Environmental Biology of Fishes **47**: 129–141, 1996.

Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations

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Received 21.6.1995 *Accepted 24.1.1996*

Key words: Sex ratio, Protogyny, Sex change, Spawning, Selective fishing pressure

Synopsis

Seasonal and spatial aspects of spawning for three commercially important grouper species in the northeastern Gulf of Mexico are detailed. These species – all of which are protogynous hermaphrodites – spawn in deep water (> 25 m for red grouper, > 40 m for gag and scamp), making it difficult to observe spawning behaviors without ROV or submersible support. They respond to intense fishing pressure in ways that are directly related to their respective reproductive styles. Species that aggregate appear to be more susceptible to such pressures than those that do not, as evidenced by marked skewing of sex ratios in favor of females. Gag, *Mycteroperca microlepis,* have suffered a drop in the proportion of males from 17% to 1% in the last 20 years; scamp, *Mycteroperca phenax,* have dropped from 36% to 18%; and red grouper, *Epinephelus morio,* which do not aggregate, have shown little change in the sex ratio over the past 25–30 years.

Introduction

The interaction of fishing pressure and reproductive characteristics of exploited species is poorly understood and rarely addressed (Buxton 1993), yet this interaction can lead to alteration of life history traits that result in impaired reproductive potential (Huntsman et al.)[1]. The changes are brought on by direct removal of gravid individuals, by rapid reduction of the average fish size, or by reduction of male:female sex ratio. The proximate consequence is reduced average fecundity of the population; the ultimate consequences include decreased effective population size, reduced population growth, and extinction, be it economic, local, or complete.

Certain species, because of their reproductive characteristics, clearly are more susceptible to overexploitation than are others. For example, species that form spawning aggregations are more susceptible than species that do not (Olsen & LaPlace 1979, Carter et al. 1994, Sadovy 1994, Sadovy et al. 1994b), and species that change sex (protogynous and protandrous hermaphrodites) are more susceptible than gonochorists (Bannerot 1984, Bannerot et al. 1987, Buxton 1993). Because all of the shallow-water groupers (family Serranidae) that sup-

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[1] Huntsman, G.R., D.S. Vaughan & J. Potts. 1994. Trends in population status of the red porgy *Pagrus pagrus* in the Atlantic Ocean off North Carolina and South Carolina, USA, 1972–1992. (Report) NMFS/SEFSC Beaufort Laboratory, Beaufort. 73 pp.

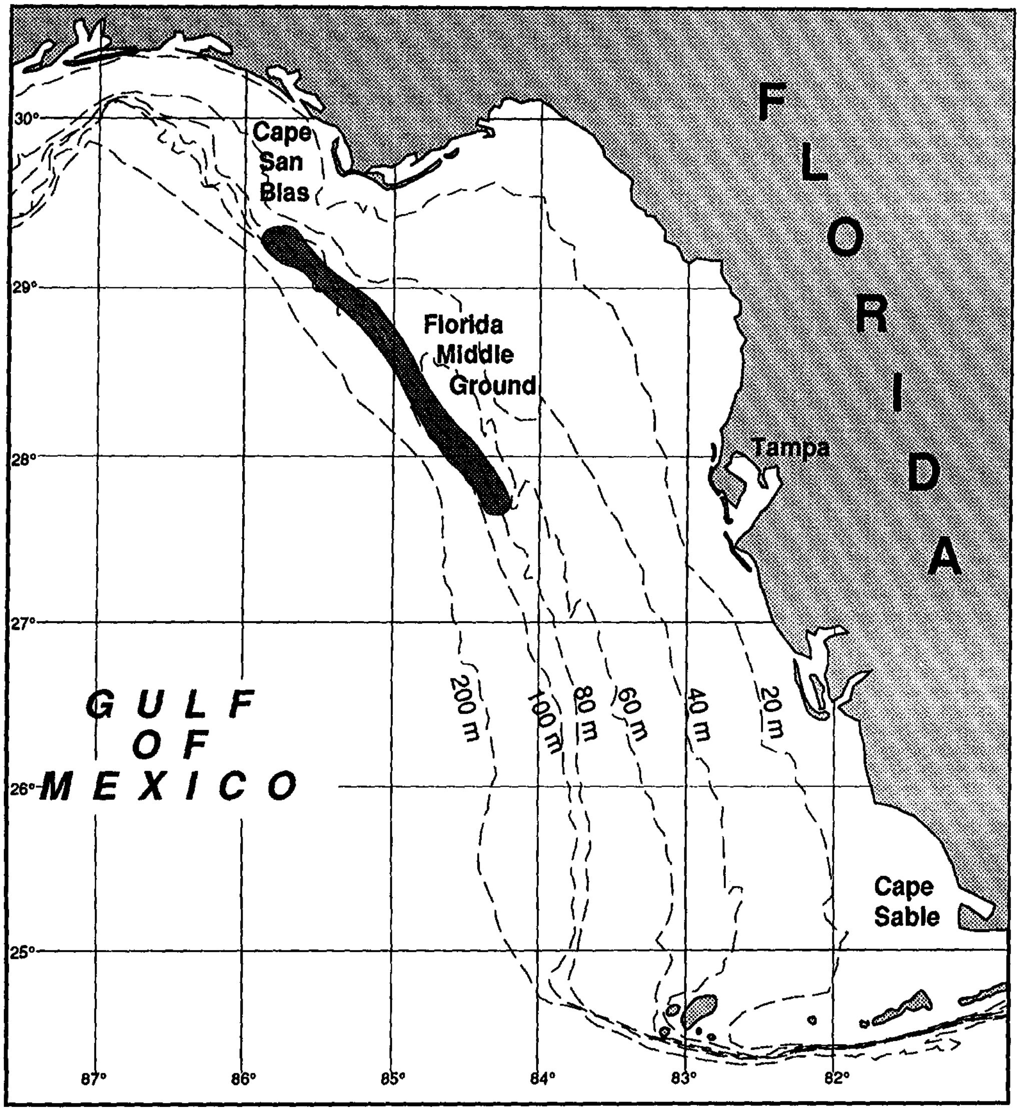

Fig. 1. Dominant spawning grounds (shaded area) for gag, *Mycteroperca microlepis*, off the gulf coast of Florida.

