

A Brief Review of Grouper Reproductive Biology and Implications for Management of the Gulf of Mexico Gag Grouper Fisheries

prepared by

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Introduction

In May of 1999, a proposal was advanced by the Gulf of Mexico Fishery Management Council to close a 423 square mile area of the northeastern Gulf of Mexico to all reef fishing and to all bottom fishing capable of catching reef fish. This year-round closure was primarily designed to counter a purported shift in sex ratio of gag grouper (*Mycteroperca microlepis*), which is thought to have been skewed by very intense fishing on gag spawning migrations, targeting primarily males. The current reproductive status of gag and the rationale behind the proposed closure were reviewed by Koenig et al. (1999). The content of this document was highly contentious, and given the socioeconomic hardships that area closures can inflict on fishers and fishing communities, several members of the Gulf Council filed a minority report objecting to the proposed closure on several grounds. One of the grounds for objection was that the proposed actions were not based on the best scientific information available. The purpose of this document is to provide the best available information on some of the more contentious issues, including:

The proximal causes of sex change in protogynous hermaphrodites, particularly groupers.

The effects of fishing on population dynamics of protogynous hermaphroditic fishes.

The relative availability of male and female gag to hook-and-line fisheries.

The role of area closures in management of grouper stocks.

For each topic, I will attempt to provide a concise overview of the general issues, then relate the available information to the gag fishery in particular. I will also provide commentary on some of the specific information on gag ecology presented in Koenig et al. (1999). My qualifications to provide this review include 12 years of research experience in the ecology and management of tropical and temperate reef fishes, including several species of Epinephaline groupers, and several years of research experience in the ecological dynamics of Marine Protected Areas.

1. Sex Change in Reef Fishes

The presumed evolutionary advantage of sex change is enhanced reproductive opportunity on spawning grounds (Shapiro 1983). The proximal causes of sex change have been studied for a number of small, territorial reef fishes, mainly labrids (Warner 1984), pomacentrids (Schwarz and Smith 1990), and Anthiine serranids (Shapiro 1983, 1987, 1989). In these fishes, sex change is sociodemographically controlled. Removal of males from the population leads to sex change in the dominant (largest) female (Shapiro 1989). In other fishes, particularly freshwater species, sex change may occur at a genetically predetermined size or age, or may be brought about by changes in temperature or photoperiod (e.g., Yeung and Chan 1987a,b).

Small reef fishes typically occupy stable social systems throughout the year and thus have continual access to information regarding local sex ratios and spawning rates (Shapiro et al. 1993). This information, which likely relates to future reproductive success, will be more obvious to species that spawn regularly over protracted periods than to those that spawn in short lived aggregations. Shapiro et al. (1993) suggest that the sex ratio of interest for a fish to assess the pros and cons of changing sex would be the spawning sex ratio in future aggregations. That sex ratio would depend upon the current spawning sex ratio within the aggregation, the proportion of adults surviving to spawn in subsequent years, and the proportion of inshore juveniles surviving to mature and enter successive aggregations.

Protogynous hermaphrodites are those in which most, if not all, individuals begin life as females and subsequently become males (Huntsman and Schaaf 1994). In some grouper populations, males are more

or less absent until the cohort reaches age 10, and in the case of red grouper (*Epinephalus morio*), the cohort sex ratio is not equal until age 15 (Shapiro 1987b). Many species of grouper can live 20 years or more (Manooch 1987). Reef fishery managers are concerned that fishing might affect the reproductive capacity of protogynous fish stocks more severely than it affects gonochoristic (separate sexes) stocks. Huntsman and Schaaf (1994) point out that both protogynous and gonochoristic populations tend to lose reproductive capacity as fishing pressure increases, since both types suffer a decrease in stock biomass and consequently in egg production. In protogynous stocks, however, increased fishing mortality might reduce the relative abundance of males by reducing the abundance of older age-classes, and diminish the probability that eggs will be successfully fertilized (Garra 1985; Burton and Clarke 1986). In extreme cases, fishing might remove all the age-classes that contain males and thereby preclude any reproduction. It is not known whether compensatory mechanisms exist in grouper populations, although Huntsman and Schaaf (1994) have modeled the effects of fishing pressure on protogynous populations with and without various compensatory mechanisms, and on gonochoristic populations also. Their work is reviewed in a later section of this document. As stated in their paper, research necessary to obtain specific information on protogyny is slow, expensive, and unlikely to be completed soon.

