

No evidence of bias from fish behavior in the selectivity of size and sex of the protogynous red porgy (*Pagrus pagrus*, Sparidae) by hook-and-line gear

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Most fisheries select the size of fish to be caught (are size selective), and many factors, including gear, market demands, species distributions, fishery laws, and the behavior of both fishermen and fish, can contribute to that selectivity. Most fishing gear is size-selective and some, such as gill nets, are more so than others. The targeting behavior of fishermen is another key reason commercial and recreational fisheries tend to be size-selective. The more successful fishermen constantly seek areas and methods that yield larger or more profitable sizes of fish. Fishery regulations, especially size limits, produce size-selective harvests. Another factor with the potential to cause selectivity in a hook-and-line fishery is the different behavioral responses of fish to the bait or lure, whether the different responses arise among different fish sizes or between the sexes.

There is reason for concern over the effect of size-selective fishing on protogynous species, i.e., sequential hermaphrodites, which begin life as females and later change sex to males. In one way, size-selective fishing affects gonochoristic (sexes separate) and protogynous species similarly: it not only reduces numbers, but also truncates size distributions. These effects can result in earlier maturation at smaller sizes and hence, at the very least, a reduction in individual fecundity (Jørgensen, 1990). Size-selective fishing can, however, uniquely affect protogynous species in at least two other ways. Because there is essentially a second maturation when sex change occurs, barring some compensatory response, size-selective fishing is sex-selective fishing. As exploitation removes the larger and primarily male members of the population, sperm limitation and decreased fertilization rates can occur. These effects could be caused by a reduction in the number of males or because rapidly skewed sex ratios disrupt the social cues for mating (Bannerot et al., 1987; Huntsman and Schaaf, 1994; Coleman et al., 1996). Naturally low sex ratios can decline precipitously in some heavily fished protogynous species, especially those that form large, temporally and spatially, predictable spawning aggregations (Coleman et al., 1996). The second potential effect of size-selective fishing that is unique to protogynous species is a decrease in population fecundity (Vincent and Sadovy, 1998), which could accompany a compensatory drop in size at sex change, because this drop in size would essentially equate to increased mortality on the largest, most fecund females (Shepard and Idoine, 1993). Such an effect, however, would only occur if at least some females were initially included in the exploited portion of the population.

The documented responses of protogynous species to fishing have varied. Significantly, fewer male daggerhead seabream (*Chrysoblephus cristiceps*) and Roman seabream (*C. laticeps*), both sparids, were found in areas open than in areas closed to fishing—a finding attributed to selective removal of larger size classes (Buxton, 1993). In contrast, the average size and age of male leopard coral grouper (*Plectropomus leopardus*), a serranid, were not consistently smaller, nor was the sex ratio consistently more female-biased in areas open to fishing than in closed areas (Adams et al., 2000).

Recent significant declines in the modal sizes and proportions of males of gag (*Mycteroperca microlepis*) and scamp (*M. phenax*)—both serranids and protogynous species—in the Gulf of Mexico (GOM) were likely due to size-selective or sex-selective harvesting, or both, that was affected by fish behavior (Coleman et al., 1996). Among gag, the proportion of males fell from 17% during 1977–80 (Hood and Schlieder, 1992) to 1.3–2.7% during 1991–93 (Coleman et al., 1996) in the GOM, and from 19.6% during 1976–82 to 5.5% in 1995 in catches from U.S. Atlantic waters (McGovern et al., 1998). Coleman et al. (1996) cited Gilmore and Jones (1992) for their conclusions about behavior-related selectivity in scamp and personal observations by Gilmore for similar conclusions regarding gag. Gilmore and Jones (1992) speculated that the bias towards large males that they noted in hook-and-line collections of gag and scamp was related to the more aggressive behavior and greater movement of males, and the higher position of males in the water column. Even though these are the only protogynous species in which behavior-related size or sex selectivity has been documented (and only by observations, not experiments), the shift in size and sex ratio in gag has often been cited as an example of how a species with this kind of mating system responds to exploitation (Vincent and Sadovy, 1998).

