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Sexual Patterns in the Labroid Fishes of the Western Caribbean, II: The Parrotfishes (Scaridae)

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ABSTRACT

Robertson, D. Ross, and Robert R. Warner. Sexual Patterns in the Labroid Fishes of the Western Caribbean, II: The Parrotfishes (Scaridae). *Smithsonian Contributions to Zoology,* number 255, 26 pages, 12 figures, 6 tables, 1978.—The interactions of protogynous sex change, coloration, and mating behavior in ten species of Caribbean parrotfishes are outlined. The species considered are *Cryptotomus roseus, Sparisoma rubripinne, S. chrysopterum, S. viride, S. aurofrenatum, S. radians, S. atomarium, Scarus vetula, S. croicensis,* and *S. taeniopterus.* For each, we outline (1) the distribution of sexual types according to size and coloration, (2) the testis weight of different types of males, (3) characteristic habitat and relative abundance, (4) the social and mating system, and (5) breeding seasonality. Non-sex-changing (primary) males are absent in the sparisomatines but present in the scarinines and prematurational sex change is much more common among the sparisomatine species. There are also very large overlaps in size and coloration among the various sexual types of the sparisomatines. Large testes are present in small males of some species, and this is related to their interference spawning strategy. In species that do not occur at high density but do have haremic mating systems, small males are rare or absent. This is probably due to an increased ability of large males to control spawning in females. Haremic species are much more common in the parrotfishes than in the wrasses, perhaps because of basic differences in the distribution of food resources in time and space.

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Sexual Patterns in the Labroid Fishes of the Western Caribbean, II: The Parrotfishes (Scaridae)

D. Ross Robertson
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Introduction

Reinboth (1968) established the occurrence of protogyny in certain scarids. Since that time, the only work on patterns of sexuality in this group has been Choat's (1969) comprehensive treatment of sixteen Pacific (Great Barrier Reef) species (published in part in Choat and Robertson, 1975). Although the basic similarity in the patterns of sex change exhibited by both wrasses and parrotfishes was discovered by Reinboth (1962, 1968) in Caribbean scarids, there has been no systematic and comprehensive examination of sexuality in the fishes of that area. Whereas Choat's (1969) Pacific study dealt with scarinine species only, parrotfishes in the Caribbean are all the more interesting since they have a strong representation from both scarid subfamilies, the Scarinae and the Sparisomatinae.

This paper comprises the second part of a study of the patterns of sexuality in Caribbean labroids (see Warner and Robertson, 1978). In these two works, we draw together what we have been able to learn of the patterns of protogyny at the population level, the relationship of permanent color pattern changes to age, sex, and sex change, and the structure of social and mating systems. From this information, we have attempted a synthetic treatment of the evolution of protogynous sex change in these fishes (see also Warner, 1975a; Warner, Robertson, and Leigh, 1975).

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Materials and Methods

SPECIES STUDIED.—We obtained sufficient numbers of the following nine species to enable us to examine population structures: *Cryptotomus roseus, Sparisoma rubripinne, S. chrysopterum, S. viride, S. aurofrenatum, S. radians, S. atomarium, Scarus vetula,* and *S. croicensis.* A smaller number of *Scarus taeniopterus* were also collected, together with a very few *S. guacamaia, S. coeruleus,* and *S. coelestinus.* We never saw the one remaining Caribbean scarid listed by Randall (1968), *Nicholsina usta.*

STUDY AREA.—Collections and observations were made in the San Blas islands of Panama, the same area as referred to in Warner and Robertson (1978). An additional sample of *Sparisoma radians* was collected farther westward at Galeta Point, in the Canal Zone.

COLLECTING.—Collections and observations were made throughout the period March 1974–May 1975. As with the labrids (see Warner and Robertson, 1978), we attempted not to take specimens during periods of sexual activity, in order to reduce bias in the population samples. Apart from some trawl collections of small species (principally *Sparisoma radians*) living in turtle grass beds, specimens were speared as described in Warner and Robertson (1978).

TERMINOLOGY AND POPULATION PARAMETERS.—In this study we follow the same scheme as used for the labrids (Warner and Robertson, 1978, Appendix 1). When there is more than one distinct adult color phase, initial phase individuals have that pattern shown by smaller adults and terminal phase fish that of the largest males. In fully sexually dichromatic species the terminal phase pattern contains color elements that are not present in the initial phase pattern. In partially dichromatic species the patterns of both phases have the same elements but some of them are more strongly developed in the terminal pattern than in the initial pattern.

