

THE MATING SYSTEM OF THE CARIBBEAN ROSY RAZORFISH, *XYRICHTYS MARTINICENSIS*

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ABSTRACT

Rosy razorfish, *Xyrichtys martinicensis*, live in isolated colonies on extensive sandbeds in the San Blas Islands of Panama. The females in these colonies are members of contiguous harems, each of which is defended by a single large male. These fish are unusual among wrasses in that females are gregarious and extremely site-attached. It is proposed that this adaptation to the lack of shelter in sandbed habitats enables large males to successfully defend groups of females and has therefore led to the development of a harem mating system in this species (female defense polygyny). Among the secondary adaptations to this mating system are protogynous sequential hermaphroditism (sex-change from female to male), the absence of non-sex-changed males, and reduced male gonad size.

Coral reef fishes have a wide variety of mating systems. This diversity is enhanced by the widespread ability of these fishes to develop hermaphroditism, either sequential or simultaneous. The ability to change sex allows sex ratios to vary radically, especially between size classes, and permits complex and unusual mating systems to evolve. Many of these mating systems have been described although few attempts have been made to discuss the ultimate factors determining which mating system will evolve in a particular situation (Robertson and Choat, 1974; Choat and Robertson, 1975; Warner et al., 1975; Robertson and Hoffman, 1977; Shapiro, 1977; Moyer and Nakazono, 1978; Warner and Robertson, 1978; Robertson and Warner, 1978; Thresher, 1979; Jones, 1981; Colin, 1982; Hoffman, 1983).

One method by which one can elucidate how the environment can mold a mating system is to compare otherwise similar species that live in differing habitats and perhaps thereby pinpoint the particular characteristics of the environment that account for the divergence in their mating systems. I chose to look at the Caribbean rosy razorfish, *Xyrichtys martinicensis*, since these fish live in exposed sandbeds, in contrast to other kinds of tropical wrasses which occupy only coral or seagrass habitats (*Hemipteronotus martinicensis* is no longer a valid name, Randall, pers. comm.). In most of their other characteristics these razorfish are similar to the many other species of small wrasses that frequent tropical waters. Comparisons between species can be made since the mating systems of many of these wrasses have been documented. I describe the mating system of the rosy razorfish and endeavor to identify which of their behavioral and life history traits are direct adaptations to the environment (primary adaptations) and which are accommodations to other less flexible traits (secondary adaptations). Warner (1980) has emphasized that if one is to predict mating systems, one needs first to determine which traits are typically primary adaptations and which are secondary adaptations.

MATERIALS AND METHODS

Four colonies of rosy razorfish living on Taintupo reef in the San Blas Islands of Panama were regularly observed between October 1982 and March 1983. In this area, rosy razorfish were always encountered in groups, which varied greatly in size (from five to over a hundred individuals for the six groups on Taintupo reef). Razorfish colonies occurred mainly on wide expanses of sand in water

deeper than 5 m. On Taintupo reef the razorfish lived only on the sand slope at the downcurrent edge of the reef. Smaller and shallower patches of sand on and around the reef were apparently avoided. Areas with silty sand or sand mixed with coral rubble were also not occupied by razorfish in the San Blas Islands.

One colony of 64 females and 5 males was selected and watched each day from 14 December 1982 to 8 January 1983. The colony was mapped at the start of this period, and the position and estimated size of each individual was recorded. During the period of daily observations, identically sized females were recorded occupying the same site each day, indicating that individual females maintained their position in the colony from day to day. Males defended a portion of the colony that contained several or more females. Males were similarly found to be occupying the same portion of the colony each day. Territorial borders of males were easily discerned because neighboring males would repeatedly dash up and down the line displaying side-by-side.

Individual males and the females within their territory were watched as a group for 30-min periods and the behaviors of the members were recorded. The identity of the male and female was recorded for each spawning observed. The relative sizes of individuals engaged in aggressive interactions with conspecifics were noted. Similarly, for interspecific interactions, the relative sizes, the species involved, and the outcome of the interaction were recorded. The use of SCUBA limited the duration of dives such that observations of entire spawning periods were not possible and specific individuals could not be monitored every day.

A colony of 45 fish was collected in its entirety. An additional sample of 42 fish, 24 of them males, was collected from other colonies on Taintupo reef at the termination of the study. The gonads from all individuals captured were dissected out, and those from the males were preserved in Bouin's solution, and subsequently weighed. The fish were preserved in 95% ethanol and subsequently measured and weighed.

