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Social system of an inshore stock of the red hind grouper, *Epinephelus guttatus* (Pisces : Serranidae)

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Synopsis

According to sex allocation theory, the decision by a female in protogynous fish species to change sex or not should be influenced by, among other things, the mating sex ratio during spawning periods and/or by factors that vary directly with the spawning sex ratio, such as relative rates of behavioral interaction with males and females outside of spawning periods. In groupers that only spawn during a few weeks of the year in large aggregations, individuals must assess the relative value of changing sex or not entirely within the aggregation unless the social system during the remainder of the year provides a behavioral equivalent of the mating sex ratio. Fifty-five individuals of the red hind, *Epinephelus guttatus,* were tagged and repeatedly located during a 152-day period within a 100 × 100 m grid on a shallow forereef off southwestern Puerto Rico. The home ranges of 22 tagged individuals sighted 10 or more times were 112–5636 m^2 in area. Individual home ranges overlapped with the home ranges of 1–18 other individuals. Home ranges of small fish were not clustered within the borders of the home range of larger fish, i.e. fish did not form spatially defined social units. At the end of the study, 31 tagged individuals remained on the grid together with five newly sighted fish. All 36 individuals proved on histological examination to be females similar in size to females in the spawning aggregation of the following year. The sex ratio of this all-female inshore stock differed significantly from the sex ratio of that spawning aggregation. Hence, information predicting the reproductive value of a sex change is not available to females in the inshore stock during nonspawning months.

Introduction

In protogynous hermaphrodites, adult individuals change sex from female to male (Atz 1964). In theory, sex change is advantageous to a female when its expected reproductive success as a male exceeds its remaining expected reproductive success as a female (Charnov 1982). Although lifetime reproductive success results both from the longevity and instantaneous spawning rate of the individual, in protogynous fishes the most studied factor influencing reproductive success is the mating system (e.g. Warner et al. 1975, Shapiro 1988a, Ross 1990). If a female could change sex and reproduce as a male with suf-