For each species, data are presented on: (1) the degree of sexual dichromatism; (2) the ratio of the number of initial phase to terminal phase fish in populations of dichromatic species; (3) the within-population overlap in the size ranges of the two color phases, based on data obtained from collections and field observations; (4) the presence or absence of males that are born as such (primary males) as opposed to males that are sex-changed females (secondary males) (see Reinboth, 1962, for criteria for distinguishing these two types histologically; when both types of males are present, the population is termed diandric, with only one type, it is monandric, see Reinboth, 1967); and distributions of the two types of males in the different size classes and color phases; (5) the distribution of recently sex-changed males (i.e., those containing previtellogenic oocytes in their testes) in the different size classes and color phases; (6) the absolute and relative (to body weight) weights of the testes of different classes of males; (7) the overall sex ratio, as determined from a combination of the color phase ratio and the within-color-phase sex ratio; (8) the characteristic habitat(s) of the species; (9) relative abundance, calculated from a series of counts of all species in a number of habitats, including (a) shallow (<5 m depth of water) stands of *Sargassum,* (b) large, shallow (<5 m) beds of turtle grass (*Thalassia* and other spermatophytes), and (c) coral reef substrates (coral, coralline rock, and sand patches dotted with coral growths), this last habitat surveyed on a series of depth profiles (<3 m, 3–6 m, 6–9 m, 9–12 m, 12–25 m, 15–18 m); (10) observations on the structure of social and mating systems; (11) breeding seasonality, as determined from observations on spawning and the collection of ripe females at various times of the year.

Results

Cryptotomus roseus.—This species is fully dichromatic (see Randall, 1968; and Chaplin and Scott, 1972, for pattern descriptions). While terminal phase males may rapidly and temporarily lose virtually all of their characteristic colors, sufficient differences remain to permit their field identification on very close inspection. Terminal phase males also have distinctly larger heads than initial phase fish. The color phase ratio was strongly biased towards the initial phase (Table 1). There was a moderate degree of within-site overlap in the size ranges of the two color phases. In six separate collections (totalling 15 terminal and 63 initial phase fish), there were two overlaps, each of 1.5 cm SL. One of those cases, however, involved two

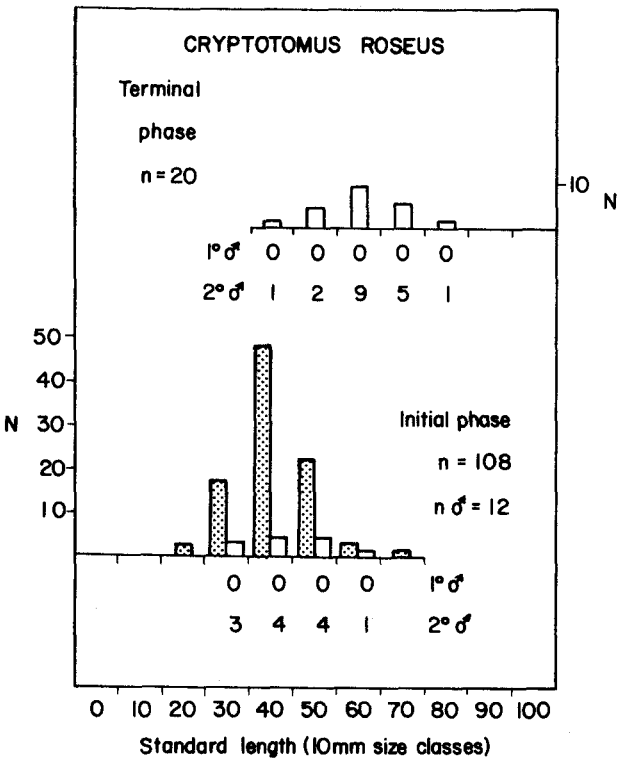

FIGURE 1.—Pattern of sexuality in *Cryptotomus roseus:* size/frequency bar graph of our sample, with indication of sexual origin of a number of the males in each size class (n = total sample size in specified color phase; 1° ♂ = primary males; 2° ♂ = secondary males; stippled bars = females, white bars = males; due to subsampling of more numerous size groups and losses during processing, the number of males histologically analyzed for sexual origin often falls short of the total number of males in the sample; placement of individuals in size classes follows the pattern of all fishes 20–29 mm SL belonging in the 20 mm size class).

small transitionally colored terminal phase individuals.