port major commercial and recreational fisheries in the southeastern United States (Bullock & Smith 1991) – including gag, *Mycteroperca microlepis,* scamp, *M. phenax*, and red grouper, *Epinephelus morio* – are protogynous hermaphrodites (Shapiro 1987), they are of particular interest in this regard. In this study we describe aspects of the reproductive biology of these species, expanding our account (Koenig et al. 1996) on gag, and discuss how the reproductive characteristics demonstrated among groupers affect their susceptibility to overfishing.

Methods

We investigated the spatial and temporal spawning patterns of gag for three years (1991–1993), red grouper for two years (1991–1992), and scamp for one year (1992). All samples were collected in the northeastern Gulf of Mexico by Florida commercial fishermen using standard hook-and-line gear. Data obtained for each fish included total length (TL; centimeters), collection date, location, and depth (meters). Florida State University (FSU) 1991 samples were taken year-round from relatively shallow waters (< 40 m) between Tampa and Apalachicola ($N_{gag} = 991$, $N_{red} = 816$); 1992 samples were taken from January through August ($N_{gag} = 633$, $N_{scamp} = 160$, $N_{red} = 510$) both in shallow water (< 40 m, 30% of samples) between St. Marks and Apalachicola and from offshore spawning sites (Fig. 1; 70% of samples). National Marine Fisheries Service (NMFS) samples were collected between Pensacola and St. Marks: gag ($N_{1991} = 440$, $N_{1992} = 319$, $N_{1993} = 623$), scamp ($N_{1991} = 137$), and red grouper ($N_{1991} = 110$). Depth of capture is unknown for these samples.

We determined the distribution of gag spawning sites by interviews and chartered trips with commercial fishermen. The shallow limit to the spawning depth range (Fig. 1) was confirmed by analysis of the distribution of gonadosomatic indices (GSI, 100 × gonad weight/total body weight) by depth during peak spawning; the deep limit was determined by the presence of suitable habitat for spawning – beyond 120 m, the substrate is sand with little relief.

Effects of fishing on spawning aggregations

To determine whether seasonal and site-specific fishing pressure on spawning aggregations caused demographic changes in grouper stocks, we compared both size- and sex-frequency distributions of mature fish (i.e., excluding juveniles and subadults) from recent catches with those from historical catches. This comparison was made for gag caught in the northeastern Gulf of Mexico and the South Atlantic. In the gulf, FSU 1992 collections were compared with those of Hood & Schlieder (1992) from 15–20 years ago. All samples were collected from overlapping geographical areas (inshore and offshore regions) and by the same methods (hook-and-line commercial and recreational catches), thus limiting bias in comparing the different data sets. From the South Atlantic, we compared recent data from the NMFS Beaufort Laboratory (samples from South Carolina; unpublished data from October 1995 gag reproductive study monthly report) with historical data (samples from South Carolina; Collins et al. 1987) from 15–20 years ago. All Atlantic samples were collected by hook and line.

Gonads were removed from freshly killed fish and either frozen or preserved in Davidson's solution. Sex was determined microscopically because we found gross examination to be unreliable, particularly for sexing reproductively inactive individuals. Freshly frozen gonads were adequate for identifying sex and staging oocyte development, but histological sections were required for distinguishing immature from reproductively inactive females.

Frozen gonads were thawed, blotted, weighed to the nearest 0.1 g, and sexed from squashes of tissue samples (Link 1980). Each squash was examined under a compound microscope for sex, stage of oocyte development (after Moe 1969), range of oocyte size per stage, and presence or absence of late-stage atresia (brown bodies), if possible. Whenever sex was questionable, we made hematoxylin and eosin stains of new squashes (Link 1980) to identify transitionals (individuals in the process of changing sex from female to male). The presence of hydrated eggs in ovaries and motile sperm in testes confirmed reproductive activity.

Sections (10 μ) of preserved gonads were mounted on slides, stained with hematoxylin and eosin, and examined microscopically for level of development according to the methods of Moe (1969): immature fish had small, extremely compact gonads consisting of oogonia and oocytes of stages 1 and 2; ripe fish contained oocytes of stage 3 or higher in the ovaries; and inactive fish (mature, nonreproductive) contained oocytes of stages 1 and 2 loosely held in a stroma or showed evidence of early oocyte degeneration. In the latter case, the gonadal wall (tunica) was typically thick, suggesting, but not confirming, prior spawning activity within the observed season or in the life of the fish. Postspawning individuals could be identified histologically by the presence of early-stage degeneration of vitellogenic oocytes or postovulatory follicles.

Gonadosomatic indices and the presence of hydrated eggs were compared across date, depth, and geographical location to determine spawning season, spawning depth, and spawning location. Weights were obtained by conversion of lengths following Bullock & Smith (1991):

gag: $W = 2.680 \times 10^{-8}\ SL^{2.958}$,
red grouper: $W = 5.420 \times 10^{-8}\ SL^{2.897}$,
where W = weight in kilograms, and SL = standard length in millimeters. Conversion for SL (cm) to TL (cm) for gag and red grouper are as follows:
gag: $TL = 1.14\ SL + 3.17$,
red grouper: $TL = 1.10\ SL + 3.30$.
For scamp, we used

$$W = 8.995 \times 10^{-9}\ FL^{3.067},$$

where FL = fork length in millimeters (Bullock & Smith 1991). We considered FL to be an adequate estimator of TL because of the shape of the caudal fin; the caudal is not forked, and the lengths of the outer caudal fin ray excertions are highly variable. Gonadosomatic indices were only determined for females. Active testes in each of these species were small and so were not used in GSI analyses. Seasonal changes in length-weight relationships for body mass are unimportant. These differences are minor relative to the enormous differences in gonad mass.