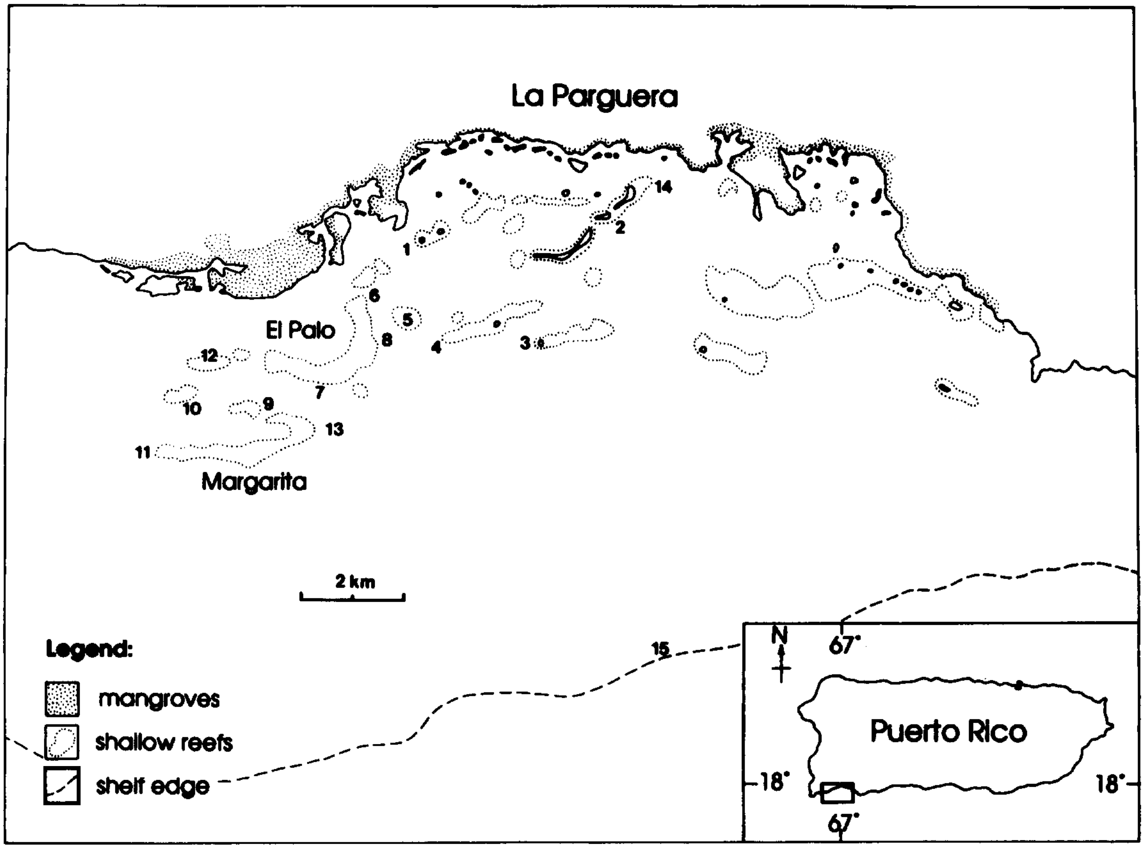

Fig. 1. Large patch reefs near La Parguera, Puerto Rico. Reefs 1–14 were surveyed for *E. guttatus*; home ranges were measured on reef 7 (El Palo); fish were removed and sexed from reefs 7, 9, and 11 (El Palo, Corona, and a patch reef near Margarita). Location 15 is one of two nearby spawning aggregation sites (the other is off the map to the west).

ficient females to more than offset the costs of gender change, the individual should alter sex (Shapiro 1989). Consequently, we expect a relationship between mating systems with female-biased sex ratios and protogynous sexuality (Charnov & Bull 1989).

The mating sex ratio may influence the physiological 'decision' to change sex directly or indirectly. In species that spawn frequently, e.g. daily, weekly, or even monthly throughout much of the year, the mating sex ratio is directly and repeatedly available to influence sex change. In species that spawn infrequently or during limited times of the year, the mating sex ratio may influence sex change indirectly whenever the relative frequency of interacting with males and females accurately reflects the mating sex ratio. Social systems reflecting the mating sex ratio include stable social groups and other spatial arrangements in which the probability of spawning with the opposite sex is similar to the probability of interacting with it outside of spawning periods. In these cases, sex change could presumably be influenced by the mating sex ratio during the mating season and/or by the behavioral or demographic equivalent of that ratio during non-mating periods.

Some protogynous groupers spawn in large aggregations during highly restricted periods of the year, sometimes as short as 1 week (Smith 1972, Colin et al. 1987, Shapiro 1987, Carter et al. 1993, Colin 1992). If, during the remainder of the year, the social system does not provide information about the mating sex ratio within the spawning aggregation, and if the decision to change sex is influenced by the spawning sex ratio, the only opportunity available to females to assess the relative reproductive values of continuing as a female or switching to a male lies within the aggregation once yearly. An important issue, then, is the degree of match between the social system outside of the aggregation and the mating system within it.

The red hind, *Epinephelus guttatus*, a protogynous grouper (Smith 1959, Burnett-Herkes 1975, Sadovy et al. 1992), spawns at the edge of the insular shelf off the southwest coast of Puerto Rico. Spawning aggregations form during approximately 1 week around the full moon each January, and infrequently during approximately 1 week around the full moon in February (Colin et al. 1987, Shapiro et al. 1993a). Within the aggregation, several females or 1 male and several females form spatial clusters. The sex ratio of intact clusters of individuals speared in a 1984 aggregation averaged 5.6 females per male (n = 34 individuals from 12 clusters), while the overall aggregation sex ratio for specimens collected with this and other techniques (n = 190) was 6.6 females per male (Shapiro et al. 1993a). Spawning has only been observed rarely, but the courtship behavior of males suggests that males spawn with females in the clusters with which they are associated (Colin et al. 1987, Shapiro et al. 1993a).

The purpose of this study is to describe the social system of a shallow, inshore stock of *E. guttatus* and to compare it with the known spatial structure and sexual composition of the local spawning aggregation the following January (Shapiro et al. 1993a). The approach was to examine the location and size of home ranges of marked individuals and then to capture and sex them. We expected that a male and several females would co-occupy a home range, resulting in a polygynous social system and a moderately female-biased sex ratio. This expectation stemmed from the social system of groupers that are not aggregate spawners (Donaldson 1991, Shpigel & Fishelson 1991), from the social structure of spawning aggregations of this species (Shapiro et al. 1993a), and from an assumption that the simplest social system would be one that is uniform throughout the year, both within and outside the spawning aggregation.

