Modeling Protogynous Hermaphrodite Fishes Workshop

August 29-30, 2012

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ABSTRACT

A workshop was convened on August 29-30, 2012 that addressed the need for improved assessment approaches of protogynous fish. The assessment of protogynous fish is challenging because current methods are limited in their ability to address species that operate first as female and then as male during different life stages. Because males occur secondarily in the protogynous species, males are larger and therefore targeted by the fishing industry. Fishing pressure on the larger males can skew sex ratios, potentially causing the age or size at transition to occur in younger or smaller fish. Further, available fishery dependent and independent data may be limited, making it difficult to provide sex-at-age or sex-at-length to support assessment analyses. Workshop participants collaborated to develop recommendations for improving data collection and modeling approaches, and to identify additional research needs for better understanding the effects of fisheries on protogynous hermaphroditic populations.

INTRODUCTION

On August 29 and 30, 2012, the Mid-Atlantic Fisheries Management Council (MAFMC) and the Partnership for Mid-Atlantic Fisheries Science (PMAFS) held a workshop on modeling protogynous hermaphrodite fishes. The workshop addressed the need for improved assessment approaches for protogynous fish, as well as data needs and modeling strategies.

The assessment of protogynous fish is particularly challenging because the same fish may operate as a male or female during different life stages. This poses challenges, for example, in the definition of spawning stock biomass (Brooks et al. 2008), the possible need for sex-specific mortality rates (Heppell et al. 2006), and the formulation of sex-specific models or models incorporating sex change (e.g., Shepherd and Idoine 1993; Armsworth 2001; Alonzo and Mangel 2004), among others. The limited information to describe this life-history strategy in black sea bass contributed to its classification as a data poor species (Shepherd 2009a). The collection of fishery dependent and independent datasets which provide functional sex-at-age or sex-at-length is particularly challenging, and may in fact prove infeasible. In addition, poorly understood behavioral processes may have important consequences for population dynamics. For example, in a laboratory study, removal of mature male black sea bass appeared to stimulate sex change in the remaining females (Benton and Berlinsky 2006). The extent to which this process may offset male-biased fishing mortality in the wild is unknown. Therefore, developing improved assessment models that are robust to assessing protogynous fish in these data limited situations is essential.

To address the need for improved assessment approaches for protogynous fish, the workshop brought together a range of fisheries scientists to provide an overview of current and innovative methods for assessing protogynous fish, and to discuss data needs and modeling strategies. The workshop objectives were to:

1. Describe and define the types of databases needed to model protogynous fish population dynamics.
2. Examine current and innovative methods for modeling the dynamics of protogynous fish, including methods for deriving biological reference points.
3. Describe the pros and cons of applying the different modeling approaches discussed under objective 2.
4. Produce research recommendations on the:
5. Types of data collections needed to more realistically model the population dynamics of protogynous fishes.
6. Future work needed to identify modeling strategies that will be robust to various data limitations or deficiencies.

The recommendations resulting from this workshop are intended to improve the assessment and management of all protogynous fishes.

PRESENTATIONS

The workshop began with an overview of the workshop objectives and agenda from Jessica Coakley. Following the introduction of participants, the workshop chairs, Kyle Shertzer and Gary Shepherd, provided some opening remarks. The first presenter, Rich McBride, summarized the diversity of sex determinism and mating systems in fish. Mikaela Provost and Olaf Jensen provided a literature review of how hermaphroditic fish species have been addressed in stock assessments. Selina and Scott Heppell outlined the problems with using traditional methods to assess hermaphroditic fish, and offered parameters to consider when modeling and managing sex changing fish. Marcel Reichert provided an overview of the survey methods and fishery independent data collected to monitor reef fish in the southeast U.S. Atlantic. Scott Heppell also provided some insight on how male-mating strategies might influence hermaphroditic population dynamics and fisheries management. Each presentation is summarized below. Where there are multiple authors for the presentation, an asterisk next to an author's name indicates the workshop presenter.

THE HOW AND WHY OF HERMAPHRODITISM

R. MCBRIDE*, M. WUENSCHEL, G. FITZHUGH

This presentation was a broad overview of sex determinism and the diversity of patterns that have emerged in many fish species. The sex of a fish can be gonochoristic (a single sex, determined by genetics or environmental factors), it could express both the female and male sex organs at one time (simultaneous hermaphroditism), or it could change sex – either from male to female (protandry), or from female to male (protogyny). Sexuality of such fishes can be simple or complex. Moe's reproductive scheme for red grouper (1969) is an example of a simple process, where all individuals mature first as female and change sex to males later in life (i.e., monandry). More complex examples include populations that have more than one male type (i.e., diandry = gonochores and sex changers), have males that changed sex but never functioned as a female (i.e., prematurational sex change), or have individuals that can change sex more than once. Protogyny is by far the most common form of hermaphroditism, but it is certainly not the only form.

Black Sea Bass
Photo Credit: Michael Eversmier

Beyond the individual sex of the fish, there are also various mating systems for different hermaphroditic species. Clownfish are monogamous, but many hermaphroditic species spawn in aggregations. Two different types of aggregations can occur, a harem or a lek. A harem is a defended territory with one mating male and several females. This mating system is common with protogyny. In a harem, removal of a dominant male will cause another male to take over the territory or another female to change sex. A lek is a spawning arena of several males. The females come and go from the area. Both a harem and lek are polygamous mating systems, causing the local sex ratio to be skewed – but the opposite way in each case. As such, sex ratio data on the spawning grounds may be a useful index of population status.

Although hermaphroditism is more prevalent in some taxa than others, the expression of hermaphroditism varies considerably between species even within the same family. For example, some parrotfish (Scaridae) form harems

and other do not; some species are monandric, whereas other species are diandric (Streelman et al. 2002). Efforts to understand the patterns and processes of hermaphroditism are emerging. Different patterns among parrotfishes are related to habitat and evolutionary history (Streelman et al. 2002). In a more general way, the sex order and timing of a sex change occurs when the reproductive advantage of one sex exceeds the other (e.g., the size-advantage model; Warner 1988).

Hogfish (*Lachnolaimus maximus*) is a good example of monandric hermaphroditism. Hogfish are female at their first maturation, but will undergo a sex change to male if they live long enough (post-maturational protogyny). Sexes are dimorphic and dichromatic, meaning the size and coloring of the female and male are distinct. In addition to these visual cues, gonad histology has been used to show that it takes several months to change sex completely (McBride and Johnson 2007). Hogfish use a haremic mating system, defending their territory (Munoz 2010) and spawning with several females per day for weeks or months (Colin 1982). Hogfish demographics are spatially dynamic. In shallower waters, they change sex at much smaller ages and sizes, in association with higher fishing pressure and episodic red tide events (McBride and Richardson 2007; Collins and McBride 2011). This demonstration of higher mortality in association with sex change at younger ages and smaller sizes is consistent with the size-advantage model (McBride and Johnson 2007; Collins and McBride 2011). The effects of sex change and fecundity on calculations of age-specific spawning stock biomass and egg production are significant (McBride et al. 2008).

Like the hogfish, gag grouper (*Mycteroperca microlepis*) are also protogynous and monandric with post-maturational dichromatic characteristics, but the gag show evidence of leking (Gilmore and Jones 1992; Koenig et al. 1996). Gag spawning sites are high relief outer shelf relic reefs tracts. The mating system is poorly understood, but the small males are thought to be reproductively disadvantaged. Because gag spawning is aggregated on the outer continental shelf, this species is a good example of the challenges inherent in designing a monitoring program of sex ratios, fish sizes, and reproductive potential for many hermaphroditic species. Sex ratios of dichromatic species can be monitored with simple visual observations of landed fish, but only if a strong link between dichromatic traits and sexuality is established, and if these data are collected with a spatial context, so as to disaggregate the landings into spawning areas.