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evidence that the behavior-related (as opposed to gear- or fishery-related) size or sex selectivity reported for gag and scamp also occurred in fishery-independent hook-and-line catches of the similarly protogynous, co-occurring red porgy (*Pagrus pagrus*) (Sparidae). In other words, at a given location, were males or larger individuals (more likely to be males in a protogynous species) more aggressive and more likely to bite a baited hook and be caught before females or smaller (more likely to be female) individuals? Such selectivity has never been experimentally demonstrated in any protogynous species.

The red porgy is found in warm temperate to subtropical waters on both sides of the N. Atlantic, including the northern GOM and Mediterranean Sea, and in the S.W. Atlantic from Venezuela to Argentina (Manooch and Hassler, 1978). This sparid is one of the most abundant, potentially exploitable reef fishes in the northeastern GOM but is only lightly fished there, entirely by hook-and-line gear. Red porgy are, however, often taken as bycatch by fishermen targeting other reef species. In contrast, the population(s) of red porgy in the Atlantic waters off the southeastern United States declined so steeply during the 1980s and 1990s (89% drop in spawning stock biomass and a two-orders-of-magnitude drop in recruitment to age 1), presumably because of overexploitation, that a one-year moratorium on their harvest and possession was enacted in 1999 (Vaughan and Prager, 2002).

It is important to establish whether behavior-related size or sex selectivity occurs in hook-and-line catches of red porgy. From a sampling (whether fishery-dependent or fishery-independent) and assessment standpoint, such selectivity could lead to very biased conclusions about population demographics and dynamics, life history traits, and stock status. In addition, the potential for this sort of selectivity to rapidly skew sex ratios, especially if it occurs in conjunction with size-selective harvesting caused by the gear and the targeting behavior of fishermen, could partly explain the apparent crash of the Atlantic population(s) of red porgy off the southeastern United States. Also, given the large number of exploited protogynous species among sparids and many other families, and the need to predict the effects of fishing, it is important to determine whether such behavior-related selectivity characterizes most fishes with this mating system or whether it is restricted to certain serranids. If demonstrated to occur in red porgy, this would be the first experimental evidence of selectivity caused by the behavior of a protogynous species other than a serranid.

Materials and methods

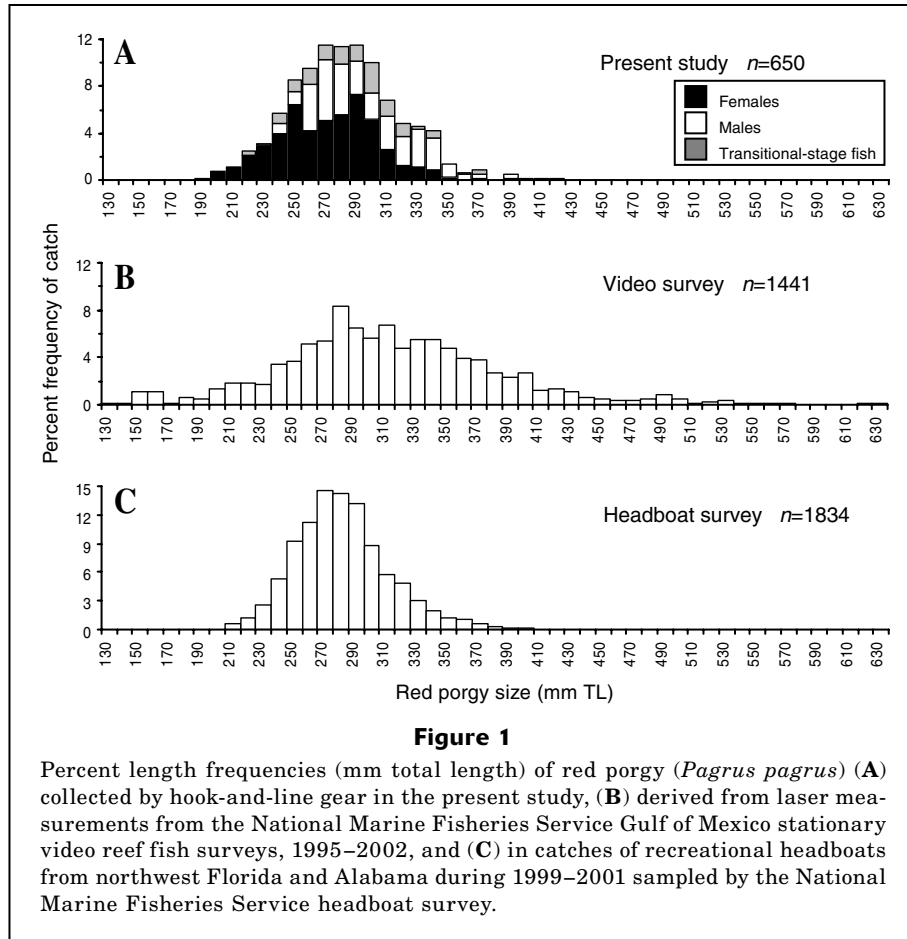
Red porgy were collected with standardized hook-and-line gear during February–November 2000 at seven low-relief (less than 0.5 m) hard (live) bottom sites at 41–67 m depths in the northeastern GOM, off Panama City, FL. The sites were a subset, and the deepest, of

