

***Review of Kenchington Document. “Management of the Gulf of Mexico Gag Grouper Fisheries: A Reconsideration.”***

***by***

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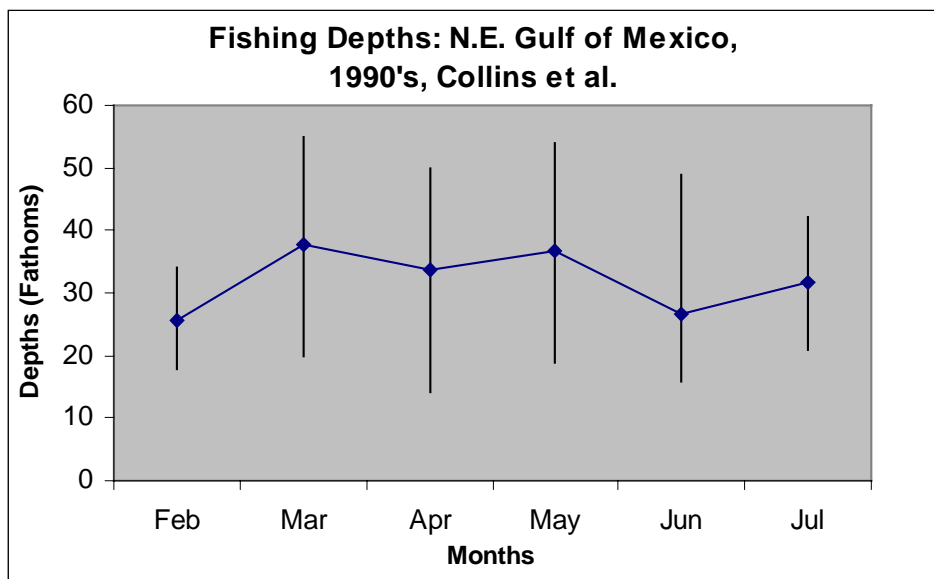
In this document, Kenchington comments on a selected group of documents and papers that represent part of a larger body of work conducted on gag grouper over the last 20 years. The Kenchington document is essentially divided into two broad sections. The first section addresses the status of the gag in the Gulf of Mexico, in which he reviews the stock assessments and work relating to sex ratios, genetic signs of inbreeding, recruitment indices and proposed management recommendations. The second section addresses a summary document prepared for the Gulf Council and the lay public that relates specifically to the effects of shelf-edge fishing on the demographics of the gag and the rationale for proposing a year round closure of aggregation sites. The substance of Kenchington’s document largely supports the need to be cautious in the management of gag and that the council will need to take action soon (e.g., p. 22). His main concerns are the change in the sex ratio and the genetics. Thus, the bulk of our comments relate to these issues.

***Comments on Sex Ratios***

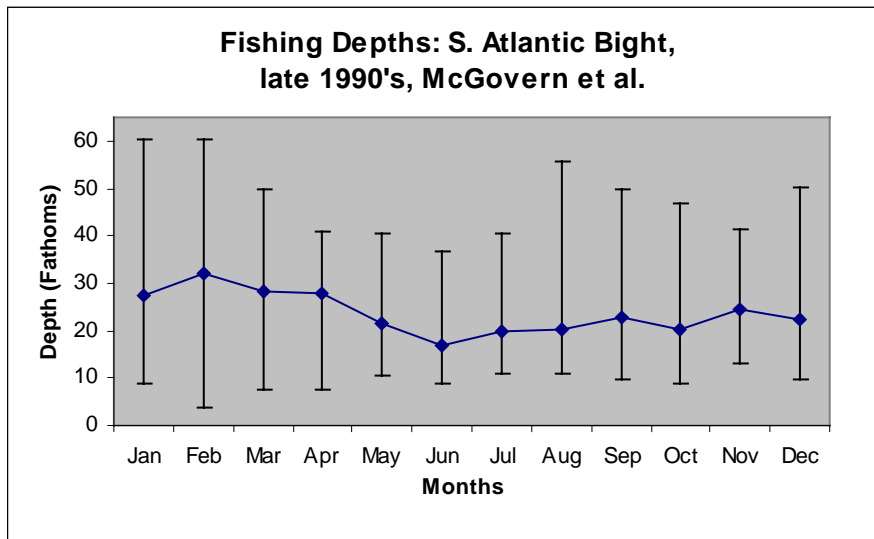
Kenchington states that the trend of reduction in males “. . . has not been seen in other, similar species” (p. 10 par.1) and “. . . similar shifts do not appear to have been reported in other groupers” (p. 11 par. 2) and again, that “. . . the question . . . is not why gag males are becoming scarce in catches but why those of other grouper species are not” (p. 12 par. 2). A very cursory literature review demonstrates these statements to be wrong. In Coleman et al. (1996) (cited in Koenig et al. 1999, not cited by Kenchington), for instance, a decline in the proportion of males related to exploitation is seen in both gag and scamp—closely related species that have very similar life history characteristics. Such declines also are reported in the Atlantic population of gag (McGovern et al. 1998), the Atlantic population of scamp (Harris, Wyanski and White in prep.), red hind (Beets and Friedlander 1992, 1999), snowy grouper (Wyanski et al in review at Fishery Bulletin), porgies (Buxton 1993, unpublished data from the South Atlantic), examined in graysby (Huntsman and Schaaf 1995), and been suggested overall for grouper species for some time (e.g., Shapiro 1978, Nagelkerken 1981, Bannerot 1984). Both red porgy and black sea bass have a greater percentage of males at smaller sizes in recent years, suggesting that they are compensating for the loss of the larger males by undergoing transition at smaller sizes. In addition, females in both these species become sexually mature at smaller sizes in recent years than during the early 1980s (McGovern pers. observ.).