Black sea bass (*Centropristis striata*) are protogynous hermaphrodites, monandric, and possibly lek forming. Components of the populations appear to be both post- and pre-maturational, suggesting complex social dynamics on spawning reefs, likely to consist of females, subordinate and dominant males. They are dimorphic and dichromatic, but these physical characteristics have not been demonstrated to be diagnostic, so there may be no simple external character to distinguish females and males. Black sea bass have regional variations in movement, size, age, and reproductive patterns, which demands spatial resolution for monitoring this species.

In sum, hermaphroditic species exhibit much biological complexity: sexuality (sex order, timing, simple or complex), mating system (sex ratio in the population, mate choice, and secondary characteristics), and reproductive potential (egg or sperm fecundity). Recent research has clarified this diversity and identified both constraints and promising avenues for monitoring practices. Continued investigation is warranted because these biological inputs can be useful for assessing hermaphroditic species.

USE OF SEX CHANGE CONSIDERATIONS IN STOCK ASSESSMENTS

M. PROVOST* AND O. JENSEN

This presentation reviewed several case studies to show the importance of knowing the sex ratio and size at transition for protogynous hermaphroditic populations. The negative consequences of a skewed sex ratio and downward trend on size at transition were also discussed. It also provided a review of how hermaphroditic species are treated in stock assessments.

Sex Ratio

In protogynous species males occur at a larger size, where the fishery tends to focus their efforts. For some protogynous species, the result is a skewed sex ratio or a compensatory response of the females by transitioning to the male sex at an earlier age or size. Fishing pressure increasingly skews sex ratios (Table 1) and can cause a downward shift in the age at transition (Table 2).

Coleman et al. (1996) examined the reproductive styles of shallow water groupers in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. Gag (*Mycteroperca microlepis)* and scamp (*Mycteroperca phenas),* both of which are protogynous hermaphrodites and form large aggregations had decreases in the proportion of males from 17 percent to one percent and from 36 percent to 18 percent, 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.

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

Species	Location	Δ proportion male	Citation
Gag (*Mycteroperca microlepis*)	Gulf of Mexico	17% to 1%	Coleman et al. (1996)
Scamp (*Mycteroperca phenax*)	Gulf of Mexico	36% to 18%	Coleman et al. (1996)
California sheephead (*Semicossyphus pulcher*)	California	25% to 20%	Hamilton et al. (2007)
Blue-throated wrasse (*Notolabrus tetricus*)	South Australia	10% to 5%	Shepherd et al. (2010)
Snowy grouper (*Epinephelus niveatus*)	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	Δ in age or size	Citation
California sheephead (*Semicossyphus pulcher*)	California	-240 mm	Hamilton et al. (2007)
Venus tusk fish (*Choerodon venustus*)	Great Barrier Reef, Australia	-409 mm	Platten et al. (2002)
Roman (*Chrysoblephus laticeps*)	South Africa	-2 years, 4 months	Götz et al. (2008)
Parrotfish (*Sparisoma viride*) (*Sparisoma rubripinne*) (*Scarus taeniopterus*) (*Sparisoma aurofrenatum*) (*Scarus iserti*)	Caribbean Islands	-7 mm -8 mm -6 mm -5 mm -4 mm	Hawkins and Roberts (2004)
Shrimp (*Pandalus borealis*)	Alaska	-2 mm	Charnov and Anderson (1989)

Gag and scamp form large spawning aggregations. A social trigger causes a sex change in both of these species (Ross et al. 1983; Coleman et al. 1996; Benton and Berlinsky 2006). For the trigger to occur, these species need to be surrounded by both males and females. Males and females co-occur only during the spawning aggregation, which lasts over a short time period. For gag and scamp, they have a short timeframe to evaluate sex ratio and change sex, versus species like red grouper where males and females co-occur much longer.

Beets and Friedlander (1998) studied a spawning aggregation closure for red hind (*Epinephelus guttatus*) in the U.S. Virgin Islands. Increased fishing mortality caused a decrease in mean length, which resulted in a sex ratio skewed towards females, which are smaller. Seven years after the no-take closure, the proportion of males increased. The size distribution of the population expanded with less fishing pressure. For this species, the size at transition did not change to compensate for change in sex ratio.

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. Males and females could potentially experience very different fishing mortality rates because of differences in reproductive behavior. Knowing sex selectivity of fishing gear will help reveal these differences.

Size at Sex Change

Sex change is affected by ambient factors and fishing pressure in some cases. Benton and Berlinsky (2006) conducted a lab study manipulating the ratio of females to males in black sea bass (*Centropristis striata*). They showed that sex change is, at least in part, triggered by social structure or sex ratios. A similar effect has been found in wild populations of other fish species (Table 1).

Scamp Grouper
Photo Credit: Don Demaria

Hamilton et al. (2007) examined the effect of fishing pressure on age at sex change in California sheephead, a heavily fished protogynous hermaphrodite. Over the span of twenty years, fishing went unregulated and increased significantly. The average female length decreased in populations of sheephead exposed to heavy fishing pressure (Hamilton et al. 2007). In exploited populations females matured at smaller lengths and the percent of males in all size classes shifted, resulting in more males at smaller sizes, further indicating that female California sheephead underwent sex reversal at smaller sizes.

In another example, the age and size of maturity and sex change in roman (*Chrysoblephus laticeps*) decreased when fishing pressure was relatively high. Gotz et al. (2008) observed roman inside and outside of a closed area. They found no change in the sex ratio because roman were able to compensate for lost males and transition earlier, maintaining an optimal sex ratio.

Effects of Skewed Sex Ratios and Downward Shift in Size at Transition

Increasingly skewed sex ratios may result in reduced fertilization rates and, as a consequence, reduced population growth. The side effects of increasingly skewed sex ratios include sperm limitation (Lessios 1988; Hines et al. 2003; Brooks et al. 2008) and reduced genetic diversity (Allee 1931; Chapman et al. 1999). Skewed sex ratios may have negative effects on the population dynamics of a species. The side effects of transitioning at smaller sizes may result

in decreased egg production, biological constraints, as well as other negative consequences for smaller males on average.

Sex Change in Assessments

Results of the most recent stock assessments for the protogynous hermaphrodites on the East Coast and Gulf of Mexico are summarized in Table 3. The summary identifies how the assessment addressed the spawning stock biomass and reports the resulting stock status. The stock assessments for these species were reviewed to determine if the stock assessment tracked sex change over time, a change in the proportion of males to females, and reports on changes in the size at transition and measures of selectivity by sex (Table 4). Table 5 summarizes whether the assessments addressed hermaphroditic characteristics for all the species listed in Tables 3 and 4.

While Table 4 shows that none of the stock assessments parameterized selectivity by sex, the importance of sex selectivity is not to be overlooked. In a black sea bass tagging study (Jensen and Provost 2012, pers. com.), 1500 black sea bass tags were released. There was a twenty percent recapture rate with half reported by fishermen. Recaptures occurred in commercial pots and hook and line gear. With a known selectivity, the probability of capturing males and females in pots and angling can be calculated. Very large males are much more likely to be captured by angling while mid-size and smaller males were more likely to be captured in pots. Pots captured a greater proportion of males at a given length, possibly due to differences in reproductive behavior between males and females.

Table 3. Hermaphrodite stock status.