nine sites that had been regularly sampled for a larger study of small-scale spatial variation in population traits of red porgy (Fig. 3.1 in DeVries, 2006). Site selection was driven primarily by logistic constraints. Locations with the most consistently high catch rates were chosen to maximize the amount of information collected and to enable among-collection comparisons. Gear consisted of one or two size-1 Mustad j-style hooks (O. Mustad and Son (USA) Inc., Auburn, NY) attached to 5–10 cm droppers on a 27 kg test monofilament leader with a terminal lead sinker of varying (depending on current and wind conditions) weight. Bait consisted of squid and occasionally cut fish. All fishing was undertaken by two to four anglers (with varying levels of experience) during daytime hours and from an anchored boat.

Target sample size each time a site was fished was 25–30 red porgy, although for logistic reasons (primarily variable catch rates) that goal was not always met. For each collection, each fish was tagged with a unique sequential identification number indicating the order in which it was captured, and then placed on ice. The next day fish were measured to the nearest mm total length (TL) and sex was determined macroscopically, after which histological samples were taken from the gonads of any fish identified as female or transitional (DeVries, 2006). Final determination of sex was based on histological findings.

Nonparametric runs tests “above and below the median” and “up and down” (Sokal and Rohlf, 1981a; Zar, 1999) were used to look for evidence of behavior-related size selectivity in individual collections. Critical values for determining acceptance or rejection of the hypothesis that the order was random were obtained from statistical tables (Sokal and Rohlf, 1981b; Zar, 1999). Total length was the variable used in both tests. In general, runs tests are used to determine whether the order of a sequence of observations is random or whether each observation is independent of its predecessor. A run is defined as a sequence of one or more like elements preceded and followed by unlike elements (Sokal and Rohlf, 1981a). In the “above and below the median” test, observations above the median are labeled pluses and those below as minuses. The order of those pluses and minuses is then tested for randomness. If fish caught at the beginning of the collection tended to be larger, as would occur if larger individuals (more likely to be males) were more aggressive and tended to bite the hook before smaller ones (more likely females), there would be fewer runs than expected. The “up and down” test, particularly designed for trend data, examines the sequence of the signs of the difference from the previous value (Sokal and Rohlf, 1981a). Again, if larger fish tended to be caught before the smaller ones, the signs would be mostly negative and therefore there would be fewer changes in sign than if the sequence of lengths was random.

A runs test for dichotomized data (Sokal and Rohlf, 1981a; Zar, 1999) was used to determine if the order in which sexes were captured in a given collection was random. Because it was not known if transitional-stage



fish behave more like males or females, this test was run two ways: one in which transitional-stage fish were considered males and another in which they were considered females. Transitional gag and scamp may be as susceptible to behavior-related sex selectivity as fully transformed males if they adopt male behaviors before completing sex change (Coleman et al., 1996). The lyretail anthias (*Pseudanthias squamipinnis*) exhibits such a shift to male behavior before any visible morphological changes (Shapiro, 1979).