Since all the males we examined were secondary (Figure 1), *C. roseus* is evidently monandric. Secondary males were detected in all size classes of mature initial phase fish, including those well below the size of the smallest terminal phase individuals. The only males with transitional gonads that we found were two small (61 and 64 mm SL) terminal phase fish that had not yet fully taken on terminal coloration. The gonads of initial and terminal phase males weighed the same absolutely, but those of the initial phase males formed a much higher percentage of body weight (Table 2). The three smallest terminal phase fish had the relatively heaviest gonads of any fishes in that color phase. The sex ratio (Table 1) was moderately biased towards females, primarily as a result of the scarcity of initial phase males. We were unable to determine size at maturity because the smallest fish we collected were sexually active.

Cryptotomus roseus was restricted to shallow dense turtle grass beds and the broad interfaces of grass beds and coral reefs. It was one of the least abundant species, both overall and in the habitats to which it was restricted (Table 3).

We saw no good evidence of strong permanent territoriality by members of either color phase. Initial phase fish moved about in pairs and occasionally in small schools of up to a dozen individuals. Some of those groups also contained a terminal phase male, and we occasionally saw several such males moving quietly about near each other.

Sexual activity was observed in the early afternoons, when intensely colored terminal phase males became aggressive to each other. They coursed actively about over areas of up to several hundred square meters, apparently defending territories. Fifteen pair spawnings involving such males were observed, each with a smaller female. There were no signs of attempted interference by initial phase males or any indications that group spawning might occur. The terminal phase male courted either a single female or an entire small school. Sexual activity was observed only on the outer edges of reefs and banks in the habitats normally favored by the species.

Breeding occurred in all months of the year (Table 4). Not all females were continuously producing eggs, since we found some large individuals with inactive ovaries.

Sparisoma rubripinne.—The two color phases of this species are figured in Randall (1968), Böhlke and Chaplin (1968), and Chaplin and Scott (1972). It is fully sexually dichromatic (see Figure 2) and terminal phase fish appear to be unable to revert to the initial pattern. The color phase ratio was moderately biased towards females (Table 1). Direct observations and a few small collections indicated that the intrapopulational overlap of the size ranges of the two phases was exceptionally high. Three overlaps occurred in seven collections (16 terminal and 43 initial phase fish in total). The largest overlap was 11.5 cm. Also, as is shown in