RESULTS

The distribution of rosy razorfish on Taintupo reef was extremely clumped (Fig. 1). These colonies were very compact, resulting in densities as high as 5 per m^2 . Females, in particular, were extremely site-attached and were rarely observed traveling more than 1 m from the center of their home range (the site of their sand refuge), unless chased and maneuvered out of the colony by a diver. A much smaller portion of this home range was defended from other female razorfish. Each colony, regardless of size, had at least one individual with a different color pattern, described as terminal phase (Randall, 1965; Roede, 1972). These terminal-phase males occupied a much larger territory than the female home range, but were still always sighted within the borders of their territory. The resident male consistently prevented other males from entering his territory.

In contrast to the consistency with which individuals were found to be occupying the same site during the period of daily observations, the positions of entire colonies did not remain the same over the entire duration of this study. Between October 1982 and the start of the daily observations in December 1982, the largest colony found on Taintupo reef appeared in an area in which I had previously recorded no razorfish. This colony presumably had moved up the sand slope from deeper water. Between the end of the daily observations in January 1983 and March 1983, the colony I had been studying was not in its original site but appeared to have merged with the largest colony which had moved nearer. I do not have sufficient observations to distinguish whether this is the result of small movements of a few centimeters each day or occasional moves of many meters.

All spawnings observed were between a terminal-phase individual and an initial-phase individual. Gonad examinations revealed that all terminal-phase fish were males and all initial-phase fish were females. The size frequencies of the two sexes indicated that sex change occurred at about 70 mm SL, while the maximum size attained by males was about 95 mm SL (Fig. 2). The gonads of males were very small, on average only 0.011 g or 0.174% of the total body weight ($SD = 0.064\%$, $N = 24$). The proportion of body weight devoted to gonads did not change with

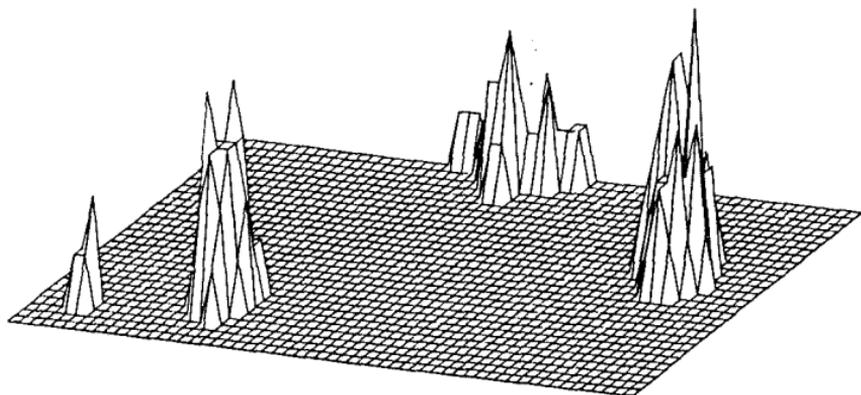


Figure 1. Three-dimensional plot of the spatial distribution of rosy razorfish on an extensive sandbed on the slope of Taintupo reef in the San Blas Islands of Panama. Each square represents 1 m². The height of each peak indicates the number of razorfish within that 1 m² (maximum height = 5 individuals).

the size of the male (the slope had no significant departure from zero, $P > 0.74$) (Fig. 3). Confirmation of sex change in this species comes from the observation that the largest female within the territory of the largest male did change from an initial-phase fish spawning as a female into a fish spawning as a male over a period of 2 weeks. Her color change, however, had not been completed by the end of the study.

Spawnings occurred late in the day, with most recorded between 1430 and 1600 h. Females were courted by the male before spawning took place. Courting consisted of a male tipping into a head-down posture in front of the female while rigidly extending his fins and intensifying his colors. This was followed by the male twitching his body once or twice, and then swooping around her into a head-up posture. The display would often be repeated and, if no consenting activity of the female was forthcoming, the male would then leave to court other females or patrol the edges of his territory. If the female responded by initiating a slow rise in the water column, the male would join her with his head touching her operculum and they would rise about a meter before returning to the substrate in a dash. The actual release of gametes occurred at the apex of the rise. The rise was noticeably slower than that of the four other wrasses I have observed in the San Blas Islands (*Thalassoma bifasciatum*, *Halichoeres bivittatus*, *H. maculipinna*, and *H. poeyi*). After 1600 h the razorfish became progressively more inactive and stayed closer to the substrate until about 1730 h by which time all had burrowed into their sand refuges for the night. Since daily observation periods were limited in duration and some females were seen consistently spawning day after day, it is likely that females of this species spawn daily.

