish *Xyrichtys pentadactylus* (Teleostei, Labridae). *Environmental Biology of Fishes* **14**:199-211.
- Olsen, D. A. and J. A. LaPlace. 1979. A study of a Virgin Islands grouper fishery based on breeding aggregation. *Proceedings of the Gulf of Caribbean Fisheries Institute* **31**:130-144.
- Platten, J. R., I. R. Tibbetts, and M. J. Sheaves. 2002. The influence of increased line-fishing mortality on the sex ratio and age of sex reversal of the venus tusk fish. *Journal of Fish Biology* **60**:301-318.
- Policansky, D. 1982. Sex change in plants and animals. *Annual Review of Ecology and Systematics* **13**:471-495.
- Policansky, D. 1987. Evolution, sex and sex allocation. *Bioscience* **37**:466-468.
- Ross, R. M. 1990. The evolution of sex-change mechanisms in fishes. *Environmental Biology of Fishes* **29**:81-93.
- Ross, R. M., G. S. Losey, and M. Diamond. 1983. Sex Change in a Coral-Reef Fish: Dependence of Stimulation and Inhibition on Relative Size. *Science* **221**:574-575.
- Sadovy, Y. 1994. Grouper stocks of the western central Atlantic: the need for management and mangement needs. *Proceedings of the Gulf of Caribbean Fisheries Institute* **43**:43-64.
- Sadovy, Y., A. Rosario, and A. Roman. 1994. Reproduction in an aggregating grouper, the red hind, *Epinephelus guttatus*. *Environmental Biology of Fishes* **41**:269-286.
- SAFMC (South Atlantic Fishery Management Council). 2004. Complete stock assessment report of SEDAR 6 (Southeast Data, Assessment, and Review) for hogfish snapper, assessment report 2. Charleston, South Carolina.
- SAFMC (South Atlantic Fishery Management Council), 2002. Stock assessment of South Atlantic red porgy, report of the first SEDAR (Southeast Data, Assessment, and Review). South Atlantic Fishery Management Council, Charleston, South Carolina.

- SAFMC (South Atlantic Fishery Management Council), 2006. Report of Stock Assessment: Black sea bass, Southeast Atlantic, SEDAR 10 (Southeast Data, Assessment, and Review), Update Process #1. Beaufort, North Carolina.
- SAFMC (South Atlantic Fishery Management Council), 2006. Report of Stock Assessment: Gulf of Mexico Gag Grouper, SEDAR 10 (Southeast Data, Assessment, and Review), Stock Assessment report 2. Charleston, South Carolina.
- SAFMC (South Atlantic Fishery Management Council), 2006. Stock Assessment for Gag Grouper, SEDAR 10 (Southeast Data, Assessment, and Review), Stock Assessment report 1. Charleston, South Carolina.
- SAFMC (South Atlantic Fishery Management Council), 2009. Stock Assessment for Red Grouper in the Gulf of Mexico, SEDAR update (Southeast Data, Assessment, and Review). Miami, Florida.
- Shapiro, D. Y. 1979. Social behavior, group structure, and the control of sex reversal in hermaphroditic fish. *Advances in the Study of Behavior* **10**:43-102.
- Shapiro, D. Y., Y. Sadovy, and M. A. McGehee. 1993. Periodicity of sex change and reproduction in the red hind, *Epinephelus guttatus*, a protogynous grouper. *Bulletin of Marine Science* **53**:1151-1162.
- Shepherd, G. 1991. Meristic and Morphometric Variation in Black Sea Bass North of Cape Hatteras, North Carolina. *North American Journal of Fisheries Management* **11**:139-148.
- Shepherd, G. R. and J. Nieland. 2010. Black sea bass stock assessment update. National Oceanic & Atmospheric Administration.
- Shepherd, S. A., J. B. Brook, and Y. Xiao. 2010. Environmental and fishing effects on the abundance, size and sex ratio of the blue-throated wrasse, *Notolabrus tetricus*, on South Australian coastal reefs. *Fisheries Management and Ecology* **17**:209-220.
- Sinclair, A. F., D. P. Swain, and J. M. Hanson. 2002. Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. *Canadian Journal of Fisheries and Aquatic Sciences* **59**:361-371.
- Smith, C. L. 1972. A spawning aggregation of Nassau Grouper, *Epinephelus striatus* (Bloch). *Transactions of the American Fisheries Society* **101**:257-261.
- Smith, C. L. 1975. The evolution of hermaphroditism in fishes. In: H. Reinboth (ed.) *Inter-sexuality in the Animal Kingdom*, Springer-Verlag, Heidelberg:pp. 295-310.
- Vaughan, D. S., G. R. Huntsman, C. S. Manooch III, F. C. Rohde, and G. F. Ulrich. 1992. Population characteristics of the red porgy *Pagrus pagrus* off the Carolinas. *Bulletin of Marine Science* **50**:1-20.
- Warner, R. R. 1975. The adaptive significance of sequential hermaphroditism in animals. *The American Naturalist* **109**:61-82.
- Warner, R. R. 1988. Sex change and the size advantage model *Trends in Ecology & Evolution* **3**:133-136.
- Warner, R. R. 1988. Sex change in fishes: hypotheses, evidence, and objections. *Environmental Biology of Fishes* **22**:81-90.
- Warner, R. R., D. R. Robertson, and E. G. Leigh. 1975. Sex Change and Sexual Selection. *Science* **190**:633-638.
- Warner, R. R. and S. E. Swearer. 1991. Social control of sex change in the bluehead wrasse, *Thalassoma bifasciatum* (Pisces, Labridae). *Biological Bulletin* **181**:199-204.
- Wenner, C. A., W. A. Roumillat, and C. W. Waltz. 1986. Contributions to the life history of black sea bass, *Centropristis striata*, off the southeastern United States. *Fisheries Bulletin* **84**:723-741.
- Wyanski, D. M., D. B. White, and C. A. Barans. 2000. Growth, population age structure, and aspects of the reproductive biology of snowy grouper, *Epinephelus niveatus*, off North Carolina and South Carolina. *Fishery Bulletin* **98**:199-218.