**Data requirements to compare sex ratios.** Kenchington suggests that eliminating biases in the sample relating to time and gear type used would make sex change mechanisms more plausible, and faults all published accounts for overlooking this. He is in error in assuming this was not done relative to gear type, location, and seasons (e.g., Coleman et al. 1996).

1. **Gear:** In the historical and contemporaneous samples taken in the northeastern Gulf and the Atlantic, all were taken by hook and line and the vast majority came from commercial fishers.
2. **Locations:** In the northeastern Gulf, historical samples came from areas around the Florida Middle Grounds (R. Schlieder, personal comm.). Contemporary samples were taken from the same area. In the Atlantic, historical samples were taken mostly from off South Carolina. Contemporaneous samples were taken from the area extending from east central Florida to North Carolina. Commercial fishers in the Gulf operate at depths ranging from 20 to 50 fathoms throughout the winter, spring, and summer (Figure 1, **data** from NMFS Panama City Laboratory). Those in the Atlantic operate within a similar depth range, although the mean depth fished is somewhat more shallow (Figure 2, data from McGovern, SCDNR). In each area the fishermen fish in depths deeper than 25 fathoms throughout the year. Thus, in both areas shelf-edge areas are fished throughout the year.



**Figure 1.** Mean depth and range of fishing locations visited by commercial fishermen in the northeastern Gulf of Mexico. Data represent monthly distribution of catch locations for eleven trips made between 1991 and 1997 aboard four different commercial hook and line grouper fishing vessels.



**Figure 2.** Mean depth and range of fishing locations visited by commercial fishermen in the South Atlantic Bight (from eastern Florida to North Carolina). Data represent monthly distribution of catch locations for hundreds of trips made by about 15 commercial hook and line fishermen between 1995 and 1998.

3. **Season:** Kenchington faults us (p. 12) for comparing our data with Hood and Schlieder's 1970s data because the latter he says was only collected from November to May and the months were not comparable. If he would look more carefully, he would see that the dates of Hood and Schlieder's collections were November 1977 through May of 1980, with essentially equal sampling throughout the 31 month period. We did in fact compare comparable seasons because we only compared catches during the spawning period.

In this document (see below), we divide the year into three biologically meaningful segments: the spawning season, December through March; the post-spawning season, April through July; and the pre-spawning season, August through November. All sex ratio comparisons to demonstrate historical and contemporaneous differences are made among like seasons.

**Sex ratio declines in gag in the last two decades.** That the sex ratio of gag has declined significantly in both the Gulf of Mexico (Gulf) and the South Atlantic (Atlantic) is clear from all the data sets comparing sex ratios from the late 1970's to the present (Tables 1 and 2). For a manager to ignore these dramatic changes in sex ratio in the gag catches while waiting for fishery independent assessments to confirm them would be unquestionably a demonstration of poor judgment. Understanding this requires an appreciation and understanding of the complexity of the fisheries issues in this region of

the country. The southeast fisheries exploit many warm-temperate reef species with complex life styles while those in the northeast rely upon such groups as the ovoviviparous rockfish and the gonochorist cod, among others.

**Table 1.** Gag sex ratio: Gulf of Mexico comparison of historical and present data. Numbers in parentheses represent percentage of males in the catch data.

		Hood and Schlieder (late 1970s)		
		Dec-Mar (15%)	Apr-Jul (20%)	Aug-Sept (19%)
Koenig et al. (early 1990s)	Dec-Mar (2%) Apr-Jul (5%) Aug-Sep (0%)	<0.001	<0.001	<0.01

**Table 2.** Gag sex ratio: South Atlantic Bight comparison of historical and present data. Numbers in parentheses represent percentage of males in the catch data.

		Collins et al. (late 1970s)		
		Dec-Mar (11%)	Apr-Jul (32%)	Aug-Sept (19%)
McGovern et al (1994-1995)	Dec-Mar (5%) Apr-Jul (10%) Aug-Sep (5%)	<0.001	<0.001	<0.001

**Mechanisms of sex change.** Behaviorally induced sex change is clearly the most parsimonious explanation for sex change in gag, as deduced from the many other studies of sex change in fishes (e.g., Shapiro 1979, Warner 1988, Ross 1990). It is far less likely to be under some endogenous control triggered at some age or size. Kenchington's disregard for a social mechanism for sex change in gag is based in part on the territoriality of other species that exhibit socially-induced sex change. The implication is that having migratory behaviors somehow precludes exhibiting territoriality or anything other than solitary behaviors. (As an aside, cod—*Gadus morhua*--are migratory, territorial, and occur in schools.) These are not mutually exclusive behaviors. Gag, in fact, are territorial (Lindberg 1998, Lindberg and Loftin 1999, pers. observation) as are red grouper, scamp, Nassau groupers, most other groupers, and most reef fish. All our observations and those of commercial fishermen indicate this to be so. We have seen no evidence presented anywhere that gag are solitary.