Rosy razorfish appear to be strictly harem. All but 1 of the 61 spawnings observed was with the male whose territory overlapped the female's territory. The exception was a spawning that took place at the border of one male's territory where, instead of rising vertically into the water, the pair rose at an angle crossing the boundary between the spawning male's territory and that of his adjacent rival. The rival then dashed over, routed the spawning male in mid-rise, and completed the spawn.

Colonies of rosy razorfish are apparently divided up into contiguous harems.

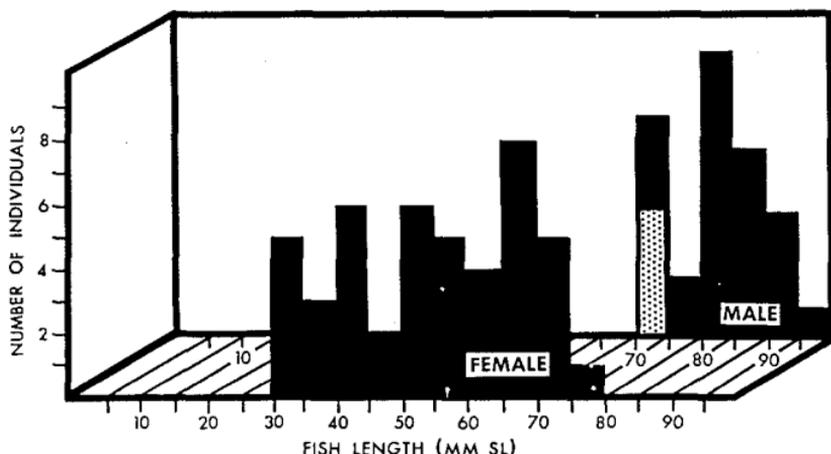


Figure 2. The distribution of the sexes in increasing size classes of rosy razorfish in the San Blas Islands. The dotted bar represents those males still in a transitional color phase.

In the colony I observed, one male had 35 females within his territory, another had 15 females, while 3 other males on the periphery had 7, 3, and 4 females apiece. The large female that changed sex during the study was a member of the harem of the top male, and he (the sex-changer) courted the surrounding females despite attacks from the larger top male. After several days, the top male ceased to attack the new male who then began to spawn with the females in closest proximity. He eventually had a harem larger than that of the three males with the fewest females and appeared to suffer no interference, despite the fact that he was conspicuously smaller than they were. Their territories, however, were not adjacent to his, and they may not have been aware of what was happening just a few meters away.

While I did not record detailed time budgets, my observations indicated that female razorfish spent most of their time foraging, primarily in the water column picking plankton, but occasionally near the substrate searching for benthic invertebrates. On days with clear water and abundant planktonic animals, the fish hovered as much as 1 m above the substrate. When females were not foraging they were usually occupied in maintaining a tiny patch of sand that was used as a refuge from predators. Maintenance consisted of removing pieces of coral or mouthfuls of sand from the site and depositing them a few centimeters away. The females occasionally would dive into the refuge and slowly rise while vibrating their body thus churning around the sand. These activities apparently kept the refuge clear of obstructions that might impede the fish when it dived in, but were certainly not necessary for a refuge since fish that were chased off into the sandbed buried themselves in any sand they happened to be over when I approached them too closely. Benthic animals disturbed by this activity were noticed and eaten, but the behavior often occurred without any obvious searching for prey.