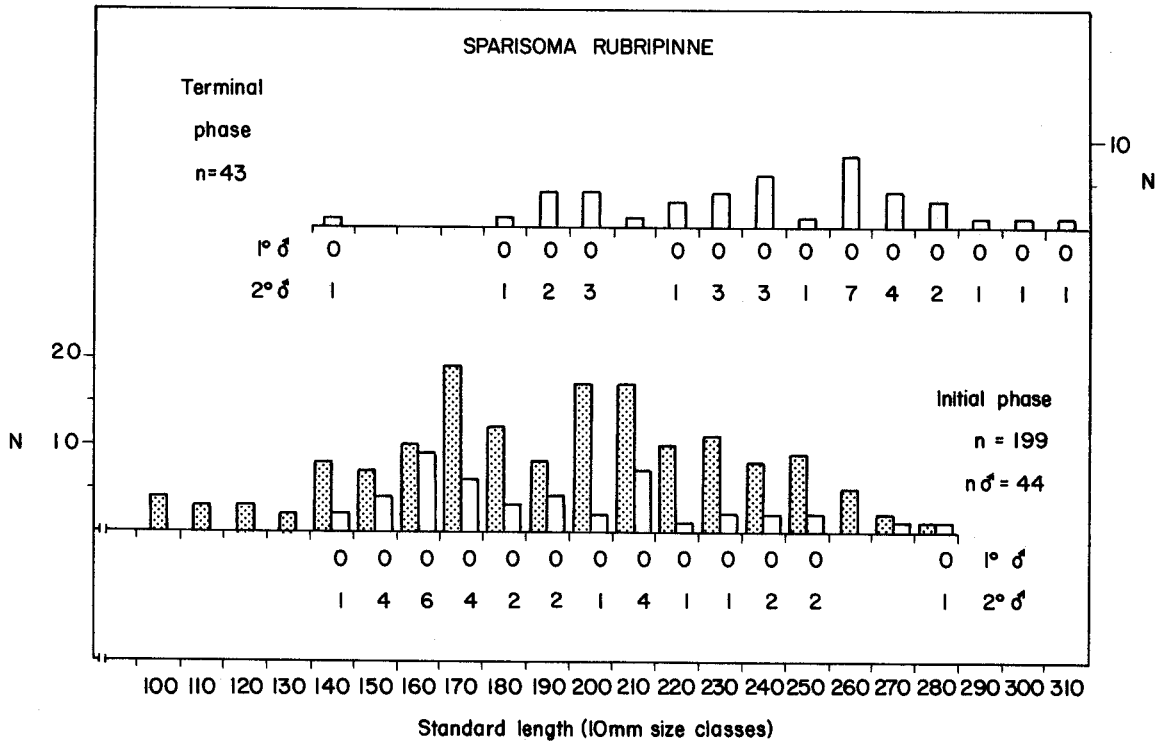

FIGURE 2.—Pattern of sexuality in *Sparisoma rubripinne* (for explanation of format, see Figure 1).

Figure 2, the largest females and initial phase males closely approached the largest terminal phase fish in size.

All males of both color phases proved to be secondary, establishing the monandric status of this species. Secondary males were also distributed throughout the entire size range of mature initial phase fish (Figure 2). Six males with transitional gonads were collected, four among the smallest size classes of initial phase males (143–169 mm SL) and two moderately large fish (235–260 mm SL) in the terminal phase. The smallest transitional individuals had changed sex prior to maturing as females. Our samples showed that females are mature beginning at about 160 mm SL. Initial phase males fell into two distinct classes: males smaller than 200 mm SL had very much smaller testes both absolutely (Figure 3) and relative to body weight, than did larger males. The gonads of the larger initial phase males weighed much more, both absolutely and relatively, than did those of terminal phase males (Table 2). In the largest initial phase males, relative testes weights equaled 6 percent of body weight, two orders of magnitude greater than that for terminal phase males.

Due to the strong representation of males in the initial phase (Figure 2), the sex ratio is not heavily biased towards females (Table 1).

This species, one of the less abundant scarids, was distributed throughout the habitats sampled with the exception of turtle grass (Table 3). Other observations indicated that it was most commonly associated with *Sargassum* beds in areas subject to heavy wave action, and on turtle grass beds close to the edges of reefs.

Feeding schools were often encountered. They consisted of up to 40 fishes of both color phases and a variety of sizes. This and the overlapping movement of individual fish strongly suggest that this species shows no permanent territoriality.

Intensely colored terminal phase males set up temporary territories and engaged in sexual activity on the peripheries of reefs facing deep water. The 27 pair spawnings that we observed involved such males, and occurred at one site in late afternoon. Sexually active males were observed by us