Kenchington errs in suggesting that females changing sex are unlikely to impose behavioral restraints on sex change in other associated females. In fact, dominant females can suppress sex change among other females in a group while the dominant fish assumes male behaviors and eventually male function (Robertson 1972, Fricke and Fricke 1977, Moyer and Nakazono 1978, Shapiro 1979, Ross 1990).

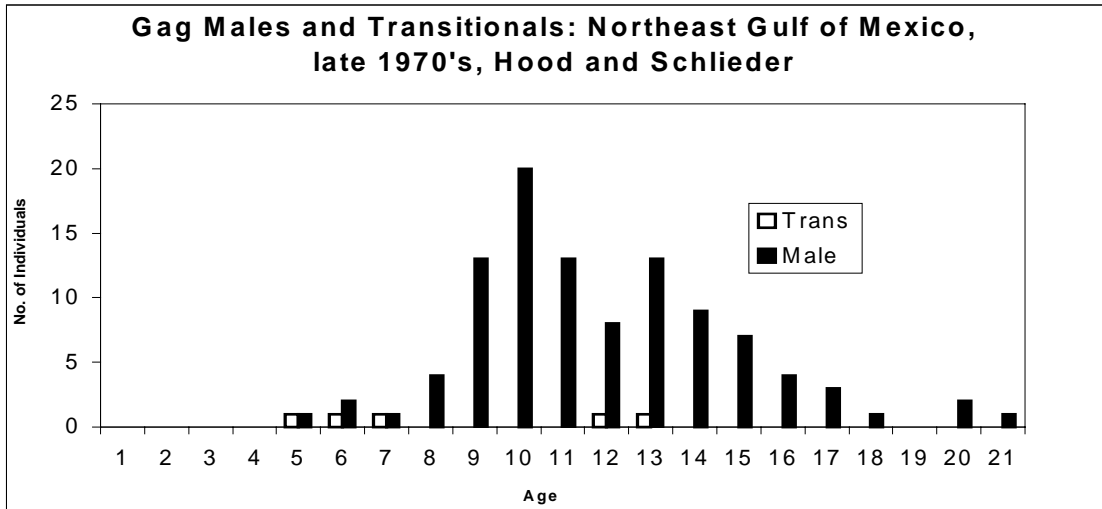
To directly infer social control in gag, certain criteria must be met.

1. Protogyny must be demonstrated, which it has (McErlean and Smith 1964, Hood and Schlieder 1992).
2. Reproduction in gag must occur predominantly within aggregations that are consistent in time and space. This has been demonstrated repeatedly in the Gulf and in the Atlantic (Koenig et al. 1996, Coleman et al. 1996, Collins et al. 1998, McGovern et al. 1998, Gilmore and Jones 1992), and is known by fishermen in both regions.
3. Relevant information, such as mating sex ratio, is available to gag at the time of aggregation when the fish are together in mating groups, and not at other times. Gag aggregations are consistent in space and time. The females disperse in April along the shelf-edge and into shallower depths while males stay at shelf-edge depths where they remain year round.
4. Sex change occurs in temporal proximity to the aggregation period. The relative proportion of transitionals to males is significantly higher immediately post-spawning than it is either during the spawning season or just prior to spawning (Table 3).

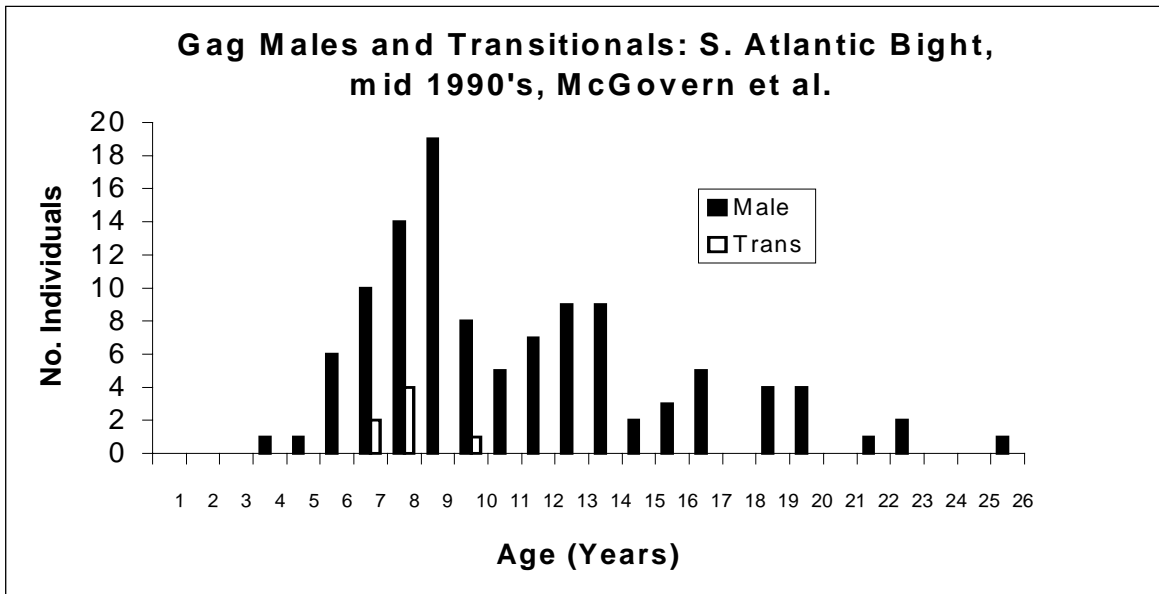
**Table 3.** Gag males and transitionals: all data combined from the Gulf and the Atlantic.