Results

Sexual maturity and sex ratio

All gag > 66 cm TL were mature; minimum size observed at maturity was 49 cm TL ($N_{mature} = 536$, $N_{immature} = 42$); 50% maturity occurred at 61.5 cm TL ± 0.96 SE, as determined by probit analysis. Insufficient samples were available for determination of size at maturity for red grouper and scamp.

Sex ratios in the three grouper species examined are given in Table 1, including sex ratios both from this study and from historical data sets.

Spawning location, depth, season, and pattern

Gag

Gag spawned on offshore reefs from southeast of Apalachicola to west of Tampa (and possibly further to the south) west and northwest of an area known as the Florida Middle Grounds (Fig. 1) at depths around 80 m (range: 50–120 m). It is unclear whether and to what extent the present spawning area exceeds the identified range, but the gulf fishery for gag is concentrated on the west Florida Shelf (Schirripa & Goodyear)[2], suggesting that this area is the major spawning area for gag grouper in the Gulf of Mexico.

All gag collected in 1991 were taken from shallow

Table 1. Numbers of individuals and proportion of males, females, and transitionals collected for northeastern Gulf of Mexico groupers; sex ratios (male:female) for each species. All fishes were mature.

Species	Collection area	Study	Collection dates	Males		Transitionals		Females		Sex ratio male:female
				N	%	N	%	N	%	
gag	N.E. Gulf of Mexico	Hood & Schlieder 1992	1977–1980	134	17	6	0.8	659	82	1:4.9
	N.E. Gulf of Mexico	NMFS	1991	12	2.7	1	0.2	427	97	1:35.6
	N.E. Gulf of Mexico	NMFS	1992	8	2.5	2	0.6	309	97	1:38.6
	N.E. Gulf of Mexico	NMFS	1993	8	1.3	2	0.3	613	98	1:76.6
	N.E. Gulf of Mexico	FSU	1992	9	1.9	3	0.6	457	97	1:50.8
	off South Carolina	Collins et al. 1987	1977–1982	51	17	4	1.3	253	82	1:5.0
	U.S. South Atlantic	NMFS Beaufort Lab	1994	44	3.4	6	0.5	1233	96	1:28.0
scamp	N.E. Gulf of Mexico	Hood, unpublished data	1970's	291	37.9	0	–	477	62	1:1.6
	N.E. Gulf of Mexico	NMFS	1991	33	24.1	0	–	104	76	1:3.2
	N.E. Gulf of Mexico	FSU	1992	26	18.3	0	–	116	81.6	1:4.5
red grouper	N.E. Gulf of Mexico	Moe 1969	1960's	109	14.4	11	1.5	638	84.2	1:5.9
	N.E. Gulf of Mexico	NMFS	1991	34	30.9	0	–	76	69.1	1:2.2
	N.E. Gulf of Mexico	FSU	1991	56	21.7	1	0.4	201	77.9	1:3.6
	N.E. Gulf of Mexico	FSU	1992	51	22.4	0	–	177	77.6	1:3.5

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[2] Schirripa, M. & P. Goodyear. 1994. Status of the gag stocks of the Gulf of Mexico. NMFS/SEFSC Miami Laboratory Contribution No. MA-93/94-61. 156 pp.