Current theory holds that sex change in fishes is induced by loss of behavioural interactions between males and females, combined with continued interaction between females (Shapiro 1983). Koenig et al. (1999) suggested that the loss of male-female interaction in gag occurs at the end of the aggregation period, when females purportedly return to shallower, inshore waters. The question of whether or not sex change in groupers is socially mediated is presently unanswered and probably unanswerable without a great deal more experimental research. Shapiro et al. (1993) outline the information needed to identify behavioral control of sex change. First, the fish must be sequentially hermaphroditic. Second, reproduction must occur predominantly within the aggregation. Third, information on sex ratios must be available only to individuals within the aggregation. Fourth, sex change must occur in temporal proximity to the spawning aggregation. Lastly, individual fish must return to the same aggregation site each year.

To date, the only species of grouper in which the proximal causes of sex change have been investigated is the red hind (Shapiro et al. 1993). With regards to the above requisites for social mediation of sex change, only red hind and coney (*Epinephalus fulva*) have been histologically proven to be protogynous (Shapiro 1987b). Colin (1992) suggested that groupers that aggregate are not necessarily protogynous. For example, neither Nassau grouper nor yellowfin grouper (*Mycteroperca venenosa*) has definitely been shown to be protogynous, although both are known to aggregate. Red hind and coney, which are proven protogynous hermaphrodites, display harem spawning (Shapiro 1987b, Colin 1992). Gag are most likely also protogynous, as evidenced by the existence of transitional males (Coleman et al. 1996, McGovern et al. 1998).

Except for the red grouper (*Epinephalus morio*), no spawning of grouper has been reported outside aggregations, but far too little effort has been spent searching for such events. Certainly, the possibility exists that groupers may spawn in small groups or pairs outside of major aggregations, and the sex ratio of smaller groups could differ from that of aggregations. Colin (1992) observed no courtship behaviour of Nassau grouper outside of spawning aggregations in the Bahamas during limited observations. However, courtship behaviour was observed in groups of only three to four Nassau grouper at South Caicos, in the Turks and Caicos islands (author's personal observations). South Caicos has abundant Nassau grouper stocks, but no known spawning aggregation sites. Of course, the occurrence of courtship behaviour itself is no proof that actual spawning will occur outside an aggregation.

Whether or not information on sex ratios is available to individual groupers outside of aggregations is unclear. The Nassau grouper (*Epinephalus striatus*) spawns in very large aggregations (thousands to tens of thousands of fish) for only a few weeks of the year (Colin 1992). Males and females of this species co-occur throughout the year. In contrast, male and female gag (*Mycteroperca microlepis*) and red hind (*Epinephalus guttatus*) co-occur only during the spawning season. The spawning season of gag is longer than that of Nassau grouper or red hind, and extends from January to April. Gag grouper are thought to spawn in relatively small aggregations (Coleman et al. 1996) and water depths of 50 - 120 m (Gilmore and Jones 1992). Females apparently leave the aggregation site in March-April and remain in shallower inshore waters until the following winter. Thus, as hypothesized for red hind (Shapiro et al.

1993), gag may only have access to information on sex ratio and population structure while aggregating at spawning sites. However, as discussed above, the existence of smaller reproductive units outside the aggregation cannot be completely ruled out.

Shapiro et al. (1993) hypothesized that red hind assess the best time to change sex within the aggregation, and actually initiate sex shortly thereafter. They therefore predicted the transitional individuals should occur predominantly shortly after the aggregation. This prediction was not supported by their results. Transitional red hind were rare, but were found during most months of the year. Koenig et al. (1999) report small numbers of transitional gag from December to July, a range not particularly indicative of sex change beginning immediately after spawning. Shapiro et al. (1993) offer a number of possible interpretations of such results. First, sex change may be initiated well before the appearance of histologically recognizable changes in the gonads of this species. There are no apparent advantages to individuals completing sex change soon after the aggregation disperses. These fish will not spawn again for another ten to twelve months and the absence of social structure in nearshore waters indicates no behavioral advantage to becoming a male quickly. Another interpretation is that individuals do not assess the best time to change sex during the aggregation. The only data available on sex ratio and social structure of gag outside of the aggregation comes from predominantly female populations in shallow, nearshore waters. However, if populations of gag exist year-round on reefs either deeper or shallower than the known spawning aggregations in groups whose structure and sex ratio are similar to those within the aggregation, then information on when to change sex would be available to them throughout the year (see Shapiro et al. 1993).