	Location	Year	SSB: sexes combined?	F/Fmsy	B/Bmsy
Black sea bass	Mid-Atlantic	2012	Combined	0.48	0.99
Black sea bass	South Atlantic	2011	Combined	1.07	0.70
Yellowedge grouper	Gulf of Mexico	2011	Combined	0.94	1.12
Gag grouper	South Atlantic	2006	Combined	1.29	0.12
Gag grouper	Gulf of Mexico	2006	Combined	1.96	Not reported (highly uncertain)
Black grouper	South Atlantic & Gulf of Mexico	2010	Combined	0.44	1.4
Scamp grouper	South Atlantic	1998	Not reported	<1.0	0.35
Red grouper	South Atlantic	2010	Combined	1.35	0.79
Red grouper	Gulf of Mexico	2006	Female only	0.73	1.27
Snowy grouper	South Atlantic	2004	Combined	(overfishing)	(overfished)
Red hind	Virgin Islands	2004	Not reported	Not reported	Not reported
Red porgy	South Atlantic	2012 (update)	Combined	0.64	0.47
Hogfish	South Atlantic & Gulf of Mexico	2004	Combined	Not reported	Not reported

Table 4. Sex change in stock assessments.

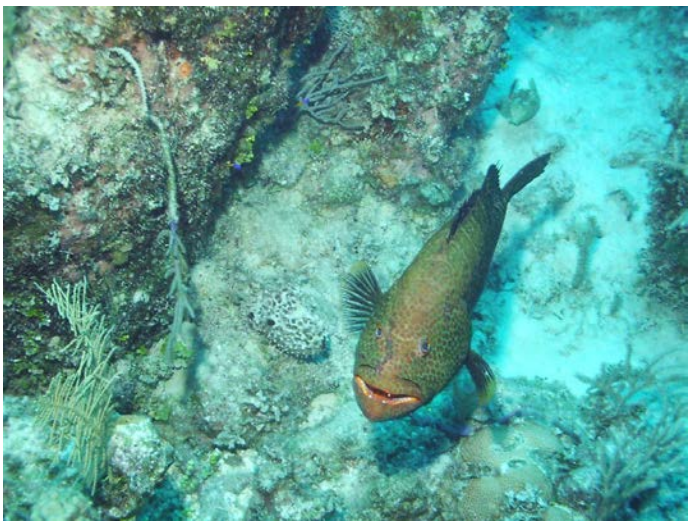
	Location	Reports sex ratio through time?	Δ in proportion male	Reports shift in size at transition?	Measures sex selectivity?
Black sea bass	Mid-Atlantic	No	Not reported	Not reported	No
Black sea bass	South Atlantic	Yes	65%-70% (1978-2010)	Not reported	No
Gulf yellowedge	Gulf of Mexico	No	Not reported	Not reported	No
Gag grouper	South Atlantic	No	21.1 - 8.2% (1976-2004)	Yes	No
Gag grouper	Gulf of Mexico	Yes	17% - 1% (1970-1992) (Coleman et al. 1996)	No decrease in size	No
Black grouper	South Atlantic & Gulf of Mexico	No	Not reported	Not reported	No
Scamp grouper	South Atlantic	No	36% - 18% (1970 – 1992) (Coleman et al. 1996)	Not reported	No
Red grouper	South Atlantic	Yes	21.4% (no change since 1991)	Not reported	No
Red grouper	Gulf of Mexico	No (proportion male pre-and post-1980)	Not reported	No decrease in size	No
Snowy grouper	South Atlantic	No	Not reported	Not reported	No
Red hind	Virgin Islands	No	Not reported	Not reported	No
Red porgy	South Atlantic	Yes, but not continuous time period	Ranges from 35% - 50% (1972-2011)	Not reported	Reports proportion male at age for different gears
Hogfish	South Atlantic & Gulf of Mexico	Yes	Not reported	Not reported	No

Table 5. Summary.

How many stocks currently experience overfishing?	6 of 13
How many are overfished?	7 of 13
How often does SSB include male biomass?	10 of 13
How many stocks track the sex ratio?	5 of 13
Reports change in proportion male?	5 of 13
Reports shift in size at transition?	2 of 13

Issues in Assessment Modeling for Protogynous Fishes

Selina Heppell* and Scott Heppell



Black Grouper
Photo Credit: Sarah Lardizabal, WaterNotes/Marine Photobank

The typical age structured assessment model includes data such as catch-at-age time series, selectivity curves, age at recruitment to the fishery, maturation ogive, fertility-weight relationship, spawner-recruit curve, constant mortality, constant catchability, and assumes a closed population. Some of the model assumptions may be inaccurate if the species is hermaphroditic. In sex changing species, the catch-at-age time series and selectivity curve varies by sex because the fishery targets older males that often have different behaviors, habitats, and desirability to the fishery. Recruitment to the fishery may be 100 percent for the youngest males. The assessment would need a separate transition probability-at-age ogive to account for the transition from female to male. A strongly skewed sex ratio, relative to a gonochoristic species, will likely limit fertility and will skew the results of a typical age structured assessment model.

To account for the hermaphroditic life-history patterns, the spawner-recruit curve may be dependent on relative abundance of males and females. Natural mortality and catchability estimates may be needed for both sexes to account for possible differences in habitat preferences and behavior. In protogynous species, the females transition to males and are removed from the female stock biomass, but not from total biomass. So the model needs to know how to address the reduction in female biomass without removal from total biomass.

Typical data-poor assessment models are based on catch history using catch time series, basic life history (natural mortality and age-at-mortality), and a ratio of current biomass to pre-fished biomass. The assessment does not account for aggregation behavior that is typical for some hermaphroditic species, which is problematic to assessments because variations in the aggregative behaviour of the fish may cause variations of stock catchability. It would also require sex-specific catch, which is possible to collect but not always available.

The Gag Grouper Model shows the effects of harvest on hermaphrodites (Heppell et al. 2006). It compares the relative impacts of protected areas that are sex-specific and time-location specific, and evaluates the benefits of protected areas with reductions in fishing pressure. The model can consider issues about spatial management, but it is not a spatially explicit model.

The most effective management strategies for hermaphroditic species depend on what aspect of the population was being measured. Different management scenarios were considered to determine how a spawning reserve could benefit a population. The most effective management measure for population recovery and conserving biomass was a nearshore reserve, followed by a 50 percent cut in fishing mortality, and then a spawning reserve. The least effective were seasonal closures and size limits. Size limits were relatively ineffective at helping the population

recover quickly. An aggregation reserve was helpful, but it was more important to protect the females. The females were the largest proportion of the population and they may eventually turn into the male. The spawning reserve most effectively preserved the sex ratio or effective population size. A spawning reserve reduces spawning mortality but there is still fishing pressure and natural mortality during the remainder of the year. Yield per recruit and harvestable biomass were not compared.

To develop an assessment that appropriately considers the life history and behaviors of a protogynous hermaphrodite, the parameters in the initial model should be based on a gonochoristic species. Once parameters are established the model can be extended to a protogynous species with fixed transition, followed by a model of protogynous species with plastic transition. The latter would need to be sex dependent. It would also need to consider sperm limitation because depensation can be caused by a skewed sex ratio. Finally, the model could also consider a species whose distribution is aggregated, a species that may aggregate at certain times of the year, and finally one that never aggregates. Additionally, consideration could be given for species that may switch its aggregation behavior to adapt to a particular situation.

For productivity, the model parameters should consider the female weight at age and fecundity, juvenile survival, size-specific reproductive success, maternal effects, and sperm limitation. Other factors that might influence the model are movement patterns (i.e., territorial v. roving, spawning site fidelity, corridors, and gender differences in movement patterns). The reproductive interactions and behavioral learning (such as juvenile to adult transition) should also be factored into the parameters.