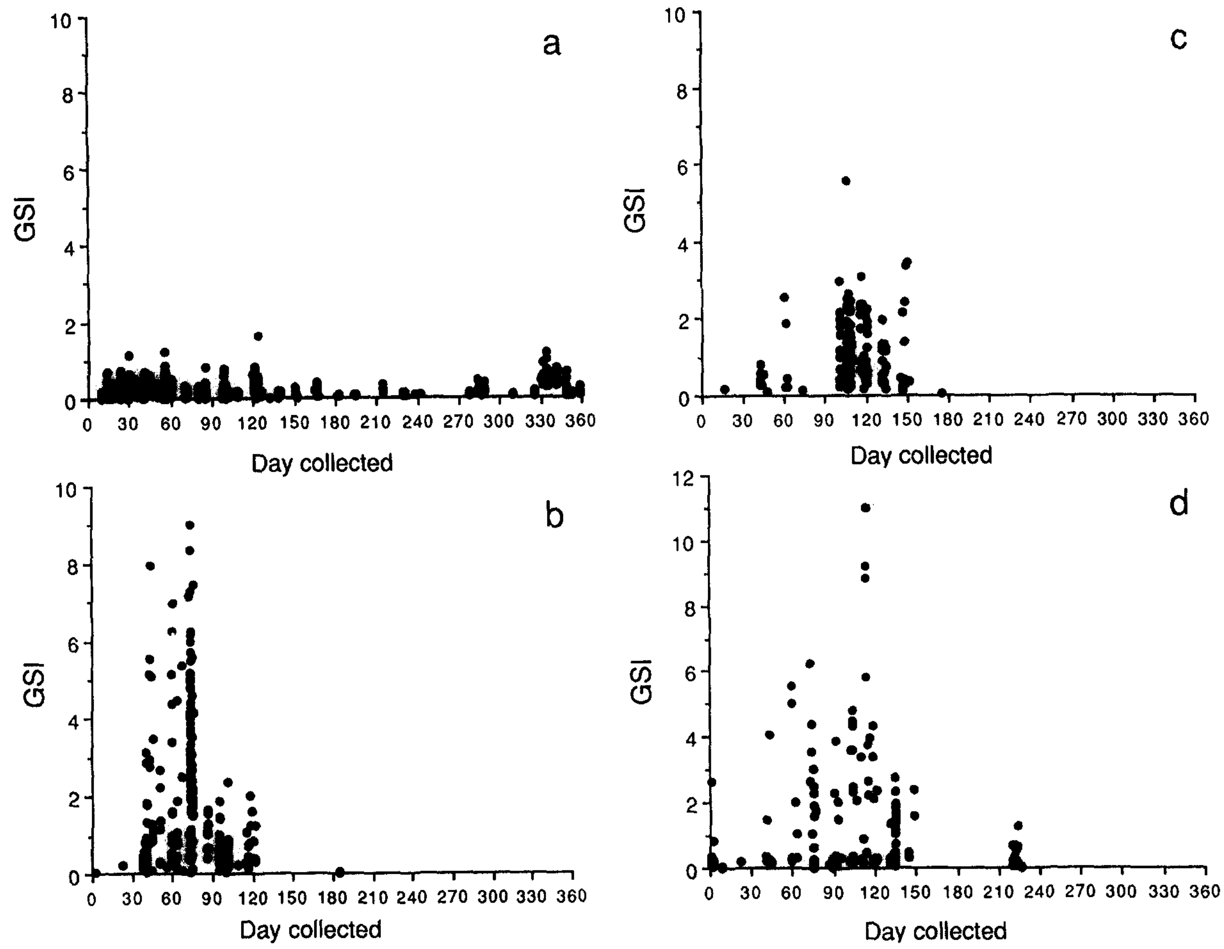

Fig. 2. Distribution of gonadosomatic indices relative to date of capture: a – gag, *Mycteroperca microlepis*, 1991 year round (n = 904); b – gag, *Mycteroperca microlepis*, 1992 during peak-spawning season (N = 252); c – scamp, *Mycteroperca phenax*, 1992 (N = 154); d – red grouper *Epinephelus morio*, 1992 (N = 223).

water and had small gonads year-round; gonad size increased somewhat between January and May (Fig. 2a). Gag collected in 1992 were taken primarily from offshore sites during the spawning period. Reproductively active individuals were found from February through April; peak spawning occurred from mid-February through March (Fig. 2b). During peak spawning, most mature females (those > 55 cm SL) caught at depths > 50 m had large gonads filled with late-stage vitellogenic and/or hydrated eggs; males had small testes with active sperm. About 80% of the females caught on spawning aggregations had late-stage atretic eggs, as indicated by the presence of brown bodies. Fish collected from spawning aggregations were larger than fish collected in shallow water (< 50 m) ($y = 58.3 + 0.295\ x$, $r^2 = 0.181$, $p < 0.05$) (Fig. 3). All gag collected in shallow water were female.

Of the gag collected in shallow water during the 1992 spawning season, 112 (110 females, two transitionals) were examined histologically for determination of reproductive state. Nineteen of the females were clearly immature, 67 reproductively inactive (47 mature but not in spawning condition and 20 of uncertain maturity), and 24 mature with ripe ova. Of the mature fish not in spawning condition, 10 females showed no indication of either imminent or past spawning activity; three collected in February had developing oocytes, suggesting that they

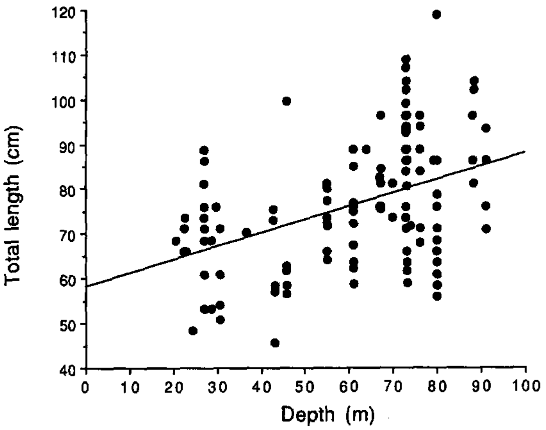

Fig. 3. Distribution of total length (centimeter) for gag, *Mycteroperca microlepis*, relative to depth of capture during peak spawning in March 1992 (N = 201). $y = 58.3 + 0.295x$; $r^2 = 0.181$.

were in prespawning condition; and two collected in March were in postspawning condition.

Scamp

Scamp frequently co-occurred with gag on offshore reefs during spawning periods, but the two groups did not intermingle (ROV observations, Koenig). Scamp were rarely found in shallow water and appeared to spawn at depths > 60 m. Scamp began spawning at about the same time of year as gag, but their season extended later into the spring (Fig. 2c); spawning peaked from late February through early June.

Red grouper

Red grouper occasionally occurred on reefs with gag and scamp but were incidental. They spawned in relatively small polygynous groups and appeared neither to aggregate nor to have depth-specific spawning sites within the 25 to 120 m depth range. We observed a male red grouper in a presumed courtship display but saw no actual spawning. The red grouper reproductive season extended from late fall to late spring; spawning peaked in April (Fig. 2d).

Seasonality of gag catches and fishery effects on population demographics

Gag

The highest catches for gag from 1986–1992 (J. O'Hop, Florida Marine Research Institute, Department of Environmental Protection, St. Petersburg, unpublished data) occurred immediately before, during, and after peak spawning (Fig. 4a). Although the mean number of trips declined during that same period (Fig. 4b), correlating with the high incidence of storms and danger associated with fishing far offshore in the winter, the catch per unit effort increased (Fig. 4c).