As discussed above, Koenig et al. (1999) attributed an increase in relative catch of transitional and male gag shortly after the spawning period to induced sex change mediated by behavioural interactions within the aggregation. However, a more parsimonious explanation of the shift in sex ratios is that male fish simply remained longer on the spawning site than female fish. Some clear differences in the residence patterns at aggregations have been observed between male and female fishes (e.g. Morgan and Tripple 1996, Zeller 1998). Males spend considerably longer at spawning sites than females, and also undertake more trips to spawning aggregation sites. Zeller (1998) found that male leopard coral grouper (*Plectropomus leopardus*) spent 8 times longer at spawning aggregations than females did. The energetic cost of reproductive development is typically much higher in female fish than in males (Weiser 1989), and female fish typically spawn fewer times and for a shorter duration than males. It is in the best interests (from an evolutionary standpoint) of male fish to be prepared to fertilize eggs during the time that females are ripe. This increases the chance that a given male can spawn with multiple females. Male fishes therefore tend to arrive at aggregation sites earlier than females and leave later than females. Thus, the assertion of Koenig et al. (1999) that sex change in gag takes place immediately following the spawning aggregation must be viewed with caution.

Tagging studies have shown that gag can migrate several hundred km (Van Sant et al. 1994, Heinisch and Fable 1999), ostensibly to spawning sites. Colin (1992) and Carter (1987) found that the Nassau grouper can also migrate several hundred km, and evidence exists that this species travels to and from spawning aggregation sites. However, there is presently no evidence to confirm that gag migrate to the same spawning aggregation each year.

In summary, of the five items identified by Shapiro et al. (1993) as necessary for behavioural control of sex change, only the first (sequential hermaphroditism) is a certainty in gag populations. Thus, while the limited evidence available may point to behavioural control of sex change in gag, it by no means beyond dispute. Another possibility is that sex change is not behaviourally mediated but is controlled by the attainment of a critical developmental stage that might occur at any time during the year. Shapiro et al. (1993) failed to induce sex change in female red hind by removing single males from caged groups. While this result does not prove developmental control of sex change, it does suggest that behaviour is not the only process mediating sex change. Shapiro et al. (1993) point out that until more is known about sex ratios and social structures of groupers outside of aggregations, no choice can be made from among these alternative explanations.

2. Effects of Fishing on Protogynous Populations

As discussed previously, the effects of fishing on protogynous populations are exceedingly difficult to measure without very complete information on the reproductive patterns, sex ratios, and other biological aspects of fish stocks. Since this information is more often than not incomplete or unavailable for groupers, we can only speculate on the response of such populations to increased fishing. Huntsman and Schaaf (1994) modeled the effects of varying levels of fishing pressure on reproductive capacity of the graysby (*Epinephalus cruentatus*), a small protogynous grouper. They provided five different scenarios concerning the reproductive patterns of graysby. The first was uncompensated protogyny, in which the neither the rate of transition or age of onset of transition changed in response to changes in sex ratio resulting from increasing fishing pressure. In the second model, the onset and rate of transition were allowed to change as fishing pressure increased, but the sex ratio in the population remained fixed. This scenario is termed number-compensated protogyny with fixed maturation. The third model was number-compensated protogyny with variable maturation. This was identical to the previous scenario except that the onset and rate of female maturation was also allowed to vary as fishing pressure increased. The fourth option was termed biomass-compensated protogyny with fixed maturation. In this simulation, the reproductive capacity of the population was compensated in response to decreases in the ratio of male biomass to population fecundity. The onset and rate of female maturation did not vary with fishing mortality. The final option was growth-compensated protogyny, in which growth rate increased in response to increased fishing mortality.