There were many agonistic interactions between individuals. Females were territorial and aggressive, usually rushing at their smaller nearest neighbors and nipping at them. Fish of equal size lined up alongside each other and bent their bodies in exaggerated S-motions before responding aggressively. Of the 126 aggressive encounters between females that I recorded, 64% were initiated by the larger of the two fish, 29% were between similarly sized individuals, and only 7%

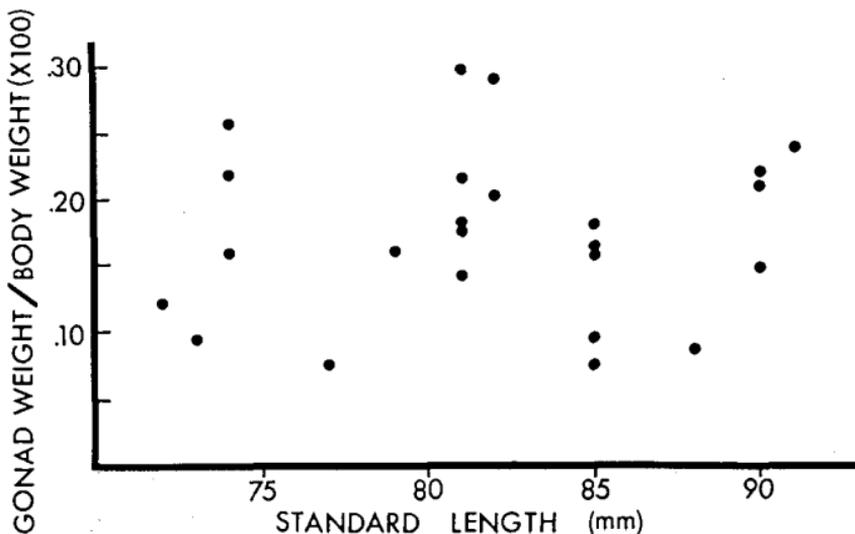


Figure 3. The relationship between the percentage of body weight devoted to gonads and standard length for male rosy razorfish in the San Blas Islands of Panama.

were initiated by the smaller fish. Males displayed to and chased neighboring males. Males rarely trespassed onto other males' territories, primarily because the colonies of rosy razorfish are sufficiently compact that the owner of a territory is virtually always close enough to repel an intruder. Males also attacked females, especially when a female had a prey item in her mouth and he could take it from her.

Interspecific aggressive interactions were also common for males (0.83 per hour of observation). Females were observed attacking intruders only once, when no male was nearby. The species chased were the yellowfin mojarra, *Gerres cinereus*, smaller bothid flatfishes, and goatfishes (Mullidae). All of these fishes are benthic invertebrate-eaters (Randall, 1983) and are therefore potential competitors. Males would not hesitate to attack mojarras several times their length. Of all the attacks observed only one, on a flatfish, was aggressively reciprocated.

Responses to predators varied with both the distance and species of predator. Certain fast-moving fishes (tunas and mackerels (Scombridae), jacks (Carangidae), and snappers (Lutjanidae)) were detected well before they came into my sight. Upon detection, a fright reaction spread through the colony almost instantaneously, as individuals lay sideways against the sand assuming a mottled coloration. Despite their reputation for burying themselves in the sand for protection, the razorfish only dived into the sand in rare cases when predators approached to within about 1 m of the hiding razorfish. Ambush predators, such as lizardfishes (Synodontidae), also elicited a panic among the razorfish, who responded by lowering themselves to the substrate in direct proportion to their proximity to the lizardfish, with those closest to the lizardfish occasionally burying themselves. Strong reactions to predators were relatively more common among razorfish (16.8 times per hour, SD = 6.04, N = 16 h) than among the reef-associated wrasses I have observed (for example, feeding schools of the bluehead wrasse, *Thalassoma bifasciatum*, on a nearby reef were recorded having a similar fright reaction only 5.1 times per hour, N = 14 5-min periods; Schildhauer, pers. comm.). Recovery

from the fright reaction was very fast, often taking place only seconds after the passing of the predators.

DISCUSSION

There are two ways for a male to monopolize a number of females in a polygynous mating system (Emlen and Oring, 1977): one is by defending resources essential to females and thereby keeping other males away from those females using the resource (resource defense polygyny), the other is to defend the females themselves from other males (female defense polygyny). These two categories are obviously not mutually exclusive, and often a male will defend females attracted to his territory because of the higher quality of the resources within his territory. There are numerous cases of resource defense polygyny in animals, while pure female defense polygyny is relatively uncommon (Emlen and Oring, 1977).