Competitive interactions may also influence model parameters, such as mate competition versus sperm competition, aggregation versus pair/haremic spawning, and male-male antagonistic feedback, which occurs when there are not enough males in the population.

Establishing reference points for sex changing species is also a challenge. Maximum sustainable yield may need to be sex-specific, though it is further complicated by the biology and behavior of the species. Yield per recruit and eggs per recruit, as well as female and male spawning stock biomass, are deterministic and may not capture non-linearity effects like skewed sex ratios. The sex ratio is also problematic for species with episodic recruitment. Age distribution can also be skewed because of the sex transition.

Management measures could have some serious consequences for hermaphroditic species. Introducing size limits may create high discard mortality. Bag limits are likely to result in differential fishing mortality by age and sex. Area closures require enforcement, and could result in a redistribution of fishing effort, which may have a different set of impacts to the population that would need to be evaluated. The correct areas would need to be identified for closures, especially since it is difficult to change an area closure once implemented. Temporal closures have the same challenges as seasonal closures, but the appropriate timing for spawning needs to be accurately identified. Determining the appropriate approach for managing a species is ultimately dependent on the available data.

Fishery Independent Reef Fish Monitoring in the Southeast

M. Reichert

Currently, there are three regional fishery independent surveys in the southeast Atlantic that work in close collaboration to monitor (reef) fish populations in the region. The Marine Resource Monitoring, Assessment, and Prediction (MARMAP) conducted by South Carolina Department of Natural Resources (SC DNR), South East Area Monitoring and Assessment Program - South Atlantic (SEAMAP-SA) also conducted by SC DNR, and South East Fishery Independent Survey (SEFIS) conducted by the Southeast Fisheries Science Center (SEFSC). All of these surveys collect fishery-independent information for commercially and recreationally important reef fish populations and associated habitats from Cape Hatteras, North Carolina to St. Lucie Inlet, Florida. The surveys provide data and analyses to state and Federal agencies, fishery management councils, the Atlantic States Marine Fisheries

Commission (ASMFC), the Southeast Data, Assessment, and Review (SEDAR), and others in support of fisheries management.

The SEAMAP Trawl Survey (in place since 1986) takes place over soft bottom habitat (sand, etc.) in nearshore areas. Catches of protogynous hermaphrodites is generally very low in this survey. MARMAP has been in place since 1972. Since 1978, it has monitored reef fish populations of live bottom habitat using fish traps and standard sampling methods. In 2009, SEAMAP-SA added a Reef Fish Survey to the program to supplement ongoing MARMAP efforts. In 2010, SEFIS was initiated, enabling a considerable (~100%) increase in South Atlantic-wide fish trap sampling efforts, and the introduction of video survey gear. With the exception of the video survey, there have been few additions to the surveys, but the consistent methodology and sampling maintains the integrity of the long time series. The time series documents impacts of fishing, provides updates and feedback as to the impact of regulations, and provides information for stock assessments and management. It can also be supplemented by fisheries dependent data where needed.

In addition to relative abundance data, MARMAP/SEAMAP-SA/SEFIS provide life-history information such as species identification (morphological characteristics), fish length and weight, age and growth information, reproductive data, diet composition, and data from various other tissue samples. Whole and sectioned otoliths and spines are processed to provide species-specific information on age and growth. The survey supplies fish gonad samples to examine reproductive data by processing and examining samples using histology or other techniques. The collection of fish samples provides data for length-weight relationships, length and age compositions, length at age, growth parameters, maximum age, sex ratios, length and age at maturity and sex transition, and other information.

Red Grouper
Photo Credit: Don DeMaria

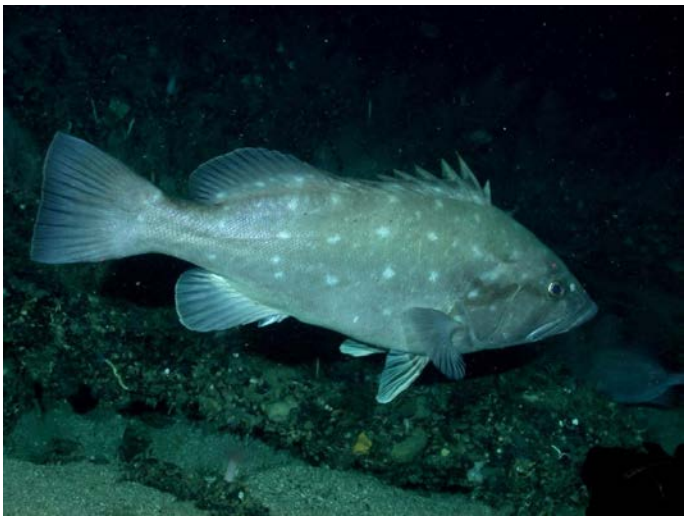
The *R/V Palmetto* (SC DNR) and *R/V Savannah* (Skidaway Institute of Oceanography, SKIO) are used for reef fish sampling by MARMAP/SEAMAP-SA and SEFIS respectively. Each vessel spends 40-60 days at sea per year with 5-14 days per cruise. In addition, the *R/V Lady Lisa* (SC DNR) is used for the MARMAP long bottom long line survey (10-25 days at sea per year) and the SEAMAP-SA coastal trawl survey (50-60 days at sea per year), spending 5 days at sea per cruise. The sampling expansion in 2010 allowed for additional investigations such as bottom habitat mapping and monitoring changes of seafloor habitat using the video surveys and sonar equipment.

Currently, the chevron fish trap (since 1990) and short bottom longline (since 1978) are the primary gears used for sampling of reef fishes. Initiated system-wide in 2011, video cameras mounted on the chevron traps were added as a survey gear. The video survey component is used to provide additional indices of relative fish abundance, investigate bottom habitat, and conduct research on fish community structure, fish behavior, catchability, and gear selectivity issues. The surveys also have used or are using long bottom longlines, rod and reels, a CTD, and underwater TV and still cameras. A CTD is deployed with every trap set to collect oceanographic information such as salinity and temperature and rod and reels are used for supplemental sampling. The underwater TV and still cameras are mostly used to investigate and verify bottom habitat type.

Chevron video camera traps are arrowhead shaped fish traps, with a total interior volume of 0.91 m^3, constructed with 35 x 35 mm square mesh wire, a single entrance funnel (“horse neck”), and a release panel to remove the catch (see details in Collins 1990 and MARMAP 2009). The traps are baited with clupeids, soaked for about 90 minutes,

and generally sampled at a depth of up to 90 meters (300 feet). Currently, over 1,200 randomly selected stations are sampled annually from a total of about 3,100 identified live bottom sampling stations in the region.

The short and long bottom longline surveys were halted in 2012 due to budget restrictions. The short bottom long line gear is used in areas of high relief, generally in depths greater than 90 meters. The gear has a 25 meter groundline with 20 gangions with hooks baited with squid, and is soaked for about 90 minutes (see details in MARMAP 2009). Annually, 100-150 stations out of about 1,000 stations are randomly selected and sampled. Snowy grouper, jacks, tilefish, and speckled hind are frequently sampled with this gear. The long bottom longline is used over smooth mud bottom around 200 depth (the so-called "tilefish grounds"). It has a 1500 m groundline with 100 gangions with hooks baited with squid (see details in MARMAP 2009). The target species is golden tilefish.