Month	No. Transitionals	No. Males	% Transitionals	P
Dec-Mar	9	189	5	<0.001
Apr Jul	43	229	19	<0.001
Aug-Nov	1	63	2	<0.001

If sex change in gag is age-related rather than socially induced, then gag stocks are in far worse trouble than we think. Without a sexually-induced mechanism for sex change, recovery of male fish is far less likely and the need for their protection more urgent. The distribution of the *ages* of males for the Gulf and the Atlantic (Figures 3 and 4), however, does not support the endogenous age-based sex change mechanism suggested by Kenchington. Acceptance of his age-at-transition of 11 years old (p. 11-12) would mean, based on the data, that 40 % of the males are “premature” in the Gulf and that 56% of the males and 100% of the transitionals are “premature” in the Atlantic. That is a significant portion of the population rather than an accidental occurrence. Kenchington’s assumption of an age 11 transition point is wrong. All conclusions throughout his document derived from that assumption are therefore invalid.



**Figure 3.** Age distribution of gag males and transitionals of the northeastern Gulf of Mexico commercial hook and line fishery, 1976 to 1980. Data from Hood and Schlieder 1992.



**Figure 4.** Age distribution of gag males and transitionals from the South Atlantic Bight commercial hook and line fishery, 1994 and 1995. Data from McGovern et al. 1998.

The distribution of *sizes* of males relative to females presents another perspective. The vast majority of males in samples are greater than 800 mm total length, although small males were reported by Koenig et al. (1996) and by commercial fishermen (e.g., Steve Smeby, Panama City, FL, personal communication). That the larger fish in a population become males is exactly what the size-advantage model for sex changing species (Ghiselin 1969, Warner 1988) predicts. The model predicts that the circumstances required for sex change are largely related to the mating system. In all protogynous species of fish that have been studied, the mating system consists of large males who monopolize the matings of females (Warner 1988). The reproductive success of these large males surpasses that of large females because it includes not only the fecundity of the female (which is the size advantage to females) but the number of females with which he mates. In other words, he can contribute his genes to many more offspring than she can. He also monopolizes the matings of those females by being large. The size at transition is probably determined by the size of the largest females in the social group, as Shapiro observed with the serranid bass, *Anthias squamipinnis* (Shapiro 1979). Of course, it is also possible that there is some genetic predisposition to change sex at sizes above a certain threshold minimum size. It would be difficult to discern between these two possibilities, but we consider the former the more likely, given the observed small males in various samples.

***Mechanism for declining sex ratio.*** It is clear from the analysis of the proportion of transitionals to males that sex change is induced within the aggregation period and not at other times of the year. Thus, information relevant to sex change (e.g., sex ratio, size ratio, dominance hierarchy) must be available only during the aggregation period. Judging from the high rates of transition immediately after the spawning season, the species is compensating for the low proportion of males by producing more males. The males occur in the catch (along with high proportions of transitionals) in the months immediately following the aggregation period. The males produced from this sex ratio compensation are lost through fishing on shelf-edge reefs at non-spawning times of the year, as all the data suggest. Thus, there is a deficiency of males in the aggregations the following spawning season. The data do not support any other mechanism for reduction in sex ratio.

***Effects of fishing spawning aggregations.*** Kenchington states (p. 22) that he cannot point to any specific reason why intensive fishing on gag spawning aggregations is undesirable. We can think of several, including the higher catch efficiencies and disruption of the spawning process, as well as loss of traditional aggregation sites. There is a fairly robust literature on this covering a host of species, from Nassau grouper to orange roughy (Shapiro 1978, Colin 1992, Shapiro et al. 1994, Sadovy 1994, Sadovy et al. 1994, Aguilar-Perera and Aguilar-Davila 1996, Domeier and Colin 1997, Sadovy and Eklund in press, Clark and Tracey 1994 among others).