Controlling access to a group of females is difficult, if not impossible, for a single male if those females tend to travel on their own to pursue their own interests. Female defense polygyny, therefore, is feasible mostly when females are gregarious and relatively immobile. Females usually aggregate where their essential resources are clumped, and there males have the opportunity to monopolize them through resource defense polygyny. However, anything that causes females to aggregate in one place will promote the monopolization of mates by males. Predation pressure, particularly in exposed habitats, can force animals to forego independent foraging for the protection that living in groups affords (Wilson, 1975; Krebs and Davies, 1978; Partridge, 1982). This may result in a mating system exhibiting pure female defense polygyny. Rosy razorfish appear to be an example of this kind of female defense polygyny. Males defend females but do not defend any clumped essential resource, since these fish depend primarily on plankton drifting by for food and use the sand itself as a shelter. The colonies occur on large and apparently uniform beds of sand, much of which is suitable for shelter since (1) entire razorfish colonies regularly move around the sandbed, and (2) individuals that are chased out onto the unoccupied sandbed can bury themselves immediately whenever approached too closely. The observation that a male deferred spawning with a female resident in his territory when she crossed the border into another male's territory indicates that females may not be the sole currency of defense. This anecdote suggests that males actually defend the site occupied by a female, but probably only because it predictably contains a particular female.

It is not immediately apparent what is causing females to aggregate so tightly in a seemingly uniform environment. The high incidence of fright responses observed in this species suggests one answer. The lack of any structural heterogeneity in this habitat makes it difficult to remain sheltered and inconspicuous to predators. Fishes living on coral reefs are always near the shelter of the structurally complex reef substrate and concomitantly would be harder to see from a distance, have fewer angles from which attacks can be made, and have a variety of refuges immediately available. In contrast, fishes in exposed areas, such as the sandbed, can be seen from a distance, attacked from all angles, and have no refuge other than the sand itself. While burial in the sand is an effective escape, it is a risky one because the hiding fish is effectively blind and cannot tell whether the threat has passed without exposing itself again. Predators on sandbeds do often stop and wait for prey to reappear. This hypothesis is supported by my observations that razorfish typically lie close to the sand on the approach of predators rather than burying themselves, and when they do bury, often remain under the sand for

some time (on occasion more than an hour) after the danger has passed. On the exposed sandbed, therefore, a premium would be placed upon the rapid detection of predators. As a result, living in a familiar and close group would be extremely advantageous (review in Krebs and Davies, 1978). The razorfish colony would thus functionally resemble a substrate-associated school of fish (Partridge, 1982). Site-attachment of the group would both reduce the likelihood of being noticed by predators as well as assure the presence of a suitable sand refuge which could be maintained to facilitate a fast escape.

It has been argued that the distribution of food resources determines much of the mating system in the other tropical wrasses that have been studied (Robertson and Hoffman, 1977; Thresher, 1979; Robertson, 1981). One example is the Pacific cleaner-wrasse, *Labroides dimidiatus*, in which females have fixed sites at which they feed on the ectoparasites of other fishes. A single dominant male defends an area that includes several females' feeding sites from other males, resulting in a strictly harem mating system (Robertson, 1972; Robertson and Hoffman, 1977). Clearly, when females are tied to a predictable source of food, a male can sequester a number of females. If the optimal spawning sites are in a different location to optimal feeding sites, the decision by females whether to migrate or not could affect the mating system (Jones, 1981; Robertson, 1981). If the species is small and traveling to a better spawning site is sufficiently hazardous, females would be selected to spawn at the feeding site with the resident male, as in the cleaner-wrasse. If females do migrate to a distant spawning site a group-spawning or other promiscuous mating system would be most likely. Razorfish do not migrate to better spawning sites as do many other wrasses. Females always spawned within the colony, where other razorfish were regularly observed eating newly spawned eggs in the water column. Spawning downcurrent of the colony (and the planktivorous garden eels usually found within the same habitat) would certainly decrease the risk of losing eggs.

Robertson and Hoffman (1977) and Robertson (1981) argue that harems arise when males are able to penalize females who are sexually uncooperative by depriving them of access to resources. They suggest that when females are mobile, males cannot deprive them of resources and thus non-harem mating systems develop. In the rosy razorfish, however, males cannot deprive females of access to their planktonic (or even benthic) food, since these foods are widely available in the sandbed and generally indefensible. Another proposed method for males to penalize females was by expulsion from the group, thus lowering her chances of ultimately becoming a male. This behavior would be advantageous only if it were difficult for females to join other harems, either by moving to another part of the colony or by leaving the colony and finding another. Furthermore, unless the supply of space or food were so limited as to prevent females from finding a place within or at the edges of a colony, such behavior by males would be selected against because the expulsion of a female who even only rarely spawned with the resident male would result in an immediate lowering of that male's reproductive success. It is more likely that the driving factor in the razorfish mating system is simply the ability of males to prevent access to females by other males.