Snowy Grouper
Photo Credit: George Sedberry, NOAA

There are several data challenges and considerations for protogynous hermaphrodites, but these are not necessarily unique to fishery independent sampling. Histology is needed for accurate determination of maturity and sex transition because it is difficult to macroscopically/morphologically determine the reproductive state of a fish, especially during the process of sex transition. Sampling often does not coincide with the spawning period, and is often the period after which the fish may transition. Transition can be rapid, in some instances taking a matter of days. The life history of some species is complicated and can make data collection even more challenging. For example, in black sea bass a small percentage of fish are primary males, and red porgy may undergo sex transition as a juvenile. A large sample size is necessary for reliable sex ratio and sex transition data. There may be a low percentage of males, especially in heavily exploited larger hermaphroditic species and those that form spawning aggregations (e.g., gag). Multiple gears (e.g., traps and longlines) and genetic techniques are often needed to obtain reliable estimates.

Incorporating ancillary factors in sampling design (e.g., month, water depth, latitude, lunar phase) is important when investigating reproduction in these species. Data collection is challenging because the number of individuals caught (especially males) can be low for many species and sampling is rarely done year-round. To get a more complete picture, reproductive and other data often needs to be supplemented by fishery dependent sampling. This supplemental fishery dependent sampling can be costly and is often limited by fishery regulations, such as size limits and trip limits, and timing, such as spawning areas and quota closures. Special projects, such as exempted fishing permits for sampling, may be needed, but would require careful design for representative samples.

Male Mating Strategies – How Might They Impact Hermaphrodite Management?

Scott Heppell

Male mating strategies can be summarized into two categories: sperm competitors (primarily group spawners), and mate competitors where males are territorial and compete directly for mates. Harems and leks are two examples of territoriality. In a lek, a dominant male defends a space, but there is no inherent value to the space. It is just a space.

With harems there is often a resource value to the area in which the male has his harem. With group spawning or a lek, males attempt to produce an excessive amount of sperm to outcompete other males.

Androgens play an important role in male reproduction by determining the primary or secondary male characteristics. There are two important androgens, testosterone and 11-ketotesterone (11-KT). The level of testosterone present can initiate sex differentiation and development, stimulates the pituitary gland to induce spermatogenesis, and is the precursor to estradiol and 11-KT. The levels of 11-KT are substantially higher in aggressive species. 11-KT stimulates territoriality, nest building, aggression, secondary sex characteristics, spermatogenesis and sperm maturation, and tactic switching. Knowing the amount of androgen present in a species can help to determine the type of mating strategy the species might exhibit. Samples of 11-KT can be obtained with a blood sample, and it may be possible to discern the 11-KT level with a tissue sample.

Male reproductive tactics, disruption of mating strategies, and "The Challenge Hypothesis"

With territoriality, there are multiple strategies for reproductive success. The primary male is aggressive, has high androgen levels and small testes. The secondary male (a.k.a. sneakers, streakers, and satellite males) is not aggressive, has low androgen levels and has large testes producing large quantities of sperm. These tend to also be the characteristics of group spawners. Wingfield (1984) and Wingfield et al. (1990) explained that with territoriality comes aggression and mate competition. He proposed "The Challenge Hypothesis" where competitive interactions are key to reinforcing the reproductive success of the dominant male. An environmental input starts the cycle for reproduction but intra-specific aggressive interactions drive up androgen levels and in turn drive up sperm production. Those challenge situations with other males are the trigger or cue for the dominant male to continue the production of the androgens, thus causing a hormone positive feedback loop.

Scamp Grouper
Photo Credit: Don DeMaria

Warner and Swearer (1991) found that when a dominant male bluehead wrasse disappears, a secondary male exhibits dominant male behaviors within minutes. The coloring will change within a day, and sperm can be present within eight days. Without the presence of a dominant male, there could be decreased individual reproductive success and population level (allee?) effects if half of the feedback loop (the "challenge male") is missing. Semsar and Godwin (2003) found that in some species this change is linked to arginine vasotocin production in the brain, and not necessarily linked to gonad production of steroids, a likely explanation for why behavioral changes can be seen almost instantaneously in species that spawn in social groups.

Whether or not another female is able to change depends on whether sex change is behaviorally plastic and socially controlled, as is seen in small, permanently haremic species and those that spawn often, or if it is more "static", for example in cases where the species spawns seasonally or annually and aggregates to spawn. In that case the only time the animal can assess the benefits to changing sex is after it has already arrived at the spawning location, likely with mature gametes. In that case the animal would not be able to spawn as the other sex until the following year and it would lose a year of reproductive capacity in the interim.

Discussion

Following the presentations, the workshop participants were divided into two breakout groups to discuss the workshop objectives. After the breakout discussions, the groups reconvened and reported on their discussions. Both groups identified many of the same issues. A summary of the two breakout groups' and the full plenary's discussions follows.

Sampling Challenges

Both groups discussed the challenges associated with collecting additional data to address the uncertainties associated with modeling protogynous species. Additionally, both groups agreed that much of the data that should be collected would also be beneficial for both protogynous and gonochoristic species. The cost associated with additional data collection on existing surveys would be challenging, and obtaining the funding for additional surveys would be an even greater challenge. Beyond the added expense and effort, any additional data collection will require careful planning to provide representative sampling.

Hogfish
Photo Credit: George Sedberry, NOAA

Many of the protogynous species mentioned in this workshop have a strong sex-spatial component that makes collecting a random sample problematic. For example, should sampling occur at a population level or on a smaller scale, such as reef communities? In the example of northern black sea bass, the stock is managed as a single unit, but data suggest there are metapopulations with different behavioral characteristics. To further confound sampling, the extent of mixing and migration between reef communities is not well understood. A sampling program would need to cover a broad geographical area, and the samples would likely need to come from a diversity of surveys.

In addition to the geographical sampling challenge, the timing of these surveys is also an important consideration in sampling design. The existing surveys that collect information on protogynous species are not necessarily synchronized with spawning periods. The group discussed whether or not it was necessary to sample during a spawning season if the catchability and selectivity by sex were known. Sampling during a spawning season would provide data on sex ratio, as well as a measure of fertilization success but sampling during a spawning season should not be done at the expense of losing information collected during the regular survey times.

Sampling should occur during periods of transition to gather information about age or size at transition. However, transition can occur over a very short period. It is also not well known if all of the individuals transition at exactly the same time. Further, transition is a multi-step process that could include morphological, chemical, and gonadal changes. Transition may actually begin prior to spawning, but the final stages of transition may not occur until after spawning. For example, when black sea bass have been sampled in the past, the results have been misleading because there was an under-detection of transitional fish (Wuenschel et al. 2012). Histologically, the tissue samples showed the samples were male, but the macroscopic characteristics suggested that 95 percent of the samples were female. In general, sex of hermaphrodites cannot be accurately assigned based upon macroscopic staging of gonads.

More directed sampling of gonads at sea (e.g., scientific observers taking gonad samples during fishery dependent collections) along with verification of sexual traits such as coloration and sexuality would be beneficial. Further, experimental studies should be conducted to determine the time frame and triggers (e.g., density dependence, environmental cues) for transition.

DATA COLLECTION NEEDS

To improve our understanding of protogynous stocks, it is important to collect both sex specific data and estimate sex ratios. These species would likely respond to exploitation by a shift in either the sex ratio or transition at size or age. A change in either of these components could be an indication of stock status. To improve our understanding of protogynous stocks, it is important to collect both sex specific data and estimate sex ratios.