Changes in the Gulf of Mexico gag population demographics occurred during the 1980's, most notably in a modal shift toward smaller fish and a decrease in the proportion of males in the population

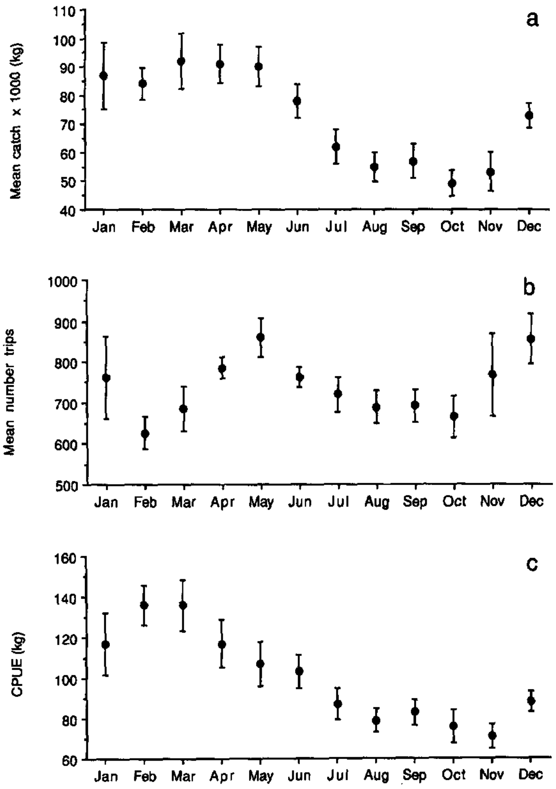

Fig. 4. Landings for gag *Mycteroperca microlepis* in the Gulf of Mexico: a – mean catch (10^3 kg); b – mean number of trips; c – catch (kg) per unit effort (CPUE). Circles represent mean values; vertical bars represent standard errors.

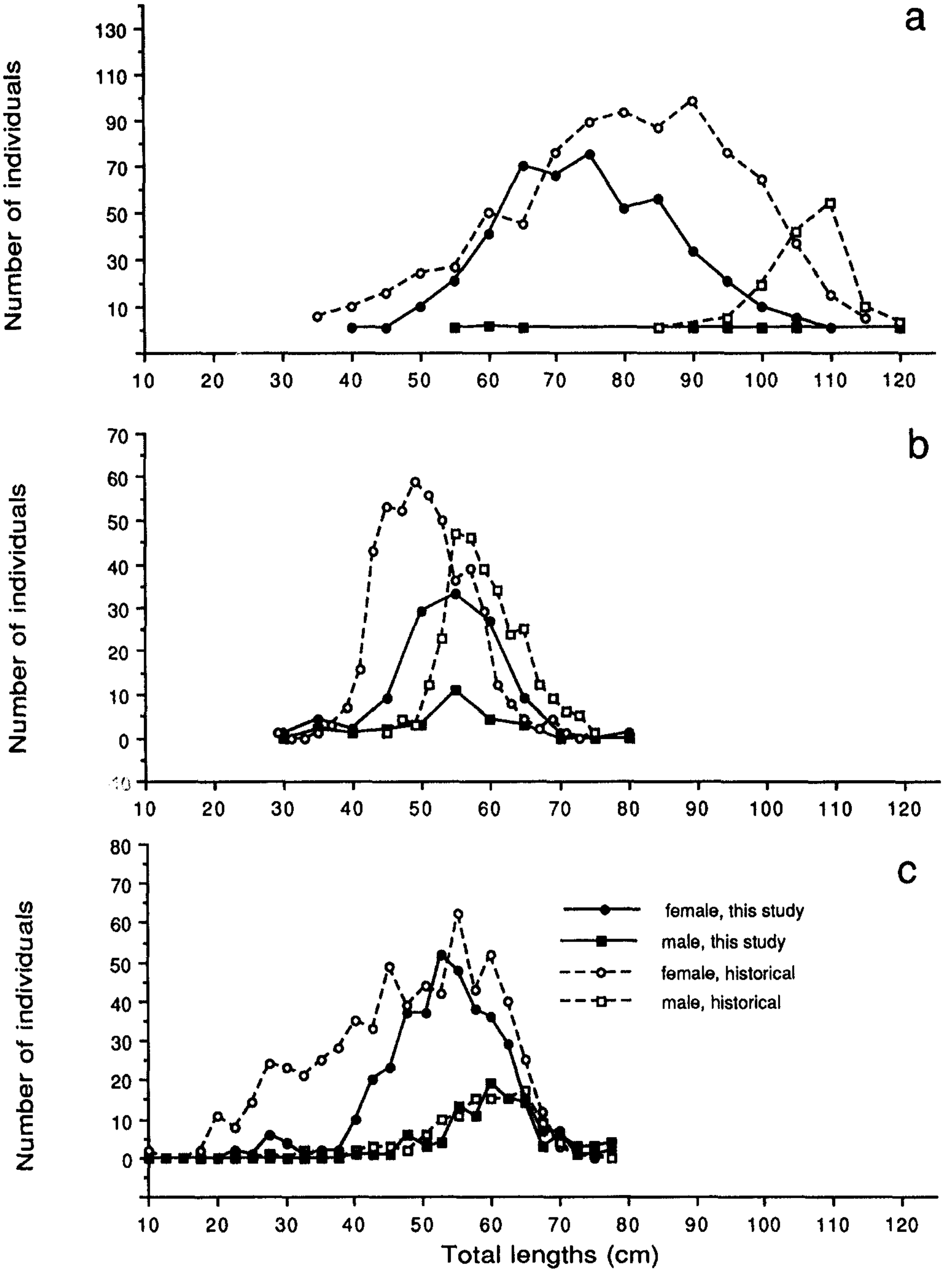

Fig. 5. Sex-by-size-frequency distributions: a – gag, *Mycteroperca microlepis*; data from this study (N_{female} = 464, N_{male} = 9) and historical data from 1977–1980, Hood & Schlieder (1992) (N_{female} = 818, N_{male} = 134). b – scamp, *Mycteroperca phenax*, data from this study (N_{female} = 116, N_{male} = 26) and historical data from late 1970's, Hood unpublished data (N_{female} = 477, N_{male} = 291). c – red grouper, *Epinephelus morio*, data from this study (N_{female} = 381, N_{male} = 107) and historical data from the 1960's, Moe (1969) (N_{female} = 638, N_{male} = 109).