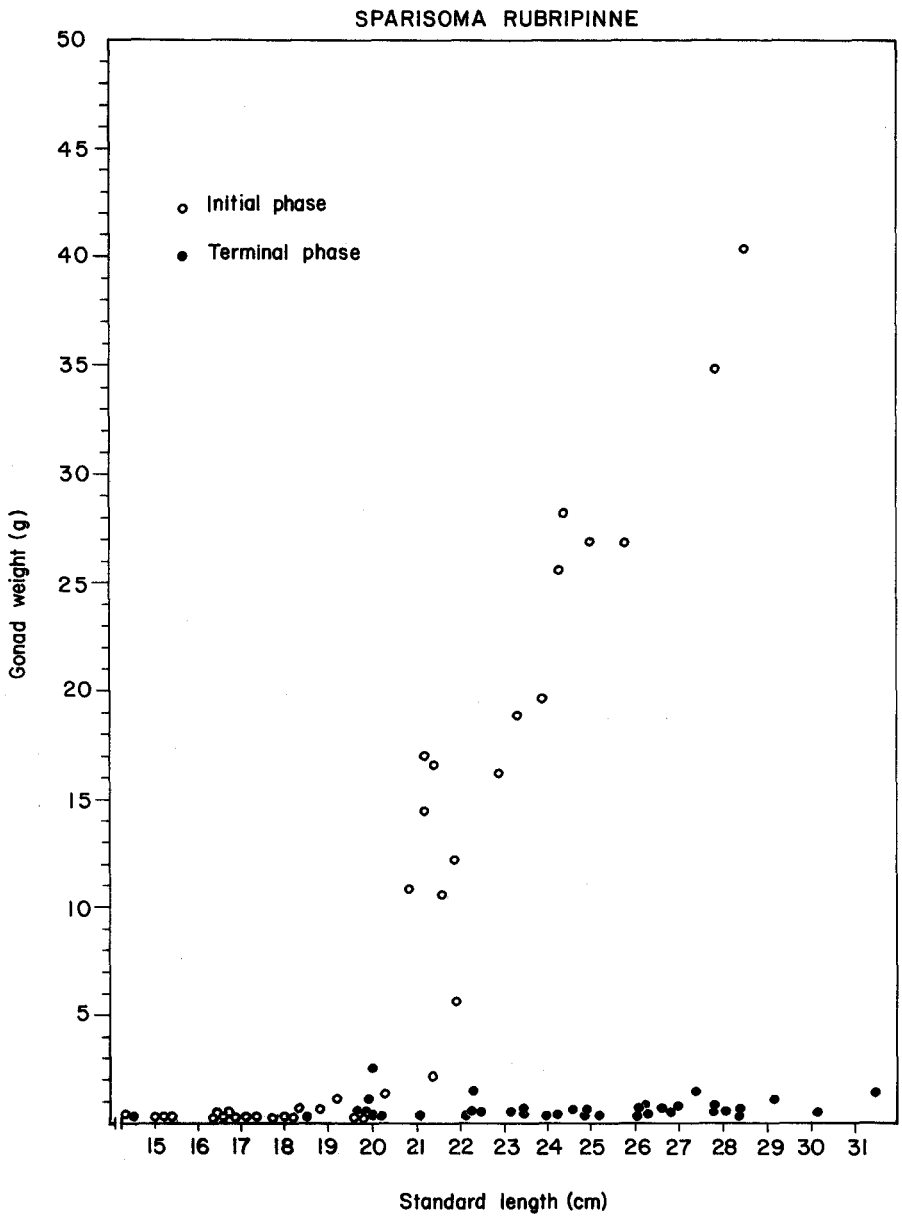

FIGURE 3.—Gonad weights for various sizes of initial phase and terminal phase males of *Sparisoma rubripinne*.

in the mornings in other areas. We observed no group spawning in this species or any participation by satellite initial phase males in the pair spawnings of territorial males. However, Randall and Randall (1963) describe group spawning in aggregations of hundreds of initial phase fish. Initial phase males were certainly present in the same areas as sexually active terminal phase fish; we speared two that were being persistently and vigorously harrassed by territorial males.

Sparisoma rubripinne probably breeds throughout the year, although our data are not quite complete enough to show it (Table 4). Females with inactive gonads were also regularly collected.

Sparisoma chrysopterum.—Although *Sparisoma chrysopterum* is fully sexually dichromatic (see

Randall, 1968, for illustrations of the two color phases), we experience some terminological difficulty in describing the bright all-male phase as a terminal coloration. Females grow to the same size as terminal phase males, perhaps even slightly larger (Figure 4). However, since juveniles bear the same coloration as initial phase adults, terminal phase individuals, at one time in their lives, have been in the initial phase. For this reason we continue to call the bright pattern of large males the terminal coloration. Terminal phase males did not appear capable of temporarily regaining the initial color pattern. The color phase ratio was quite equable (Table 1). Direct observations and a series of small collections indicated that the degree of color phase size overlap within a population was high. Overlaps of up to 6.3 cm SL were found in six of eight collections, comprising 21 terminal and 45 initial phase fish.

Sparisoma chrysopterum is evidently monandric, since all the males of both color phases that we examined were secondary (Figure 4). The few initial phase males were restricted to the lower end of the initial phase size range. Most of those males also had transitional gonads, as did seven of the terminal phase males. These terminal phase males were also quite small individuals (145–194 SL). For females, the onset of maturity appears to occur at about 140 mm SL. Secondary males smaller than the smallest mature females were collected. The testes of males of both color phases were small, with no significant size differences between the two phases (Table 2). Our initial phase male sample, however, is small and thus does not rule out the possibility that some such males have large testes. Although there were few initial males, the sex ratio was not strongly biased towards females due to the low color phase ratio (Table 2).