Results

A total of 27 collections of red porgy were made, both during and outside the spawning season, which runs November–March but peaks December–February (DeVries, 2006). Sample sizes were >20 in 21 of 27 instances (range: 10–31). Mean sizes and 95% confidence intervals (CI) of males, females, and transitional-stage fish were 296 ± 4 mm, 270 ± 3 mm, and 291 ± 7 mm TL, respectively. The overall size distribution is shown in Figure 1. Mean proportion and 95% CI of males in 19 collections from five of the seven sites was 0.39 ± 0.07, assuming transitional-stage fish were males, and 0.24 ± 0.05,

assuming transitional-stage fish were females. The two remaining sites were persistently and significantly more male-biased than the other sites (DeVries, 2006). Mean proportions of males at the eight collections from the two remaining sites were 0.66 ± 0.10 (transitional fish as males) and 0.53 ± 0.08 (transitional fish as females). For further details on the temporal and spatial distribution of the collections, see DeVries (2006).

The order in which red porgy were caught in each of 27 collections was random with respect to both size and sex, i.e., there was no evidence that larger fish or males were more likely to be caught before smaller individuals or females (Fig. 2). In both the “above and below the median” and “up and down” runs tests, the hypothesis that the sequence of lengths was random could not be rejected at $\alpha=0.05$ for any of the collections (Table 1.1 in DeVries, 2006). Whether transitional-stage fish were considered males or females, the hypothesis that the order in which sexes were caught was random could not be rejected at $\alpha=0.05$ for all but four of the collections (Table 1.2 in DeVries, 2006). In each of those four collections only one male was caught. The statistical table used for determining critical values (Table 28; Sokal and Rohlf, 1981b) required a minimum sample size of two for both of the dichotomous variables used (number

of males and number of females); therefore these four collections could not be tested.

Discussion

The absence of any evidence of behavior-related size or sex selectivity indicates that hook-and-line sampling can provide reasonably unbiased information on the population biology and stock status of red porgy. As hook size approaches the extremes, vulnerability will decrease and bias will increase, and therefore choice of hook size is critical. There is evidence in some reef fishes that, across at least a moderate range of hook sizes, selectivity can be relatively constant (Ralston, 1982; Dalzell, 1996). Size-1 Mustad j-style hooks were chosen for this study on the basis of considerable experience of the author in catching many species of reef fishes in the study area—experience that indicated that such hooks would readily catch all sizes of red porgy typically observed in both recreational and commercial catches in the GOM. During the study, red grouper (*Epinephelus morio*) that were much larger than the largest red porgy collected and that had considerably larger gapes were caught on the same hooks, as were many tomtates (*Haemulon aurolineatum*) which were similar in size and had similar gapes as the smallest red porgies caught.

A critical assumption of this study was that all sizes of red porgy present at a location when a given sample was collected were equally vulnerable to the gear. If, because of gear selectivity, smaller individuals were considerably less vulnerable than larger ones, and significant numbers of small fish were present at a site being sampled, then it would be possible for behavior-related selectivity for larger fish to occur undetected, or at least its magnitude would be underestimated.

Several lines of evidence indicate that the aforementioned scenario is very unlikely. Size data from the eastern GOM, collected during recent annual National Marine Fisheries Service (NMFS) reef fish surveys with the use of stationary video cameras equipped with laser measuring devices, showed no evidence of noticeably greater proportions of small fish than those seen in the hook-and-line samples of the present study (Fig. 1). Although the size distributions were statistically different (Kolmogorov-Smirnov 2-sample test, $P < 0.001$)—not surprising given the very large sample sizes—the primary difference appeared to be that the distribution of red porgy sizes shown in the video data, which should have had little or at least much less bias, was shifted towards larger, not smaller fish. Although a few (3.6%) individuals in the video data were smaller than the smallest (193 mm TL) in the hook-and-line samples, it is important to note that the proportion of large fish (>360 mm) was almost 10-fold greater than in the hook-and-line samples, i.e., 21.6% versus 2.5%. Thus, if anything, the size distribution in the