Both groups agreed that sex data should to be collected for the principal hermaphroditic species (Table 3). Existing surveys should conduct additional sampling, if necessary, to collect data for estimation of the sex ratio, information on sex at length or sex at age, as well as the age at transition. The data will need to be sampled from both fishery independent and dependent surveys, and should be initiated as soon as possible. Hybrid surveys (i.e., cooperative and sentinel surveys) might be the most successful means for collecting representative data. New surveys may be needed to collect data on key species not currently covered by existing surveys, to collect sex data (i.e., length, age, transition) that cannot be collected on existing surveys, or to collect data at different times of the year, specifically during spawning seasons.

Given the challenge to accurately identify the sex of a protogynous hermaphrodite species (Wuenschel et al. 2012), some investment should be made to develop some quality controls on sex determination. The most cost effective methods for sex determination and age or size at transition should also be evaluated. The methodology employed would need to determine if the fish was an active male, active female, juvenile, maturing, mature, or unknown. The sex data could be collected using hormone levels, but the hormone levels of a fish in transition may not provide clear results. Some species will be very difficult to sample with high error rates and others may be easier to sample.

Two methods for collecting sex data are immunoassay and histopathology. The utility of an immunoassay is restricted to specific times of the year when these fish are in transition, whereas histology could be conducted at any time as long as the specimen's gonads are present. An immunoassay measures the reproductive hormone levels in a fish and determines if the species is undergoing maturation. Histology more accurately detects the specimen's ability to reproduce, and may also provide information about past spawning events. Immunoassays are conducted using a blood sample that can be taken during tagging a specimen or from muscle tissue that could be taken from a fish gutted at sea where the gonads are no longer present. Obtaining histology samples is a more laborious process requiring the presence of gonads, and could mean landing fish intact or killing specimens on research cruises. Both methods provide information on sex determination, but also have their challenges.

Some species do have morphological differences between female, juvenile male, and mature male, but transitioning individuals may not exhibit different characteristics. Beyond hormones and observing superficial differences, macroscopic examination of the gonads could be used to determine if the specimen is an active male or active female.

Fishery dependent catches are another possible source for sex data. Catch data may come from diverse areas, so the sex ratio may represent the entire population, not just a community or individual reef. To obtain valid statistical samples, sampling the catch for sex data will need to be carefully designed to take a representative sample from the entire distribution of lengths or ages. Further, obtaining fishery-dependent sources of gonad samples for histology is challenging because the fish are either gutted upon catch or inadequately maintained (e.g., not immediately preserved in formalin).

The selectivity of the gear is an important piece of information, particularly with the use of multiple surveys to collect sex data. In the fishery independent surveys, sex data should be collected in addition to total length to determine gear selectivity. The videos taken on the MARMAP/SEFIS survey could also provide some insight on selectivity. For black sea bass, new pot surveys and tagging studies could help establish the selectivity in the fishery.

The variability within the population, as well as fishing effort, should be monitored over both space and time. The variability in the population might include changes in sex ratio, age at maturity, transitional period, behavior, and sex changing patterns. Much information could be collected for these species, but the most important data to begin collecting within the next five years would be sex ratios (both in spawning aggregations and population wide), fertility rates, and information on sperm limitation or mate competition. Currently, most of the empirical data on sex ratios, fertility rates, sperm limitation or mate competition comes from small coral reef species or aquaculture (Petersen and Warren 2002; Petersen et al. 1992; Shapiro et al. 1994; Thorsen et al. 2003; Trippel 2003; Lambert and Thorsen 2003; Uusi-Heikkilä et al. 2012). There is a need for more experimental systems to address questions about how to collect this information from wild stocks.

Model Parameters

Sex-specific data would be useful in many ways to estimate or define model parameters. Sex data could be used to establish a transition function for sex change in the models. Also, the sex data would inform whether or not sex-specific selectivity patterns are important in the model. The model's selectivity patterns would ideally match the empirical data from the catch and surveys. Sex-specific natural mortality is also important. A spawner-recruit relationship, if modeled, should be based on the relevant portion of the spawning biomass, and may need to account for fertilization rates that depend on sex ratio. These are all ways in which simulation models would use the sex data to determine what is driving the output of the model.

Data should also be collected to determine sex-specific fishing mortality and natural mortality. In most protogynous fish, the males tend to be highly aggressive. This aggression may result in catchability differences; for example, males attacking a hook in the hook and line fishery. In addition to fishing mortality, there may be sex-specific differences in natural mortality caused by three processes all occurring within a narrow timeframe. The males undergo transition, migrate to the spawning grounds, and then spawn all within a short period. The level of stress is probably high, potentially increasing the rate of natural mortality. While not a protogynous species, Nassau grouper has a higher natural mortality after spawning due to parasite loads. The terminal males may experience a higher natural mortality, because they defend their territory. All of these behavioral differences emphasize the importance of conducting more research to determine the different sex-specific F and M for use in modeling protogynous species.

The shape of the fertilization curve should also be examined to understand how it changes in response to a shift in sex ratio. To establish a fertilization curve, post spawning eggs need to be collected and evaluated. There is an experimental technique to analyze the presence of haploid or diploid cells in eggs collected from spawning aggregations, which may provide some insight on the rate of fertilization success. A one year study could provide the necessary information related to fertility and reproductive potential, but a longer time series would be needed to evaluate recruitment and sex ratios.

Depensation occurs when the survival of the mature spawning portion of the population decreases, or when egg production decreases because of the allee effect, predation, or some other cause. Changes in the sex ratio could be indicative of depensation or compensation in the population. Factors such as stochastic recruitment can also cloud the detection of depensation. Ideally, a sex ratio threshold would be known, below which, the population is at risk of depensation.

Plasticity of sex transition may enable a species to more readily adapt to fishing pressure. The models should include a sex change function because the age or size at which transition occurs could influence the sex ratio over time.

Without the transition function, it would appear as though males are spontaneously created and females suddenly experience unusually high natural mortality.

Many protogynous species have a strong behavioral tie to specific habitats. While most assessments do not consider habitat, it is a critical element to the spawning dynamics of protogynous species. Numerous artificial reefs have been created to increase habitat for black sea bass, but the increased habitat is not translating into an improved status. The artificial reefs may be concentrating the fish, and creating a habitat bottleneck. The group recommended exploring the possibility of including habitat in the assessment.

Modeling Approaches

A range of modeling approaches is needed. One model construct will not answer all of the questions. Some information from one modeling approach may inform other modeling approaches. Several modeling approaches should be conducted and compared, such as management strategy evaluations (MSE), stock assessment models, and theoretical simulation models. Not only will the models inform one another, but the simulations will also inform data collection needs.

MSEs could be useful for determining which management measures could improve stock performance or for examining if regulations are creating some type of feedback on the biology of the stock. An MSE is particularly important for protogynous fish when a fishery targets a specific sex or size in the population, for example, as a result of size limits. An MSE can be used to look at a sex ratio that never varies and then introduce F to determine how the population responds.

Theoretical simulations and analytical models would provide insight to how the unique life-history characteristics of these species respond to different mortality schedules or management measures. Running different scenarios will reveal which characteristics are critical for modeling population dynamics and defining biological reference points. For example, the simulations could reveal that with certain sex ratios, the population should be modeled as a single sex. Simulation models could also be used to determine if species-specific models are needed or if generalizations can be made. If generalizations are possible, the models could identify the assumptions that can be applied across species. For example, Ellis and Powers (2012) conducted modeling that incorporated a density-dependent sex change function, and found a reduction in the sex ratio when compared to model simulations where the sex change was fixed.

Stock assessments should also be evaluated to determine the sensitivity of the model to sex-specific data versus combined sex data. The answer may be that 'it depends,' but that will inform the next modeling experiments and may provide insight to which life-history characteristics are most important for stock status.