This species was most commonly encountered in turtle grass beds, typically close by reefs, to which it retreated when threatened. It was moderately common overall (Table 3).

Feeding schools of *Sparisoma chrysopterum* containing up to about a hundred adults of various sizes and both color phases were commonly seen in turtle grass areas. We saw no indications of permanent territoriality by members of this species.

In midafternoon, we regularly observed strongly

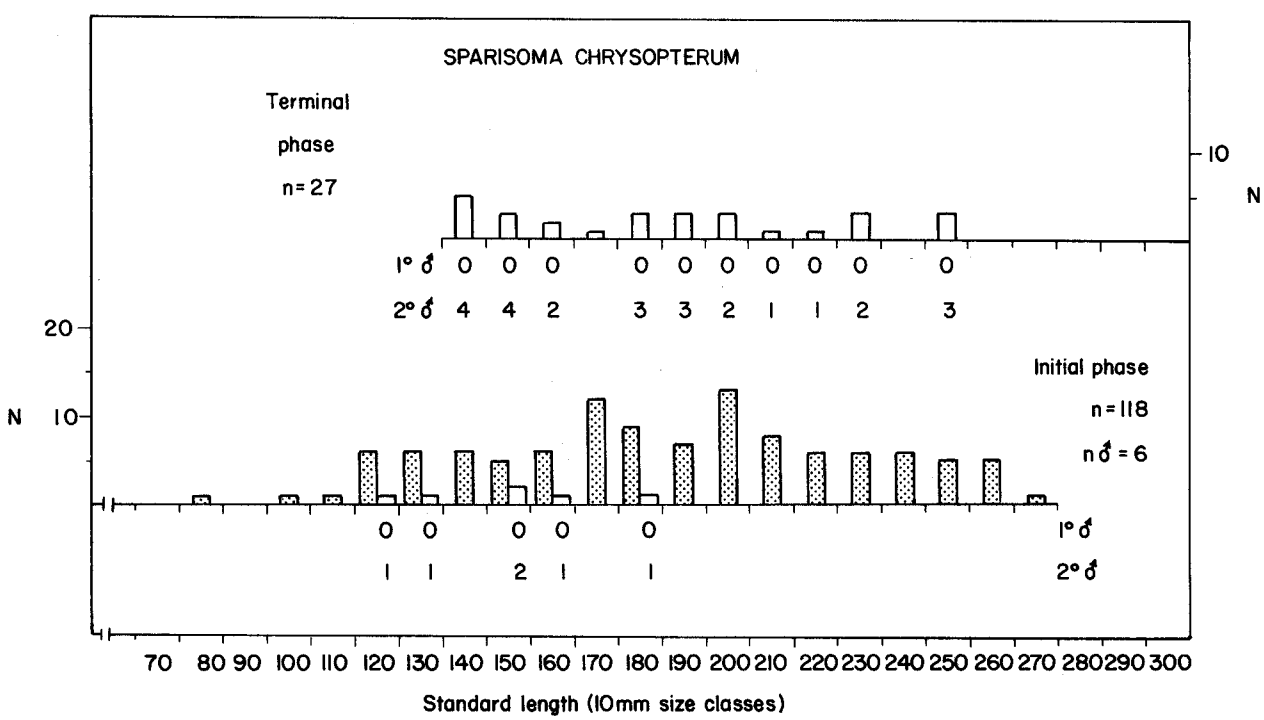

FIGURE 4.—Pattern of sexuality in *Sparisoma chrysopterum* (for explanation of format, see Figure 1).

colored terminal phase males defending temporary territories scattered along the shallow rims of reefs in areas of good coralline rock cover. Small groups of females moved about through the territories of these males. The males courted them and, on two occasions that we observed, pair spawned with them. We never saw anything to suggest that males of either color phase might interfere in pair spawnings or participate in group spawning.

The species bred during both main seasons (Table 4), probably throughout the year. Inactive as well as active females were collected at all times of the year, indicating a lack of continuous egg production by females.

Sparisoma viride.—Full sexual dichromatism is shown by *Sparisoma viride* (see Randall, 1968, for color illustrations). Our observations have shown the terminal coloration is permanent. The color phase ratio was moderately biased towards the initial phase (Table 1). There was a high degree of intrapopulational overlap in the size ranges of the two phases. We observed this directly and it is shown by some of our collections: overlaps of up to 11.2 cm SL occurred in five of seven collections comprising 14 terminal and 73 initial phase fish.