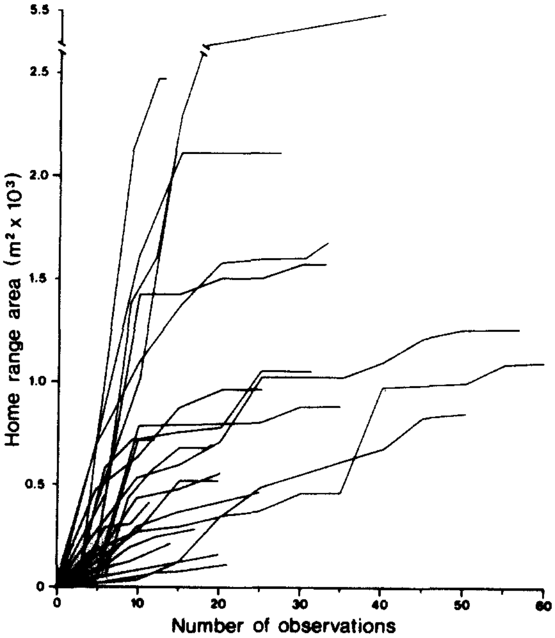

Fig. 2. Home range area (m^2) as a function of number of observations for 22 female *E. guttatus* in a 100 × 100 m grid on the El Palo forereef.

Methods

Fourteen large patch reefs near La Parguera, Puerto Rico, were surveyed initially and three with dense stocks that were infrequently fished were selected for study (Garcia-Moliner 1986): El Palo, Corona, and a patch reef near Margarita (Fig. 1). The three study reefs were approximately 8.5 km from each of 2 known spawning aggregation sites on the edge of the insular shelf, one to the southeast and one to the southwest of the study reefs. Midway along the El Palo forereef, a 100 × 100 m grid of polyethylene rope was laid on the bottom in depths of 6–10 m (average 8 m). The grid was subdivided into nine 33 × 33 m squares. Bottom topography consisted of patches of *Acropora cervicornis*, sand, soft corals, gorgonians, and variously sized coral aggregates.

Individual *E. guttatus* were caught within the grid by divers dangling small hooks baited with squid in front of the fish. The standard length (SL) of captured individuals was immediately measured to the nearest mm, a colored Floy 'spaghetti' tag was inserted at one of three positions into the dorsal mus-

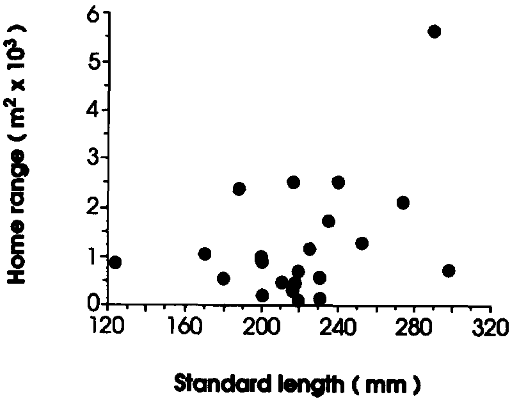

Fig. 3. Home range area (m^2) as a function of body size (mm SL) for 22 female *E. guttatus.*

culature on the right or left side of the fish, natural tail markings were noted, and the fish was released at the precise site of capture. Fish retained their tags 1–152 days, with a mean of 37 days. When a fish lost its tag or an untagged fish appeared for the first time on the grid, it was captured and retagged. Fish with lost tags were identified by location of the tag scar, body size, and tail markings. All red hinds (N = 55) observed in the grid during the study were tagged.

From April to August 1983, inclusive, the location of each fish within the grid was recorded by two divers during 2.5 h morning dives 4 or 5 days a week, totalling approximately 600 observation hours over 152 days. The starting point on the grid and the direction of swimming by divers (parallel to grid lines) were selected haphazardly in each dive. Divers then swam slowly back and forth across the grid 1.5 m off the bottom. When a fish was seen it was identified and its location recorded as the X and Y distances from the nearest grid lines. Locations were plotted later on a map of the grid in the laboratory.