(Fig. 5a, Table 1). These results are particularly notable in view of the methods of data collection. Hood & Schlieder (1992) were not aware of spawning-site locations and thus did not concentrate collections in these areas. As a result, their samples cover both inshore and offshore sites, and their data represent the low end of the scale for that time period for average fish size and male abundance, given that larger fish are concentrated offshore and males are known to occur only on spawning sites. Our collections, on the other hand, came almost exclusively from spawning aggregations and so represent the high end of the scale for the more recent time period. Thus our estimates of the reduced size and reduced proportion of males in the population are probably conservative.

Similar changes in six ratios have occurred in the Atlantic. Before the 1980's, the gag population off South Carolina contained about 17% males; in more recent samples, the proportion of males had declined to about 3.9% of the stock of mature fish (Table 1).

Scamp

A comparison of size frequency data for males and females from this study with historical data (P. Hood, unpublished data from late 1970's) shows a pattern similar to, but less dramatic than, that of gag (Fig. 5b).

Red grouper

The frequency distributions of male and female red grouper have changed little in the past 25 to 29 years (Fig. 5c). Except for the absence of size classes smaller than the legal limit (50 cm TL) in recent catch data, the distributions nearly superimpose.

Discussion

Reproductive characteristics vary among grouper, but on the basis of the limited data available, it is clear that all of the northeastern Gulf of Mexico species discussed here – gag, scamp, and red grouper – are similar in being polygynous and having naturally female-biased sex ratios (Moe 1969, Colin 1992, Gilmore & Jones 1992, Shapiro et al. 1993, and the present study). The males all have small testes containing small amounts of milt when reproductively active, suggesting that they pair-spawn. Species having males with large, milt-filled testes (e.g., Nassau grouper) exhibit multiple-male-multiple-female spawning in which males compete for access to females and sperm competition is a factor (Colin 1992). These species differ from each other, however, in the degree to which they aggregate and the length of the spawning season. Gag and scamp migrate to specific spawning sites, where they form small (10's to 100's of individuals) aggregations over a large area. Red grouper, on the other hand, do not aggregate and appear to spawn in small groups. In this, they are more closely allied with coney, *Epinephelus fulvus,* and graysby, *E. cruentatus,* which spawn within territories defended by the male (Sadovy et al. 1994a). Red grouper and scamp are similar in having more protracted spawning seasons than gag.

Given the variation in life-history characteristics among protogynous species, we became interested in how population demographics were affected by exploitation. Fishing on spawning aggregations of gag and scamp, for example, results in a decrease in the average size of fish caught, a decrease in size of sexual transformation, and a significant decline in the male:female sex ratio. Fishing apparently affects red porgy *Pagrus pagrus,* a protogynous sparid, similarly (Huntsman et al. 1994), yet similar fishing pressure on spawning aggregations of red hind, *Epinephelus guttatus,* while causing a reduction in the average size of fish, does not appear to affect sex ratio (Shapiro et al. 1993). In red grouper, fishing has caused neither a marked size- nor a marked sex-ratio change in the last 25 to 30 years, even though it is one of the more heavily fished grouper species in the eastern Gulf of Mexico (P. Goodyear & M. Schirripa 1993, The Red grouper fishery of the Gulf of Mexico, prepared for the Gulf of Mexico Fisheries Management Council). What mechanisms cause these different responses, and when does fishing pressure have its greatest effect on population demographics? We suggest that the answer is directly related to the mechanism and timing of sex change in these fishes, making some species far more susceptible than others to overexploitation.

Bullough (1947) and McErlean & Smith (1964) assumed that sex change in sequential hermaphrodites was age- or size-mediated and therefore under endogenous control. Shapiro (1987), however, suggested that sex change was more probably mediated socially (under exogenous control) on the basis of evidence from a number of families (e.g., Shapiro 1980, Warner 1982, Ross et al. 1983, 1990). Although the sex-change mechanism has not been studied in a single grouper species, our data showing a decrease in size at transition in gag and scamp supports social rather than size-mediated sex change.

Current theory suggests that socially mediated sex change occurs either through size-ratio assessment (Ross et al. 1983, Lutnesky 1994) or through sex-ratio assessment (Shapiro & Lubbuck 1980). In size-ratio assessment, a given female changes sex when she perceives some ratio of smaller to larger individuals within the social group. Sex-allocation theory suggests that sex-ratio assessment determines the rate at which sex change occurs (Charnov 1982): when males are relatively abundant, the proportion of individuals changing sex will be low and, alternatively, when males are rare, the proportion undergoing transition should increase. In this way, a normal sex ratio is maintained in response to environmental change (Carter et al. 1994). We feel that sex-ratio assessment is the more likely proximate mechanism for sex change in groupers. Not only does it account for the production of new males in the presence of existing males, but certain features of the sex-ratio-assessment hypothesis provide the clearest explanation of the differing responses to fishing pressure seen among groupers and explains how these responses could lead to disruption of the sex-change mechanism.

Sex-ratio assessment can only occur when both sexes are present, so the window of opportunity for assessment and successive sex change will be limited temporally or spatially in some species, such as gag and red hind, but not in others, such as red grouper and Nassau grouper (Fig. 6). Red hind exhibit reproductive characteristics similar to those of gag – that is, they are polygynous, they pair spawn, males and females co-occur only during the spawning season, and females occur in relatively shallow water outside of the spawning period while males remain offshore (Shapiro 1987, Sadovy et al. 1994b). They differ from gag in that they have a more restricted spawning period that occurs within a week of the full moons of January and February, and their behavior is such that the males do not appear to be selectively fished (Shapiro et al. 1993).