Related to this are the effective fishing depths. Kenchington questions how well the depth distribution of gag (p. 22) and the shelf edge habitat (p. 23) are known. Let's review the information on depth distribution of gag. First, there is a comprehensive collation of fishermen's knowledge for hook-and-line fishing offshore Florida (Moe

1963), which puts gag in the depth ranges given by Koenig et al. 1999, at least historically. Then, there are descriptions of the long-line fishery for the eastern Gulf of Mexico that put the depth range for the long-line reef fish fishery at between 18 and 129 fathoms (noting an average fishing depth of 48 fathoms) (MARFIN 1995, Prytherch 1983). A report summarizing 24 years of exploratory fishing (NMFS surveys) puts the deepest depth range for gag at 60 fathoms (110 meters) (Roe 1976). Interestingly, a comprehensive review of data on deep water reef species for the South Atlantic (covering depths from 55 to 164 fathoms (100 to 300 meters)) that documents catches on 5 grouper species and 4 snapper species does not even mention gag--the most economically important grouper species for that region (Parker and Mays 1994). And finally, a survey of the western Gulf of Mexico reef fish assemblages gives distribution of *Mycteroperca* species to depths of 55 fathoms (100 m) but not beyond (Dennis and Bright 1988). The probability that we are missing deep-water gag is remote and the study required that would satisfy Kenchington's request would return little additional information for the dollar spent. More relevant is the species' behavior over time (Errington 1956). The behavior in question for gag is their migration to shelf edge reef sites to spawn. This they clearly do, as do many other species of grouper.

There is much more in Kenchington's document on which we could comment. We suggest, however, that the author might review the literature (e.g., try Biosis Previews or Citation Index) regarding fish behavior, hermaphroditism (both evolutionary and ecological aspects), and the effects of fishing on protogynous species or on spawning aggregations.

### ***A response to the critique regarding the genetics of gag***

The Kenchington document arrived in Chapman's hands while he was attending the Annual Meeting of the American Society of Ichthyologists and Herpetologists (ASIH). Because the most knowledgeable fish geneticists in the world attend this meeting, the opportunity was taken to circulate the document and copies of Koenig et al. 1999. What follows is a consensus of the joint deliberations of those scientists.

We address five major points from Kenchington's document.

1. Data sufficiency and statistical analysis.
2. The potential for cryptic species in the currently recognized species.
3. Natural Selection as a driving force
4. The sweepstakes hypothesis and the biological process that could drive it.
5. Other grouper data.

*Data sufficiency and statistical analysis.* The critique discusses four items of note here, including samples sizes, the number and distribution of alleles at each locus, the number of loci employed, and the method used to estimate the inbreeding coefficient  $F_{is}$ , or its equivalent

These issues are easily rebutted, but in point of fact they are not even relevant. They relate to the power of statistical tests, which is the ability to reject the null hypothesis when it is in fact false. The null hypothesis in this and every other survey of genetic variation in wild populations is that there is a single stock that is a Mendelian population. This is the null for gag in the southeastern United States, as well. That gag represented a Mendelian population was flatly rejected in our paper. Had we failed to reject, the comments of the critique would be meaningful. As it is, they simply do not apply. Nonetheless, let us consider them as substantive to our case.

The sample sizes needed for statistical analysis depend entirely upon the distribution of variance within and between populations. If all of the variance is between populations, then a sample size of one is sufficient. However, one needs to examine about 30 individuals to confirm that this is the case. All of our sample locations, except NC, were at least this large and NC is near it.

The critique mentions the fact the number of alleles per locus was a little low in this study compared to other surveys in other species. This is true, but it is most important. With increasing allele numbers, the sample sizes have to increase geometrically to generate any statistical power. The major drawback application of micro's in population analyses is the extreme polymorphism at many loci. The absence of this level of polymorphism in gag only strengthens our case. The critique also mentions the unusual distribution of alleles at the Gag 038 locus. Unusual, yes, unprecedented not at all. We have seen the same thing in a number of other species and a paper at the ASIH meeting by Jan McDowell reported a similar finding in sailfish. What we fail to understand is why the critique suggests throwing this locus out of the analysis. This is the locus that shows no evidence population subdivision, or departure from Hardy-Weinberg, and supports their interpretation. It does so because the distribution of alleles provides little statistical POWER. The critique wants us to dismiss it because the most common allele is in 85% frequency? If we do that then we have to ignore 99% of the allozyme studies of the 1970's and 1980's, because they all used loci with similar allelic distributions.

The critique also questions the use of Wright's  $F$  instead of  $R$ ,  $p$ , and  $\phi$ . The actual metric is the Weir and Cockerham (1993)  $F$ -statistic. We do not like the use of the alternative metrics as they assume a step-wise mutation model of microsatellite evolution. The analysis of Estoup and Angers (1998) points this out and their results are dependent upon this assumption holding. The use of  $R$ ,  $p$  and  $\phi$  burdens the analysis with a nearly untestable assumption. This is not all that important. What  $R$ ,  $p$ , and  $\phi$  accomplish is to finely tune the  $F_{is}$  estimate. They do not reverse the sign and it is the direction of the heterozygote deviation that is important.