There are many apparent secondary adaptations in the razorfish mating system to the seemingly inflexible primary adaptation of female gregariousness. Since females can be defended, large males can assemble a number of mates and thereby lower the mating success of smaller males. If the mating system is strictly harem (all females mating with the male in whose territory they live), the mating success of small males incapable of defending a territory against larger males goes to zero. Natural selection would then select for the loss of gonochorism, and, in the absence

Table 1. Gonadal weights and gonad indices (gonad weight/body weight(100)) of males of wrasse species with various mating systems. The list is arranged in increasing order of the amount of interference by other males in the spawning act, from harem to group spawning. Pair = pair spawning; int. = interferred pair spawnings; group = group spawning. References: 1, Warner and Robertson (1978); 2, estimated from Robertson and Choat (1974); 3, Colin (1982); 4, this study; 5, Robertson (1981); 6, estimated from Jones (1981); 7, estimated from R. M. Ross (1984)

Species	Mating system	Gonad wt (g)	GW/BW(100)	Ref.
<i>Bodianus rufus</i>	Harem	0.18	0.09	1
<i>Labroides dimidiatus</i>	Harem	0.02	<0.30	2
<i>Lachnolaimus maximus</i>	Harem	—	<0.20	3
<i>Xyrichtys martinicensis</i>	Harem	0.01	0.17	4
<i>Clepticus parrae</i>	Pair	0.16	0.12	1
<i>Halichoeres garnoti</i>	Pair	0.07	0.14	1, 5
Terminal-phase males				
<i>Halichoeres maculipinna</i>	Pair/int.	0.04	0.18	1, 5
<i>Halichoeres pictus</i>	Pair/int.	0.02	0.14	1
<i>Halichoeres poeyi</i>	Pair/int.	0.07	0.27	1
<i>Pseudolabrus celidotus</i>	Pair/int.	2.0	low	6
<i>Thalassoma bifasciatum</i>	Pair/int.	0.03	0.23	1
<i>Thalassoma duperrey</i>	Pair/int.	—	0.10	7
<i>Halichoeres bivittatus</i>	Pair/int./group	0.11	0.79	1
Initial-phase males				
<i>Halichoeres maculipinna</i>	Int.	0.03	0.54	1, 5
<i>Halichoeres pictus</i>	Int.	0.02	0.49	1
<i>Halichoeres poeyi</i>	Int.	0.04	0.53	1
<i>Pseudolabrus celidotus</i>	Int.	1.1	high	6
<i>Halichoeres bivittatus</i>	Int./group	0.04	1.59	1
<i>Thalassoma bifasciatum</i>	Int./group	0.12	2.65	1
<i>Thalassoma duperrey</i>	Int./group	—	0.67	7

of any genetic constraints, all individuals would mature as females and only become males when they have reached a size at which they can successfully compete as males (Ghiselin, 1969). Rosy razorfish fit this scenario well: a few males garner most of the mates, all males are secondary (there are apparently no initial-phase males), and males are larger than most of the females.

Among the other secondary adaptations in the razorfish mating system is the small size of the male gonads. When more than one male is involved in a spawning, the one that releases more sperm fertilizes more eggs (sperm competition). All razorfish spawnings are purely pair spawnings. Razorfish males are therefore not in perpetual competition with other males to produce relatively more sperm, and thus need only produce enough to reasonably guarantee complete fertilization (Warner and Robertson, 1978). As a result, these males have relatively small gonads, the smallest in absolute size of all the wrasses that have been examined, although matching some other harem and pair-spawning wrasses in gonadal weight relative to body weight (Table 1). Similarly, because of the lack of sperm competition between males, there is no selection for increased gonadal investment in different size classes or male types (Fig. 3), as is typical of non-harem wrasses (Table 1). These other wrasses suffer some interference from small males when pair spawning and on average have more than one male per spawning. A few species have large numbers of initial-phase males who spawn in groups. In these cases, sperm competition ensues and the size of the male gonad increases in response (Warner et al., 1975; Warner and Robertson, 1978).

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