Huntsman and Schaaf (1994) found a rapid decline in reproductive capacity as fishing mortality (F) increased regardless of reproductive mode. Even the gonochoristic stock lost over 90% of its intrinsic fertilized egg production if F was set at 0.4 and 70% if F was as small as 0.17. Increased fishing mortality caused substantially higher losses of reproductive capacity in the stock exhibiting uncompensated protogyny than in the gonochoristic stock, but some forms of compensation prevented or reduced these losses. Biomass-compensated protogyny resulted in a reproductive decline identical to that of the gonochoristic stock. Numerical compensation allowed much greater reproductive capacity with increasing F than was exhibited by the uncompensated protogynous stock. Stocks displaying uncompensated protogyny lost reproductive capacity as fishing increased and failed reproductively at a lower fishing mortality rate.

In summary, conservation of the numerical sex ratio somewhat reduced the impact of protogyny, and compensation through the conservation of the cohort male biomass: fecundity ratio erased all effects of protogyny (Huntsman and Schaaf 1994). Koenig et al. (1999) suggest that loss of male gag is compensated by sex change soon after the spawning period, and that the rate and age/size of transition and maturation is variable in this species. If this is true, then Huntsman and Schaaf's model suggests that populations of gag subjected to heavy fishing pressure should suffer less of a decrease in reproductive capacity than a typical gonochoristic population.

3. The relative availability of male and female gag to hook-and-line fisheries.

Koenig et al. (1999) suggest that male gag may be more vulnerable to hook-and-line fishing than female gag during spawning periods. They attribute this to the aggressive behavior demonstrated by male gag at spawning sites, citing a greater propensity of males than females to take baited hooks. While some studies do mention intraspecific aggression of aggregating groupers (e.g. Gilmore and Jones 1992), none mention aggression towards other species, and there is no published evidence that male gag (or any other male grouper) are more apt to take a baited hook than female conspecifics.

4. The role of area closures in management of grouper stocks.

Areas closed to fishing have been advocated as a management practice in areas where typical fisheries management programs are not feasible, particularly in developing nations where budgets are tight and little information is available on the population dynamics of multi-species reef fish assemblages (Roberts and Polunin 1991). Marine reserves have generally been successful in increasing biomass of small, site-attached reef fishes such as grunts (Tupper and Juanes in press), that typically move no more than a few hundred m during foraging. Marine reserves have been highly touted by many as a means of increasing grouper biomass and production (e.g. Coleman et al. 1996, McGovern et al. 1998, Sluka and Sullivan 1998). However, the evidence from experimental studies of protection of grouper does not support the praise given to area closures as a management tool. For example, Sluka and Sullivan (1998) found no significant influence of spear fishing outside the Florida Keys National Marine Sanctuary and John Pennekamp Coral Reef State Park on the relative abundance of targeted grouper species. Similarly, Polunin and Roberts (1993) found no significant difference in abundance of grouper between fished and protected areas around the island of Saba, and no significant difference in biomass of grouper between fished and unfished areas in Belize, although grouper abundance was higher within the protected area. A study by Rakitin and Kramer (1996) found no difference in the density of coney between fished and protected areas in Barbados, where the coney is targeted by the trap and spear fisheries. Ferreira and Russ (1995) found no significant differences in mean size and age of leopard coral grouper (*Plectropomus leopardus*) between protected and unprotected reefs in the Great Barrier Reef 3-4 years after protection was established.

Another factor reducing the usefulness of area closures in management of gag is the distances over which this species migrates. In order for protective management to have any effect on gag stock abundance and biomass, the fish must spend most of its time within the boundaries of the protected area. According to the tagging data presented by Koenig et al. (1999), most of the South Atlantic Eight and northeastern Gulf of Mexico would need to be closed to achieve this.

While area closures may appear to be a worthwhile precautionary measure, they pose a number of problems that render them a poor choice in the absence of solid evidence for increased fish biomass both within the protected area and on the surrounding fished grounds. Closures of the size proposed by Koenig et al. (1999) might cause serious hardship and loss of income to fishers whom rely on that area for much of their income. This is especially true in the case of species that aggregate to spawn. Fishers dependent on these species often generate the majority of their annual income by fishing for 2-3 months over a few square miles. The issue of gag migration is also troublesome in the context of area closures. Much more information is needed on spawning migration routes and spawning aggregation sites of gag before such a drastic measure is taken.

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