*The potential for cryptic species in the currently recognized species.* The critique also suggests that gag may be a species complex. We discussed this with some of the leading ichthyologists in the southeastern U. S. who were astonished by the suggestion. Certainly Jack Randall and Phil Heemstra (authors of the recent Food and Agricultural Organization, FAO, publication on the groupers of the world) would be. No one acquainted with Serranids—the fish family in which the groupers occur--has ever

suggested a species complex for any grouper, much less gag. The occurrence of species complexes in rockfish of the genus *Sebastes* cited by Kenchington is not at all uncommon for this group of fishes, the Scorpaenids. In fact, it is the rule rather than the exception in the Pacific Northwest. But a grouper is not a Scorpaenid. Kenchington is unaware of the extensive *mtDNA* data we have on groupers that show extremely low (often zero) within-species variation in groupers. All of the *mtDNA* variation in groupers seems to be packed between species. Our *mtDNA* analysis on this species failed to find any variation in over 500 individuals. Unusual for other fish species, but the rule in groupers. We therefore dismiss the notion that gag are a complex of anything.

*Natural Selection as a driving force.* We fought the battle of the selectionist-neutralists controversy in the 1970's and early 80's and everyone finally gave up due to the sheer impossibility of detecting the effect of natural selection on gene distributions in wild populations. As George Williams once said, "Adaptation is a special and onerous concept in biology. It should be applied only where needed and at no higher level of organization than that demanded by the evidence."

The suggestion that natural selection operates against heterozygotes in the wild is puzzling. We suspect that the author of the critique had not thought this one through. Selection against heterozygotes can lead to polymorphic equilibria, but they are unstable. It is difficult to imagine how such selection could be operating against heterozygotes and microsatellite loci maintain so many alleles. In fact, it cannot. For polymorphic equilibria to exist under selection, the following conditions must be met:

- 1) No heterozygote can be less fit than all homozygotes
- 2) No heterozygote can be less fit than both associated homozygotes
- 3) At least  $n-1$  heterozygotes (where  $n$  is the total number of heterozygotes) must be more fit than all homozygotes
- 4) No more than one heterozygote can be less fit than any particular homozygote.

For six alleles at a locus, the proportion of fitness sets leading to equilibria with all alleles present is less than 0.03 (Lewontin et al. 1978), and these fitness sets all include some measure of heterozygote advantage. If the suggestion in this critique were correct, it would be thundering proof of the validity of the Neutralist position (*cf.* Lewontin, 1974 *The Genetics of Evolutionary Change*)

*The sweepstakes hypothesis and the biological process that could drive it.* Over the past decade there have been numerous indications that the effective population sizes of marine species were 3 to 5 orders of magnitude smaller than the census sizes (Hedgecock 1994, Chapman et al. 1999a). Indeed, a presentation by Tom Turner and John Gold at the recent ASIH meeting suggested that red drum effective population sizes were about three orders of magnitude smaller than their absolute numbers. For many of us involved in this research, the conclusion has been reached that there is extreme variance in reproductive success among individuals, which produces the equivalent of a population bottleneck. The mathematics of this can be found in any introductory text on population genetics. Coupled with the extreme skew in sex ratio, the consequences for hermaphroditic species

are dire. The critique includes a statement that heterozygote deficiency caused by such bottleneck would require limited genetic variation in both sexes and a footnote stating that this needs to be checked by mathematical analysis. As the author does not seem to be aware that anyone has done this, allow me to enlighten. The reference is Wright (1931). The actual situation in iteroparous species is a little more complex and is the subject of several articles by Nunney over the last decade. The end result is that genetic diversity erodes slowly, but inexorably and measures of inbreeding such as  $F_{is}$  will reflect the bottlenecks. This leads to the very cohort effect the critique discusses.

We do not disagree over the existence of a cohort effect. The issue is what is driving it. Given the propensity for gag to travel long distances (recent tags return indicate that 100's of km are usual and a 1000 km is not unknown), it makes little sense to suggest a metapopulation structure for this species. The cohort effects we are seeing are quite compatible with the phenomena we discussed in our paper and at the Council meeting. The available fishery data and sex ratio changes reported by a number of investigators support them. Why go through torturous and unsupported hypothesis regarding the biology and behavior of this species to conclude something else?

*Other grouper data.* Since this manuscript was submitted, we have accumulated three data sets that bear on this issue. Nassau grouper, black sea bass and black grouper have similar life history patterns as gag, but the available data do not show significant departures from historical sex ratios. These species show no evidence of population structuring and inbreeding that characterize the gag data.

In summary, we find nothing substantive in this critique to warrant a re-evaluation of our position presented in Chapman et al. 1999b. None of us has suggested that the genetic diversity of gag has been narrowed because we have no direct evidence that this has occurred. Rather, we note that the signs of inbreeding in the stocks are cause for concern. Inbreeding leads inevitably to losses of genetic diversity, the consequences of which are severe.