Meta-analyses should be performed to look at all of the available life-history data for marine and tropical hermaphroditic species. There are a lot of data sets and a lot of knowledge that could provide insight on transition types and other behavioral characteristics. Another meta-analysis would be to compare time-series data from gonochoristic stocks and protogynous stocks that otherwise have very similar traits to understand how the populations have responded to fishing mortality. This type of exercise could provide managers with some indication of how a species might respond to different management approaches.

The discussion above is certainly not exhaustive. Other modeling approaches, such as a gene based selectivity model (Powell et al. 2011), might also be considered.

Modeling Exercises

Stock assessments for protogynous hermaphrodites have an unknown degree of uncertainty because the implications of not including the unique life-history information are poorly understood. We do not know if

maintaining the spawning potential for a stock provides the same rebuilding goals as maximum sustainable yield. Therefore, the group agreed that modeling was an important step towards understanding how the species may respond to different management measures.

Using the same models for protogynous species as used for gonochoristic species may not achieve the same goals. For example, surplus production models were ruled out for black sea bass in the Northeast (NEFSC 1998), because of concern that removing the large fish might have a greater implication for protogynous stocks than for gonochoristic fishes. While using the same model may be ineffective, there may be some lessons to learn from the configuration of the model and biological reference points. For example, snow crab and king crab are two species with sex specific assessment models and may provide some input on appropriate biological reference points.

Using the most data rich species on the Atlantic and Gulf coasts, an assessment should be conducted with and without the sex specific information to discern what happens in the models without the specificity. This exercise has yet to be done because the sex specific information for these species is not being collected. In the absence of this much needed information, sensitivity analyses should be conducted and concurrently, data should begin to be collected to calculate sex ratio and fertilization rates.

Sex specific models that do not incorporate sex change should be explored. It is important to focus on the age diversity in the terminal phase of a protogynous species because younger or inexperienced males would have a lower reproductive value. Most model results will show fishing pressure and abundance of mature males, but may not provide the age diversity in those males. There is an added value in the older mature males. The challenge is how to account for the added value of the older males without skewing the assessment. While arbitrary, it may be possible to add a fertility coefficient equivalent of 100 percent for the oldest males and then step it down for each year class.

Heuristic models are recommended to better inform and guide the structure of assessment models, and it may even help to determine the appropriate assessment. These heuristic exercises should look at a range of parameters (i.e., sex ratio, fertility, density dependent function for juveniles). The model could go through several iterations to determine different life-history patterns and mortality on adults. This type of modeling allows assessment scientists to explore the response surface of different life-history characteristics, and identifies which factors might be most critical to understand.

Experimental Research

The third prong to the integrated approach would be experimental research. Experimental studies will provide more resolution to what is currently known about these protogynous species. Experimental studies are needed to evaluate the plasticity in size and age of transition, fertilization effects, as well as the degree of reproductive success at a given size and age. Genetic techniques should be employed to determine the effective population size of these protogynous species.

Management Measures

Size selective harvest can make a protogynous species stock status more susceptible to fishing pressure. Experimental studies show that a greater yield can be sustained over a longer period of time if the fishery focuses the effort on smaller fish (Heppell et al. 2006; Hamilton et al. 2007). Using basic data (i.e., sex and size), a benchmark for the status of the older males could be developed. A diversity of males seems to be an indicator of a healthy stock. A management objective for large males would also be a way to ensure the presence of large females.

The current regulations for protogynous species may not actually achieve the intended goal. Bag limits are set based on catch information, rather than the available population. The effect of a size limit on the life-history patterns of a species is not thoroughly understood. These species would be better served to consider the differential fishing

mortality on ages. Being able to generate the age selectivity patterns for protogynous fisheries would be an important step.

Spawning closures are another management tool often used to maintain a sustainable fishery. To appropriately establish a spatial (as opposed to temporal) spawning closure, one needs to know the most important area(s) to protect. The use of protected areas may be species-specific depending on the consistency of spawning locations. Establishing spatial spawning closures would require the collection of additional information because the location of these spawning sites and site fidelity are not well known for many of these species.

Given the difficultly of accurately establishing the boundaries of a protected area, the ability of fish to move in and out of the area, and the difficulty of changing the boundaries once set, closed seasons may be a more viable option than closed areas. Of course, closed seasons are not without challenges too. The fishery tends to target the large males. When fishing occurs after the species has spawned, the population may not have time to respond to a change in stock structure. The females may not receive the environmental cue to transition if the species is no longer aggregating, but the large males have been removed. Most species go through transition at the end of the spawning season when they get the cue, but some species have already begun the transition prior to entering the spawning ground. The challenge of managing to maintain a sustainable, mature male portion of the population is further evidence that the models need a metric for the age diversity for the terminal phase of a protogynous stock.

There are a few species (e.g., red porgy and black seas bass in the South Atlantic) for which there is enough information on size at age of transition to estimate the spawning potential ratio (SPR). SPR may provide a useful metric in calculating a biological reference point, but calculating the SPR is not without challenges. Plots comparing SPR for red porgy calculated based on all mature biomass, mature female biomass, and mature male biomass demonstrated large differences between calculations (Figure 1).

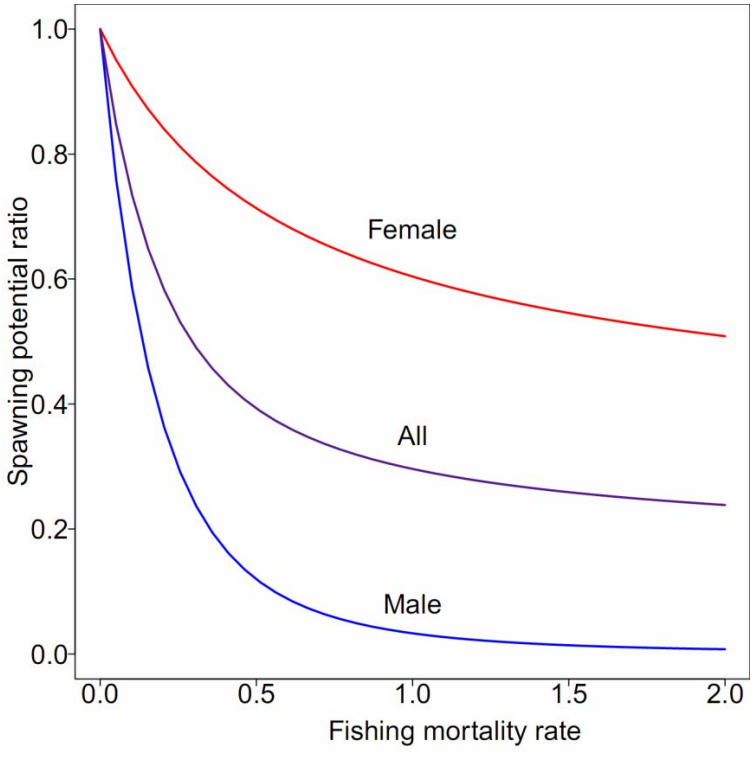


Figure 1. Sex-specific spawning potential ratio (SPR) in the protogynous species red porgy. Calculations are based on mature male (bottom, blue line), mature female (top, red line), or all mature biomass (middle, purple line) (prepared by N. Klibansky and F. Scharf of UNCW).

Because fisheries target larger red porgy, which are primarily male, SPR based on male biomass declines quickly with increased F leveling off at a very low value. By contrast, SPR based on female biomass declines much less quickly and levels off at a much higher value. Current stock assessments use SPR calculated based on all mature biomass, which has a relationship with F intermediate between the two sex-specific calculations.