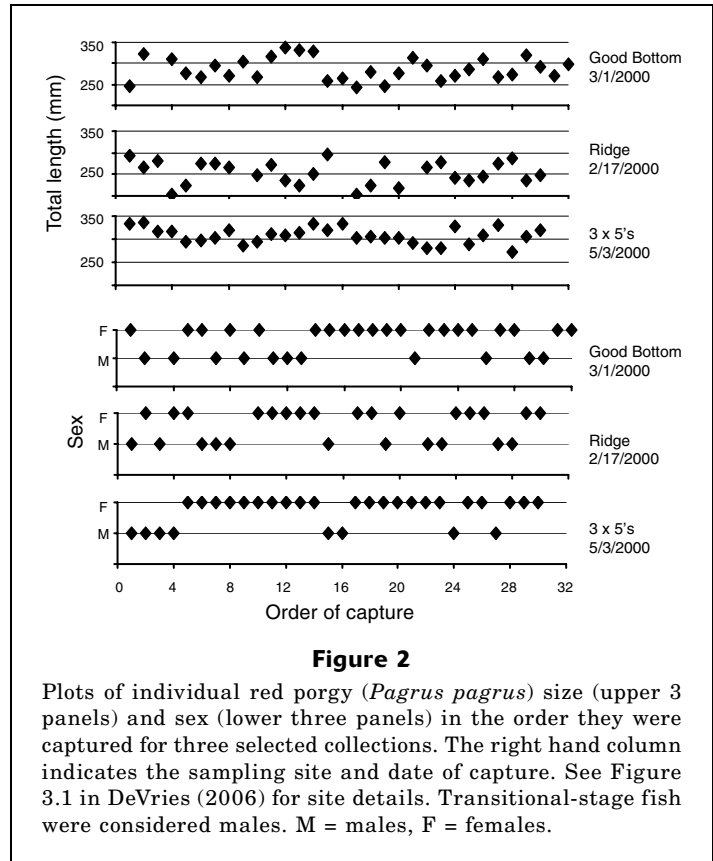


Figure 2

Plots of individual red porgy (*Pagrus pagrus*) size (upper 3 panels) and sex (lower three panels) in the order they were captured for three selected collections. The right hand column indicates the sampling site and date of capture. See Figure 3.1 in DeVries (2006) for site details. Transitional-stage fish were considered males. M = males, F = females.

hook-and-line data is biased downwards, not upwards. The higher proportion of larger fish in the video data probably reflects spatial and bathymetric differences in the sampling more than different gear selectivities. The video survey focused on the hard bottom, high-relief habitat along the 73-m (40-fathom) isobath and inshore of that isobath in the Florida Middle Grounds. In contrast, all fish in the present study were caught between 41 and 67 m and on low-relief habitat. Larger red porgy have been found in deeper water and in the Florida Middle Grounds (Harris and McGovern, 1997; Hood and Johnson, 2000).

Red porgy size-structure data from the NMFS recreational headboat survey collected during 1999–2001 in northwest Florida and Alabama almost mirrored the data from this study (Fig. 1). The headboats regularly catch red snapper (*Lutjanus campechanus*) as large as or larger than the largest red porgy taken in this study, and their fishing grounds completely overlap the area, depths, and habitats sampled in the present study. If significant numbers of red porgy larger than those collected in the present study inhabited the area sampled in this study, it seems very unlikely they would not show up in the NMFS survey samples of headboat catches from the same region. Larger red porgy are in fact caught regularly by headboats fishing the Florida Middle Grounds off the central west coast of Florida (Hood and Johnson, 2000).

On many occasions over several years while scuba diving on hard-bottom habitat in the study area in depths from 25 to 30 m, I have observed red porgy of the size that dominated the distribution of those collected in the present study, but virtually none of the size in the left-hand tail (smaller fish) of the distribution from the NMFS video survey (Fig. 1). Similarly, individuals smaller than that typically seen in hook-and-line samples have rarely, if ever, been observed by personnel from the Panama City NMFS Laboratory, either from ROVs or stationary camera arrays at many sites in the N.E. Gulf of Mexico.

Lastly, juvenile red porgy have been found primarily on sandy bottom and typically in shallower waters than those inhabited by adults (Manooch and Hassler, 1978; Labropoulou et al., 1999). These findings, together with the scuba and video observations, support the validity of the assumption that the range of sizes of red porgy in a given collection in this study were the same or at least very similar to those actually present at the site at the time the sample was taken.