### ***Comments on the Juvenile Recruitment Index***

Kenchington states that sampling methodologies and study sites are unclear based on the Koenig and Coleman project report. A quick review of the document reveals several pages describing the techniques and sampling sites, and cites a published paper on development of the index (Koenig and Coleman 1998) that Kenchington does not cite.

- 1) The 76% and 86% are very significant. The p-value of F-tests for significance of the two models are 0.0002 and 0.019 respectively.
- 2) The increase of 8% is significant too, which is indicated by the significance of the estimated coefficient 8.68 (with a p-value 0.0129). Here we use 0.05 as our significance level. Any p-values less than 0.05 mean that the corresponding coefficients are statistically significant.

3). The two fitted models are based on small samples, as pointed out. Models based on small samples are likely not robust and that is why we need to collect more samples.”

The survey index and the commercial catches are significantly correlated. That the differences in abundance determined through the index and the VPA are not is not altogether surprising, at least at this point in time. It certainly doesn't invalidate the use of either technique. Rather, it suggests that a longer time series and a more integrative approach are required. We have not stated otherwise.

This incongruity has occurred in other species as well, most notably Atlantic cod (*Gadus morhua*). For instance, the long term abundance of Atlantic cod determined using VPA and the abundance determined through research surveys over the past 30 years differ significantly (Myers et al. 1997). Myers et al. 1997 provide explanation in that the VPA overestimates the abundance and underestimates the fishing mortality. It also assumes that commercial catch-per-unit-effort varies with abundance, and underestimates the effects of discarding and nonreporting of undersize fish.

By Kenchington's standard, any juvenile survey would be a poor estimator of adults as he claims that there would be major year-to-year differences in survival between the post-settlement juvenile stage and recruitment to the fishery three years later. That rather goes against a major finding of recruitment research for the last two decades or more. It is not clear what he supposes could be a mechanism for mortality that can be so annually variable between those stages, given that year-class strength is likely established by the time of settlement (e.g., Koenig and Coleman 1998, Sissenwine 1984, de Lafontaine et al. 1992).

***Comments relating to Dr. Fitzhugh's unpublished data.***

Kenchington takes exception to what he terms Dr. Koenig's "strident objection to Fitzhugh's unpublished data being taken into account on the grounds that it is not comparable to historical data" (p. 34).

Dr. Fitzhugh's unpublished data was an update report sent only to the port samplers with whom he works. Dr. Fitzhugh, a member of the reef fish Scientific and Statistical Committee (SSC) for the Gulf of Mexico Fishery Management Council, stated that ". . . the information in the memo was very preliminary and should not be considered . . ." because the data represented ". . . a small sample size that had inadvertently concentrated on longline caught fish, and was not completely randomly collected data." (quoted from, *Partial Summary of the Standing and Special Reef Fish Scientific and Statistical Committee, Gag Stock Assessment Review – September 9, 1998, New Orleans, LA*, which was distributed to all council members before the Gulf Council meeting in March 1999).

It is clearly the prerogative of the principal investigators to determine when a study has been completed and is ready for distribution, the public nature of the study not

withstanding. This work is part of a collaborative effort that we are conducting with the National Marine Fisheries Service. Thus, it is neither strident nor objectionable that Dr. Koenig or Dr. Fitzhugh, both principal investigators in that project, would take issue with that information being circulated.

***Comments relating to the relative intensity of studies on gag.*** Kenchington finds that because we consider gag intensively studied, we have demonstrated “. . . ignorance of the volume of work done on many other exploited fishery resources, as well as of the vastly greater body of research needed before even those will be well understood.” Perhaps Kenchington has confused intensity with volume or with history. The fisheries for salmon and cod, for instance, benefit in some respects by having historical information dating as far back as the 1300s for salmon (Neboy 1968) and, in this country back at least a hundred years for cod. These species have clearly been studied intensively for a long time. It is also clear that neither the intensity, the history, nor the volume of work has done much to effect sustainability of the Atlantic cod, which once supported the largest cod fishery in the world and is now collapsed.

Fishery statistics for the gag fishery, by way of contrast, have only been available for about a couple of decades. Gag and other groupers, in fact, were avoided off Florida before the turn of the century because they were considered a species not worth exploiting. More recently, the groupers were considered in aggregate rather than as separate species, and gag were reported as “black grouper” by many fishermen when in fact black grouper is a distinct species, *Mycteroperca bonaci*. The historical information for gag admittedly is a snapshot relative to the evolutionary history of the species but is, in fact, quite substantial relative to the history of the fishery. However, to suggest that the fishery has not been intensely studied since that time is in error, as the many biologists and stock assessment scientists can affirm. The length of time it has been intensely studied is not at issue.

***Comments relating to observational studies.***

Throughout the document, Kenchington casts doubt on the validity of observational information. Yet, Charles Darwin--widely regarded as the greatest biological scientist who ever lived-- was almost exclusively an observer (Hilborn et al. 1995). Experimentation, logic, mathematics, and computation, of course, support observations. But some fields and some situations do not provide opportunities to incorporate all these elements. The time and logistic scales required for conducting replicated experiments on some species, for instance, are beyond those considered prudent for precautionary management. Waiting for their availability would precipitate delays that could lead to destruction of the resource (e.g., Butterworth 1989, Walters and Collie 1988).