Home ranges were drawn for each fish using the convex polygon method (Brown 1975). When home range area was plotted against number of sightings, the curves for most individuals began to flatten by the tenth sighting (Fig. 2). Consequently, for final analysis, data were used only from individuals (n = 22) observed on at least ten dives (Garcia-Moliner 1986).

In the third week of September, all red hinds remaining in the grid were speared or captured on hook-and-line by divers (N = 36). Gonads were removed, fixed for 24–48 h in paraformaldehyde, washed overnight, dehydrated in ethanol, cleared, embedded in paraplast, sectioned at 6–7 μm, mounted on slides, and stained with Harris' hematoxylin and eosin. Individuals were sexed by microscopic examination of the slides. All individuals from the two additional patch reefs (Fig. 1) were speared, in November 1983 on the Margarita patch reef and in June 1984 on Corona, and sexed using the same histological technqiues.

Results

During any single dive, 0–16 tagged fish (mean = five fish) were observed. For the 22 fish observed at least ten times, individuals were seen on 13–57 days, with the median fish observed on 23 days. The residence time, i.e. number of days between day of tagging and last sighting, was 54–143 days. Sightings were not equally distributed among the nine grid squares ($\chi^2 = 109.8$, df = 8, $p < 0.0001$), with fewer sightings in squares dominated by open sand bot-

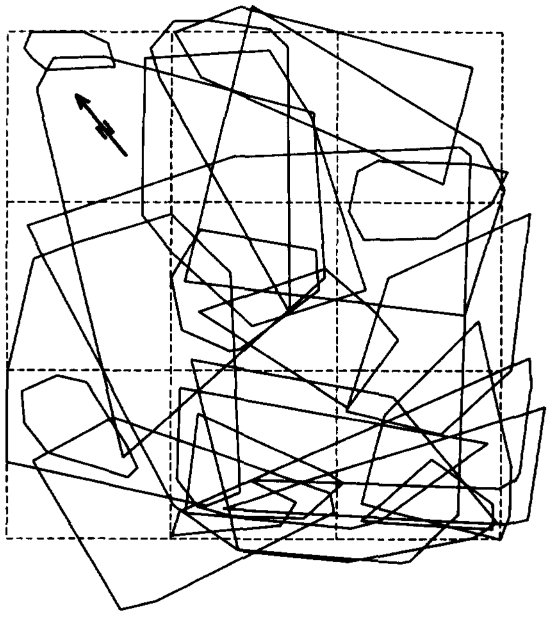

Fig. 4. Home ranges of 22 female *E. guttatus* in a 100 × 100 m grid on the El Palo forereef. Each polygon represents the outer limits of an individual's home range.

tom and more sightings in squares with much coral cover.

Home ranges for fish observed at least ten times (n = 22) were 112–5636 m^2 (median = 862 m^2). These fish measured 124–298 mm SL (median = 217 mm). Fish size correlated neither with the number of times individuals were seen on the grid (Spearman $r_s = 0.148$, n = 22, NS) nor with home range area (Spearman $r_s = 0.262$, n = 22, NS). When the data were examined with linear regression (Fig. 3), an almost significant trend appeared between home range area and body size ($r^2 = 0.164$, $p = 0.06$). However, the trend was primarily due to a single outlier with a very large home range. When the outlier value was removed, the trend disappeared ($r^2 = 0.024$, $p = 0.51$). Overall, then, home range area was not a function of body size.

Virtually the entire area of the grid was incorporated into the cumulative home ranges of the 22 individuals (Fig. 4). Home ranges overlapped heavily. The number of home ranges overlapped by the home range of each fish ranged from 1–18, with most fish overlapping the home range of 6–10 other fish (Fig. 5). The number of home ranges overlapped by an individual correlated significantly with the individual's body size (Spearman $r_s = 0.43$, df = 20, $p < 0.05$). Otherwise, we found no pattern to the overlaps, e.g. the home ranges of several smaller fish did not fall within the home range of one large fish, as one might find in a polygynous social system.

At the end of home range observations, 36 fish were collected from the grid, 31 of which had previously been tagged. All 36 were gonadally female. In addition, 23 fish were collected from a small patch reef near Margarita and 23 from Corona. These fish represented all individuals seen on both reefs and ranged in size from 116–268 mm SL, with median 186 mm on Corona and from 146–262 mm, with median 180 mm, on the Margarita patch reef. All 46 were gonadally female.