Red grouper and Nassau grouper are similar in that males and females co-occur year round. They differ in that red grouper do not aggregate, whereas Nassau grouper form very large aggregations (thousands or tens of thousands of individuals) over a restricted area (Colin et al. 1987, Colin 1992) during an extremely restricted, lunar-phased spawning season, similar to red hind.

Male:female sex-ratio will be driven down either if fishing selects for males or if, in the absence of male selection, fishing pressure overrides sex-ratio regulating mechanisms. When sex-ratio controls operate year-round on and off spawning sites, fishing pressure is unlikely to alter sex ratio. This appears to be the case for both red grouper (sex ratio = 1:2 to 1:3, Table 1) and Nassau grouper (sex ratio = 1:1).

The presence of low numbers of male gag and scamp in the 1992–1993 catches suggests that fishing pressure is either size selective, sex selective, or both. Gilmore observed sex-selective fishing on male gag (Gilmore personal communication) and scamp (Gilmore & Jones 1992) while the fish were in spawning aggregations and postulated that fishing selection based on male behavior resulted in differential fishing mortality for males. Males of both species remained relatively high in the water column during courtship behaviors and appeared to take baited hooks more aggressively than did females.

The presence of fewer males should cause a compensatory response on the part of females, resulting in a greater number of transitionals in the population, but transitionals will be rare either if the social mechanism for sex change is disrupted, in which case compensatory sex change does not occur, or if transitionals, like males, are preferentially caught by hook and line. Shapiro (1987) demonstrated that sex-change initiation in *Pseudanthias* (ex. *Anthias*) *squamipinnis* was heralded by the female's adopt-

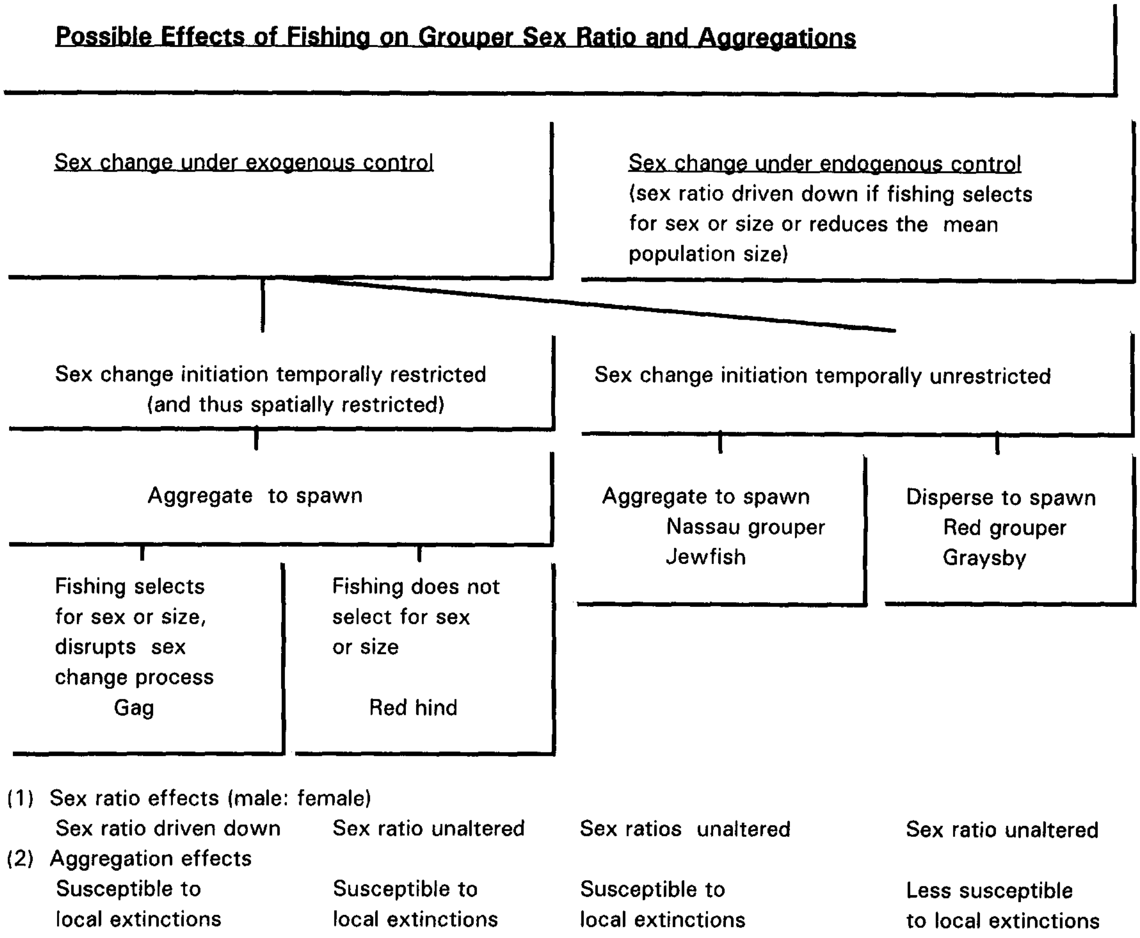

Fig. 6. Flow diagram of possible mechanisms for changes in sex ratio due to fishing pressure.

ing stereotypical male behaviors before any morphological evidence of impending sex change occurred. This finding strongly suggests that, for gag and scamp, early-phase transitionals may be as susceptible to capture as males.

Clearly loss of males has not diminished female reproductive capacity – females are large and well fed and have allocated considerable resources to reproduction – but male loss could have serious consequences for female reproductive potential. We find that some females either remain inshore during the entire spawning period, and thus never enter the spawning stock, or migrate to spawning sites, commit large numbers of eggs to vitellogenesis (an energetically expensive undertaking), and either do not spawn at all or spawn incompletely. Unspawned eggs, indicative of failed spawning opportunity, are resorbed, leaving behind evidence in the form of atretic bodies. Although high incidences of atretic bodies occur in other species in response to poor diet (Scott 1962) and termination of spawning (Hunter et al. 1986), in gag atresia is probably a response to the reduced number of males on spawning sites. This appears to be the case in white sucker, *Catostomus commersoni*. Reduction in the proportion of males in an Ontario lake population caused significant increases both in the incidence of atresia and in spawning failure (Trippel & Harvey 1990). The only way to demonstrate conclusively a similar effect in gag or scamp is to compare fished stocks (those with altered sex ratio) with unfished stocks (those with unaltered sex ratio), which we have been unable to do because no unfished aggregations are known.