Scientists and managers are often forced to accept that the characteristics of the system of interest are such that their only recourse is to develop management approaches that are robust to population fluctuations (Hilborn et al. 1995). That is the reality of fisheries management and the basis for the development of the precautionary approach, as outlined by the United Nations and adopted by the National Marine Fisheries Service in the Magnuson-Stevens Fishery Conservation and Management Act. Scientists also accept

that we cannot always determine how a population will respond to a management approach until the approach is implemented. This has proved true in virtually all circumstances (e.g., Hilborn and Ludwig 1993, Ludwig et al. 1993). Managers use the best available evidence presented them and have to make very difficult decisions about how exploitation is to be pursued, or not pursued, in the case of jewfish and Nassau grouper, two grouper species that are protected following serious declines related to heavy aggregation fishing.

### ***Marine reserves as a management tool.***

As Kenchington outlines in his initial arguments, it is almost impossible to measure the actual rate of natural mortality ( $M$ ) in exploited fish. This is due primarily to the fact that we rarely have information on these rates in unfished stocks (Beverton and Holt 1957, Gulland 1983). One of the earliest and most reasonable estimates, however, came from studies of the North Sea plaice by Beverton and Holt (1957). The reason they were relatively successful where others had failed is that they had access to age-frequency data in this species both before and after a 6-year closure of the North Sea to fishing during the Second World War. In fact they found that the mortality rates were different in males and females. Such heterogeneity of survival probabilities can lead to biased estimates of survivorship in many species (Johnson et al. 1986).

A somewhat similar opportunity was afforded Russ et al. (1998) in examining mortality rates in coral trout, *Plectromus leopardus*, in and outside of a marine reserve closed to fishing. This is an extremely important value of having marine reserves for many species because it could give appropriate values of  $M$  for use in stock assessments, thus strengthening significantly the determinations of those assessments. Based on Kenchington's strong interest in developing reality-based estimates of  $M$ , we are somewhat surprised at his strong objection to any sort of boundary management that might provide him with such numbers.

From a management perspective, Kenchington completely misses the point of the Koenig et al 1999 document. The document does not argue for or against management measures for the entire fishery or for or against allocation assignments. These are not discussed nor are they relevant to the issue of sex ratio change. The document simply outlines the rationale for using marine reserves to protect males in the population. The fact is that declines in the proportion of males occur as a result of fishing on spawning aggregations and that commercial, not recreational, fishermen for the most part, fish on those aggregations. The aggregation sites represent source populations and the very heart of production in the fishery. The inshore sites represent sinks. Fishing pressure on these inshore populations is not even in the same realm as fishing pressure that cuts into the reproducing population. To suggest that the levels of exploitation in these different areas on different stages of the life cycle are comparable is to ignore a very substantial body of evidence to the contrary throughout the fisheries science literature.

What management measures are appropriate for the protection of sex ratio in gag? Given the mechanism of sex ratio decline and the related problems with reproductive output and

inbreeding, the most appropriate management approach is to protect the aggregations (or a portion of them) and to protect the males that are produced within the aggregations at the non-spawning times of the year. A spawning season closure would protect the aggregations, but would not protect the males. Even a seasonal closure that extended into the four months following the spawning season would only displace the removal of males to the following months. On the other hand, areal closures would protect males and the spawning aggregations in the selected places of the reserves. Other species such as scamp which also have shown declines in sex ratio (Coleman et al. 1996) would be protected as well under this same umbrella. Traditional management measures such as trip limits and size limits would appear to have minimal impact on the core problem, the sex ratio of the spawning aggregations.

The marine reserve proposed for gag is not intended to reduce  $F$  in any significant way. Its sole intent is to protect a very important component of the population—males—so that whatever other measures are taken to ensure larger populations sizes are met with a capacity for reproduction. How reductions in  $F$  are to occur is up to the National Marine Fisheries Service and the Council. This is very clearly a distinct, stand-alone issue.

In essence, we find that regardless of the deficiencies Kenchington may find in the body of work presented on gag, the observations, the logic, and the historical perspective point to marine reserves protecting spawning aggregations and male gag as a sound, defensible management approach. We would be remiss if we asked managers and the fishermen to cast caution to the wind and continue to exploit this species in the manner in which it has been exploited for the last 20 years. This is particularly true in the face of the information provided in the stock assessment, the published papers on gag, the history of exploitation of a number of related species, and the ultimate dire consequences that would ensue. Kenchinton is in grave error if he supposes that the government has no proper role in testing and evaluating resource management methods—particularly when other management measure are found to be lacking. That is in fact the province of government and the directed drive of science. He is also in error if he thinks that the sole beneficiaries of the resource are the current local fishing communities. To assume such ignores completely the rights of future generations of fishermen and the rights of every citizen of this nation to expect sustained resources and healthy marine ecosystems.

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