Discussion

The social system of this inshore stock, at least that portion of it closely associated with patch reefs, was weakly structured. Individuals moved over areas occupied by as many as 18 other individuals. This degree of home range overlap might suggest that *E. guttatus* is highly social. However, behavioral interactions among individuals on the grid were rare, and most sightings were of single fish. Individuals tended to remain alone in one position for many minutes at a time, often partially hidden in crevices, behind coral aggregates, or at cleaning stations, and we observed nothing to indicate that individuals were influenced by the movements of other individuals on the grid.

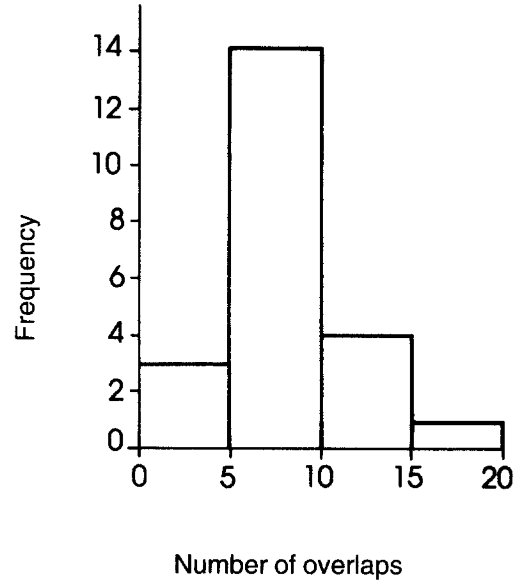

Fig. 5. Frequency distribution for the number of home ranges overlapped by the home range of each of 22 female *E. guttatus* in a 100 × 100 m grid on the El Palo forereef.

Surprisingly, all individuals on the grid and on two other patch reefs were female. While these individuals were statistically somewhat smaller overall than females from the spawning aggregation of January 1984 (for individuals placed in three size classes, $\chi^2 = 35.4$, df = 2, $p < 0.001$), all inshore females fell within the same size range as females in the aggregation (Shapiro et al. 1993a). The all-female nature of the inshore, patch-reef stock contrasted sharply with the sex ratio (n = 190) of 6.6 females per male in the January 1984 aggregation ($\chi^2 = 10.4$, df = 1, $p < 0.01$).

Do females move regularly between shallow patch reefs and slightly deeper areas where they encounter males in numbers proportional to the mating sex ratios within the spawning aggregation? On any single dive most tagged individuals were not encountered. Individuals either were frequently ensconced within crevices on the grid and simply not visible or some fish occupied home ranges centered off the grid, so that we encountered them only sporadically. If the latter is true, then the home range sizes provided here underestimate the actual home ranges of these individuals. When fish were collected at the end of the study, only 31 of the 55 originally tagged individuals were retrieved. Thus, some individuals probably moved off the grid, either temporarily or permanently, during the study.

In adjacent waters, the sex ratio of 321 individuals obtained from the commercial, inshore fishery at biweekly intervals between November 1982 and June 1984 was 11.3 females per male (Garcia-Moliner 1986). While this sample contained significantly more males than the all-female stock on the three patch reefs ($\chi^2 = 5.82$, df = 1, $p < 0.02$), the inshore sex ratio tended to be higher than the spawning sex ratio ($n = 190$) of 6.6 females per male in the 1984 aggregation ($\chi^2 = 2.86$, df = 1, $p = 0.09$). When data from a longer, 29 month sample ($N = 609$, including the 321 specimens from the above data) were considered (Shapiro et al. 1993b), the sex ratio in nonaggregation months from the commercial, inshore fishery (10.8 females per male, $n = 463$) was significantly higher than the combined sex ratio from three successive, annual aggregations (4.9 females per male; $\chi^2 = 7.22$, df = 1, $p < 0.01$). Consequently, even if females moved off the grid and into adjacent waters the sex ratio encountered there would not reflect the spawning sex ratio in aggregations. During the 11 nonspawning months of the year, males were probably located over the edge of the insular shelf in deeper water.