If the size structure of the hook-and-line samples in this study accurately reflect the true size distribution at the site at the time of the collection, then the sex ratios of those samples should also accurately reflect true values, and hence the finding of no evidence of sex selectivity is also valid. The absence of behavior-related size or sex selectivity in hook-and-line samples means that any evidence of truncation in size structure or skewing of sex ratios in exploited red porgy populations should not be attributed to greater aggression or "hook attraction" in males. Instead, such size truncation or skewing of sex ratios can be easily explained as the result of simple size-selective harvesting caused by the targeting behavior of fishermen, not by the behavior of the fish, and is a common phenomenon not unique to protogynous fishes.

Although there is historic evidence of such size-selective harvesting in red porgy fisheries off the southeastern United States, there is none indicating that behavior-related selectivity contributed to the crash of those fisheries in the 1980s. From the late 1970s through the mid 1990s, annual mean weights of red porgy in the southeastern United States were roughly 20–30% less in the recreational headboat fishery than in the commercial hook-and-line fishery (Fig. 2 in Vaughan and Prager, 2002). Such size-selective harvesting (taking larger individuals more likely to be male) may have skewed sex ratios temporarily, but there was no evidence of a long-term effect, i.e., an increasingly female-biased sex ratio. Males composed 15.8%, 13.3%, and 20.4% of red porgy taken in a fishery-independent survey in U.S. Atlantic waters during 1979–81, 1988–90, and 1991–94, respectively (Harris and McGovern, 1997). The increasingly female-biased sex ratios observed in gag catches in the 1980s and 1990s have been attributed to behavior-related selectivity (Coleman et al., 1996; McGovern et al., 1998). An increasing trend in the proportion of males in smaller size classes off the southeastern United States indicates that red porgy

compensated for the effects of fishery-driven selectivity for size by changing sex at smaller sizes (Harris and McGovern, 1997).

The targeting behavior of fishermen has produced selectivity in red porgy fisheries in the GOM, as well. Mean lengths of recreationally and commercially caught red porgy from the Florida Middle Grounds and off west central Florida have differed significantly (321 vs. 350 mm TL) (Hood and Johnson, 2000), in a manner similar to the pattern in weight differences in the Atlantic fisheries noted by Vaughan and Prager (2002). It is unlikely these length differences are related to fish behavior. More likely they reflect gear selectivity as well as spatial differences in areas fished. DeVries (2006) found persistent, significant, small-scale (<10 km) spatial differences in size structure and many other demographics and life history traits of red porgy in the N.E. GOM—differences that indicate that the species has a complex subpopulation or metapopulation structure. Further analysis of data from Hood and Johnson's (2000) study indicated that sex ratios also differed between the two fisheries: males composed 40.5% of the recreational and 49% of the commercial samples, although the sex of 78 of the 274 fish collected from the latter samples was not determined and these 78 fish were not included in the calculations. These differences in sex ratios likely reflect, and are consistent with, the differences in size structure. Additionally, as in the Atlantic, there was no evidence that sex ratios have become increasingly female biased. In 1978 and 1979 males composed 30% and 38%, respectively, of red porgy sampled from charter boat and headboat catches in northwest Florida (Salomon and Fable, 1981). Two decades later Hood and Johnson (2000) found that males composed 40.5% of recreational and 49% of the commercial samples, and in the present study the percentage of males averaged 39% from five of the sites and 66% at the remaining two sites.

Size or sex selectivity resulting from fish behavior does not appear to characterize the hook-and-line fisheries of all exploited protogynous species. Besides the apparent absence, in the case of red porgy, of selection for males with the use of hook-and-line gear, there is also no indication of such selection in the hook-and-line fishery for the red hind (*Epinephelus guttatus*), a seranid (Shapiro et al., 1993; Coleman et al., 1996). It may be that rapid skewing of sex ratios in protogynous fishes caused by behavior-related size or sex selectivity is the exception rather than the rule. The evidence that aggressive behavior in large, primarily male scamp and gag can lead to sex selection in their fisheries and rapidly skew sex ratios (Gilmore and Jones, 1992; Coleman et al., 1996) is primarily circumstantial or observational and there have been no controls or statistical tests. Although the case for behaviorally caused sex selectivity in gag is fairly convincing, more statistically rigorous and direct testing of the hypothesis would strengthen these conclusions. Until more studies, like the present one, are conducted on other species, the prevalence of

this phenomenon and whether it is unique to serranids will remain unknown.

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