We suspect that the reproductively inactive shallow-water female segment, like the high incidence of atresia, is related to male limitation, which results in disruption of social hierarchies and indicates failed spawning opportunities. This process could potentially lead to larger-scale spawning failures through what is known as the Allee effect, reduced population growth at low population size (Allee 1931). That is, if females rely on localized spawning cues from males or other conspecifics, which in this case are either absent or below some critical threshold population size, then total reproductive failure is possible.

The consequences to males of fewer males in the population may not be so clear. More females per male could mean enhanced reproductive potential for the remaining males, but the remaining 2% males in the gag population, for example, are not likely to be able to increase their gamete output to fertilize ten times the number of females they ordinarily encounter. As a result, some females probably go unspawned or, if males attempt to apportion sperm among available females at spawning sites, fertilization success is reduced (sperm limitation) (see Nakatsura & Kramer 1982, Levitan 1993, Shapiro et al. 1994 for examples of sperm limitation in fishes and invertebrates).

Intense aggregation fishing does not have to select for males in order to threaten the stability of grouper social groups. Removing significant numbers of individuals of either sex can be disruptive, particularly when members of the group depend on each other for spawning cues. Individual fish of several species of grouper (including scamp) have been observed to return to the same spawning sites in consecutive years (Waschkewitz & Wirtz 1990, Gilmore & Jones 1992). Spawning sites are therefore assumed to be traditional, and a spawning aggregation at a given site is assumed to consist of a distinct social group. Newly recruited, inexperienced fish learn the location of a particular spawning site by migrating with experienced fish. Fishing a site until no individual remain (a common practice among fishermen) leaves no experienced fish to entrain recruits into the social group. This process is believed to have caused the collapse of Nassau grouper fisheries throughout the Caribbean and western Atlantic (Olsen & LaPlace 1979, Bannerot et al. 1987, Sadovy 1994). Aggregations fished out decades ago have not been reestablished.

Commercial fishermen contend that gag spawning aggregations were once far more extensive than they presently are, occurring on sites southeast of Pensacola through the Middle Grounds to at least as far south as Tampa. Recent studies in the Atlantic support loss of spawning aggregations through overfishing. In the 1980's, hundreds of individuals of scamp and gag aggregated to spawn on Jeff's Reef (3600 m^2) off Fort Pierce, Florida (Gilmore & Jones 1992); by 1995, however, during the peak spawning season, no gag and only one small (8-individual) aggregation of scamp could be found during extensive submersible dives in the same area (Grimes, Koenig & Gilmore unpublished data), which is now part of a marine reserve established by the South Atlantic Fisheries Management Council. It is unknown whether spawning aggregations will reform in the absence of fishing.

Management needs

It is clear that we need to answer specific questions about the structure and function of spawning aggregations, male reproductive capacity, the effects of male removal, the degree of selectivity of hook-and-line fishing both during and outside of the spawning season, and the degree to which fishing on traditional spawning sites causes local extinction. Unfortunately, this is difficult to do for a species like gag. The fish is large, it spawns in deep water far offshore during the roughest weather of the year, and currents around the spawning sites make testing fertilization success *in situ* difficult or impossible. Two not necessarily mutually exclusive choices remain: (1) relying on smaller, more easily manipulated model species for experimentation and (2) setting up marine reserves.

It is imperative that model species be chosen carefully, that is, that the life history of the model be similar enough to that of the species of interest that results based on one will be at least broadly applicable to the other. Poor models result in misleading interpretations. This has been a recurrent problem in stock-assessment models that were developed with temperate gonochorist species but applied to protogynous warm-temperate and tropical species. These models are entirely fecundity based and thus do not respond to loss of male biomass. As a result, reproductive failures can occur before the stocks are recognized to be in jeopardy.

A major impediment to understanding the effects of fishing on groupers has been the lack of unfished stocks (controls) with which to compare fished stocks. It we accept the strong, but often circumstantial, evidence that fishing spawning aggregations has dramatic negative effects on reproduction, then it is clear that spawning stocks require immediate protection. Scientific investigations based on comparisons to controls or references allow changes due to some manipulation (e.g. fishing) to be detected. The most prudent management approach should involve immediate closure of selected portions of the gag spawning area. This action will not only insure protection of gag males, a portion of the spawning stock, and associated fish community structure, but it will also provide opportunities for field experiments and the monitoring of fishing effects in general.

Acknowledgements

We would like to thank the following people for their participation in this study. P.L. Colin participated in the initial stages of the project. Y. Sadovy, M.P. Chasar, Ann Kiefert, Shawna Stewart, Lou Spataro, and Shannon Owens provided technical support. Sandy Handy and Dan Marciewicz volunteered many hours. Peter Hood supplied unpublished data on gag. Lew Bullock provided field support on offshore trips. Jim Bohnsack provided advice and support during various phases of this project. We are indebted to many commercial fishermen, who were invaluable in providing gonads and leading us to the spawning grounds but prefer to remain unnamed. The Marine Fisheries Information System of the Florida Marine Research Institute, Department of Environmental Protection, St. Petersburg, supplied grouper landings data for the gulf coast of Florida. This research project was funded by MARFIN (NA90AA-H-MF748), the Florida Department of Environmental Protection (formerly the Department of Natural Resources, Grant No. 90-039), and Florida Seagrant (Grant No. R/LR-B-32).

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