Thus, sex ratio and social system differed substantially between the inshore stock and the spawning aggregation. Information predicting expected mating success for a female that changed sex and became a male is simply not available to females in the inshore stock outside of the aggregation itself.

The persistence of tagged females on all-female reefs in inshore areas raises the question of the proximate cause of sex change. Why did females not change sex in the absence of a male? In all other protogynous hermaphrodites for which there are data, sex change is induced by alterations in the behavioral interactions between the sexes, generally by separating females from males (Ross 1990). One possible explanation for persistence of females is that sex change is not controlled simply by the absence of a male but by disappearance of a male that was previously present (Shapiro 1988a). If juveniles settled inshore initially and remained there until they were ready to spawn for the first time, and if the inshore females of our study had not yet experienced a spawning aggregation, then these females would have had little prior exposure to males. All-female social units are known in one other protogynous serranid, which spawns in stable social groups. In that species, sex change occurs immediately after male disappearance from bisexual groups but only after lengthy delays in all-female groups (Suzuki et al. 1978, Shapiro 1984, 1988b).

This explanation needs additional evaluation, however. The size range of inshore females from the three patch reefs fell within the size range of aggregating females, so some or all of the inshore fish may have participated in the previous spawning aggregation. In another study of this species, at least one small, tagged female migrated from a shallow, inshore site to a spawning aggregation (Sadovy et al. 1992). None of the gonads of our inshore, patch reef females contained muscle and connective tissue bundles indicative of prior spawning (Shapiro et al. 1993b). However, such bundles generally remain within the gonads for fewer than 160 days after spawning and most of our inshore specimens were collected more than 160 days after spawning. Thus, we cannot be certain whether these females had prior exposure to males or not.

A second possibility is that sex change in this species is not controlled by separation of females from a male. In an experiment designed to simulate conditions in which females of other protogynous species were induced to change sex, male and female red hinds were captured from within a spawning aggregation and held in cages in the sea for up to 18 weeks. Each cage contained one male and six adult females. After one week, the male was removed from experimental cages but not from control cages. Eighteen weeks later, the incidence of sex change did not differ between experimental and control cages. Thus, separation of females from males under these conditions was not successful at inducing sex change, at least within the time frame of the experiment (Figuerola 1987).

Our results point to the need for additional studies of both the proximate and ultimate causes of sex change in this species. According to existing theory and our results, the information needed for inshore individuals to evaluate when to change sex is available only within the spawning aggregation. However, one prediction that follows from this result proved false: transitional individuals, as determined by histological examination of the gonads, were not clustered in time soon after the aggregation, as predicted, but were found throughout the year (Shapiro et al. 1993b). The dilemma seems resolvable but only with data on the social system of deeper stocks than have thus far been studied, i.e. in regions containing males, and with further study of the earliest stages of sexual transition. Such data might reveal a social system in deep water that does reflect the mating sex ratio or might indicate that early onset of sexual transition (prior to the appearance of histologically recognizable testicular tissue) did, in fact, occur predominantly soon after the spawning aggregation.

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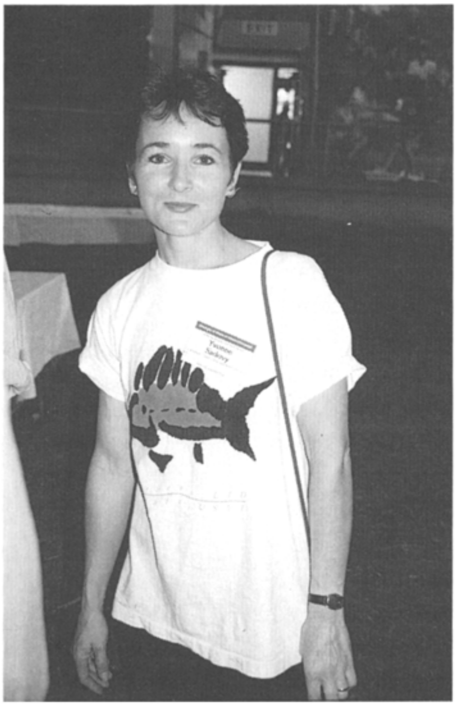

The junior author Yvonne Sadovy at the 1992 ASIH meeting at Champaign-Urbana. Photograph by E.K. Balon.