McBride et al. (2008) calculated sex-specific SSB for hogfish, and although the outcome for each sex was similar, the age-specific schedules of each sex were very different.

The sex-specific calculations illustrate how fishing pressure affects male and female gamete production differently and re-emphasized one of the emergent themes of the workshop: it is not clear how egg fertilization rates are affected by decreases in male biomass. If fertilization rates are very strongly or weakly affected by decreased male biomass, then male- or female-specific SPR, respectively, may more accurately reflect the true spawning potential of a stock.

CONCLUSIONS

The Magnuson-Stevens Fishery Conservation and Management Reauthorization Act of 2006 was signed into law on January 12, 2007, following its 2006 passage by the U.S. Congress. This reauthorization included new requirements for annual catch limits and accountability measures and other provisions designed to prevent and end overfishing (16 U.S.C. §1853(a)(15)). The Productivity and Susceptibility Assessment (PSA) approach was developed to evaluate the vulnerability of stocks. The PSA uses qualitative or quantitative data (if available) and assigns a value of risk to the species. The workshop participants agreed that it would be useful to develop a similar approach for the protogynous species listed in Table 1 of this report. The PSA-like table will outline the characteristics that make these protogynous fishes susceptible (i.e., mating system, patterns of sex change, spawning site fidelity, fixed or plastic transition, etc.), aspects of the fishery (i.e., catchability and gear selectivity), and management strategies. The individual species would then be rated for the productivity or vulnerability.

The workshop participants also agreed that a model should be developed to compare both ends of the complexity range. This exercise will identify how complex and robust the models need to be to provide adequate management advice. The model inputs would need to be sex specific for age and length. It should look at whether space is important, as well as the mating strategy of the species, sex based selectivity, and natural mortality. The model should consider density feedback in the population. The complex model would identify the critical information that drives conclusions. After identifying the critical information, data sets could be reviewed for the available information. The complex model would then be compared with simpler models to determine the adequacy of the information, and if management advice can be developed. If the data are not adequate or are not available, then their collection becomes a priority. The focus should be on the components that are unique and specific to hermaphroditism.

Many of the recommendations from this workshop will take several years to develop. They are intended to provide much needed insight into the unique characteristics of protogynous fishes that influence assessments, and how management measures influence the populations. While modeling is an important step forward, data collection needs to begin now to make these models more robust in the future. Because the collection of additional data may be expensive, the first step should be to review the data currently collected for the listed protogynous hermaphrodites. Using the available data, some of the heuristic models could already be conducted. This integrated approach using field-based surveys, modeling, and experimental research is necessary to provide the greatest insight to how the life-history characteristics of protogynous species influence assessment results and respond to different management measures. Modeling efforts should be coordinated and integrated with data collection efforts. It will be an iterative process to better understand the importance of considering life-history characteristics of protogynous species in stock assessments and reference points.

RECOMMENDATIONS

❖ Conduct simulation studies to determine the critical data and model components that are sensitive to the unique life-history characteristics of protogynous species. The modeling should make use of any sex-specific data currently available. This first step will help to prioritize data collection to fill in the gaps.

❖ Aggregate the life-history data for all of the listed protogynous species. Consolidate and review all the assessment information for protogynous species (SIS). Conduct meta-analyses on these data sets.

❖ Conduct management strategy evaluations (MSEs) to better understand the implications of a broad range of management strategies. These need to determine how simple a model can be while still providing useful management advice.

DATA COLLECTION RECOMMENDATIONS

➢ **Determine sex ratios from both catch and population**

- For the key protogynous species identified in this report, the sex ratios should be determined from both the catch and the population.
- Data collection should include sex (female, subordinate male, dominant male), length, and age.
- There should be more directed sampling of gonads at sea (e.g., scientific observers taking gonad samples during fishery-dependent collections).
- Data collections should occur during key spawning periods to discern the operational sex ratio, as well as during other times of the year to discern sex ratio of the population.
- Secondary traits, such as coloration and sexuality, should be verified.
- Collecting this information for gonochoristic species would also be beneficial (e.g., dimorphic growth in summer flounder).
- Other cost effective means for obtaining sex should be explored.
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➢ **Both fishery independent and dependent collections are necessary**

To collect spatially and temporally representative data, both fishery independent and dependent surveys may be needed. Designing a survey to obtain a valid and representative statistical sample will be a challenge because incorrect sub-sampling for protogynous species may result in skewed observed sex ratios.

- Existing surveys should be expanded to occur during spawning time periods.
- Explore use of the cooperative research program to collect additional information.
- Determine the most cost effective methods to evaluate sex and maturity stages of protogynous fish.
- Incorporate additional fishery independent and dependent collections into existing surveys, where possible, to minimize costs.

- Establish gear and survey selectivity by sex and length or age.

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RESEARCH PROJECT RECOMMENDATIONS

➢ **Explore the consequences of sex ratio on fertility**

- What are the effects of sex ratio on fertilization success? Sample eggs to determine the fertilization effects.
- Is there increased reproductive success with increased length and/or age?
- Does the species exhibit behavioral competition? And who is typically successful (e.g., dominant male and sneakers versus dominant male inhibits sneakers)?

- **Evidence of depensation or compensation in response to fishing morality**
  - How are the sex ratios skewed in a population that has a fixed size at transition?
  - When the size at transition is variable do the sex ratios remain relatively stable?
  - Is it possible to stage transitional fish, and what is the best method to do so?
  - Are there critical sex ratios below which fertilization is diminished, and how can this information be used to determine population status?
- **Develop sex-specific natural mortality (M) and fishing mortality (F)**

  With protogynous species, it is a challenge to address natural mortality because it appears as though a portion of the population has suddenly disappeared or died, but in reality it has transitioned to a secondary sex. For any species, one needs to know the natural mortality to accurately determine the fishing mortality.
  - How does natural mortality influence size at transition?
  - Can observed sex ratios be explained by natural morality or is it a function of transitioning to another sex?

MODELING RECOMMENDATIONS

- **Conduct a management strategy evaluation (MSE)**
- **Develop a model to include sex specific information:**
  - Transition function for sex ratios
  - Sex ratios for estimated fishing mortality; internal versus external to model
  - Selectivity (catch and survey); internal versus external to model
  - Gear based selectivity model
  - Sex specific natural mortality
  - Spawner-recruit relationship
  - Biological reference points (BRPs)
- **Review time series to understand how gonochoristic versus hermaphroditic species respond to F**

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Last Name	First Name	Organization
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APPENDIX 2: ACRONYMS

11-KT	11-ketotestosterone
ASMFC	Atlantic States Marine Fisheries Commission
B	Biomass
B_{msy}	Biomass at Maximum Sustainable Yield
BRP	Biological Reference Points
F	Fishing Mortality
F_{msy}	Fishing Mortality at Maximum Sustainable Yield
M	Natural Morality
MAFMC	Mid-Atlantic Fishery Management Council
MARMAP	Marine Resource Monitoring, Assessment, and Prediction
MSE	Management Strategy Evaluation
NMFS	National Marine Fisheries Service
PMAFS	Partnership for Mid-Atlantic Fisheries Science
PSA	Productivity and Susceptibility Assessment
SC DNR	South Carolina Department of Natural Resources
SEAMAP	South East Area Monitoring and Assessment Program
SEDAR	Southeast Data, Assessment, and Review
SEFIS	South East Fishery Independent Survey
SIS	Species Information System
SKIO	Skidaway Institute for Oceanography
SPR	Spawning Potential Ratio
SSB	Spawning Stock Biomass
UNCW	University of North Carolina at Wilmington