Reinboth (1968) found that this species is protogynous. Our large sample of males of both color phases shows that *S. viride* is monandric (Figure 5). Although males comprised a high proportion of the smaller initial phase fish, they were absent from the larger initial phase size classes. Only two of the males examined had transitional gonads; one was the smallest terminal phase male obtained (110 mm SL) and the other a moderate sized terminal phase male (199 mm SL). Females mature at sizes greater than 160 mm SL. Secondary males smaller than the smallest mature females were also obtained. Six males whose terminal coloration had not yet fully developed were collected; none of these six had transitional gonads. The size range of the transitionally colored individuals in our collection was 130–200 mm SL, on the lowest end of the terminal phase size range. Larger, similarly colored fish, however, were seen. Terminal phase males had testes that weighed much less than those

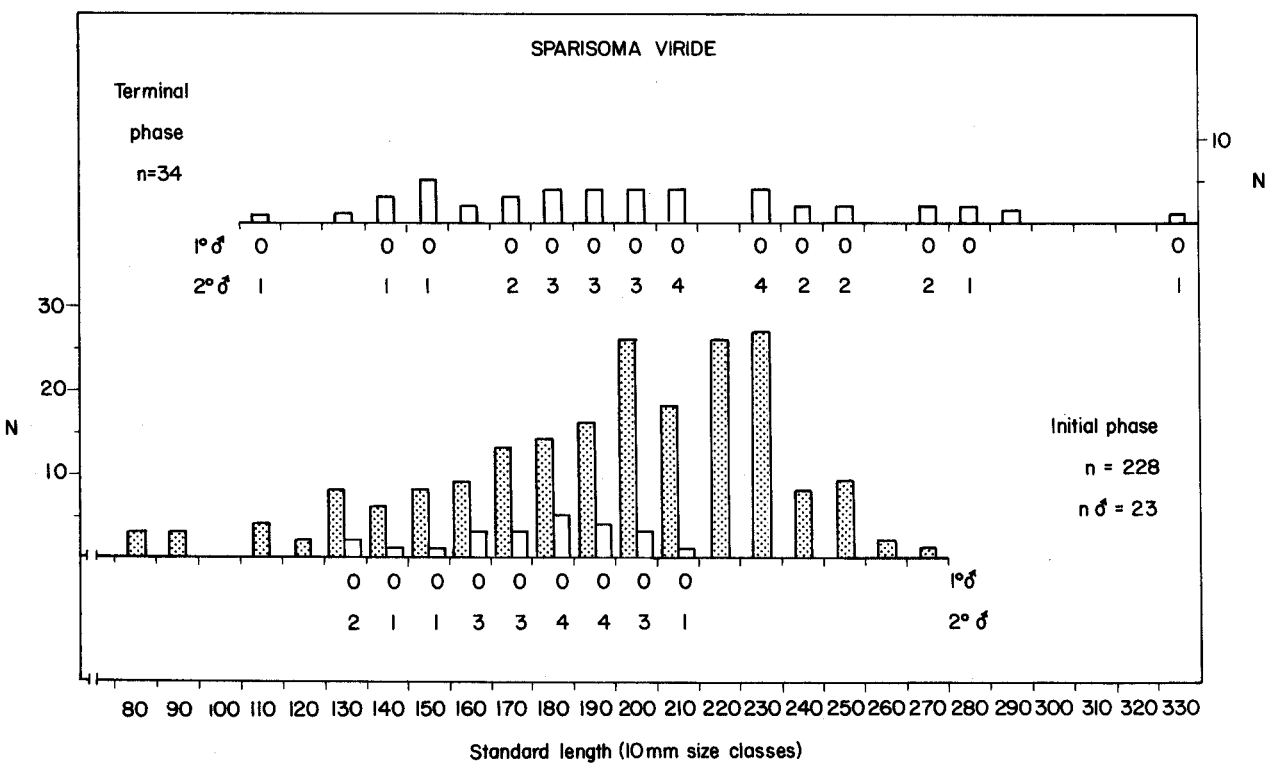

FIGURE 5.—Pattern of sexuality in *Sparisoma viride* (for explanation of format, see Figure 1).

of initial phase males, both absolutely and relatively (Table 2). The sex ratio was moderately biased towards females in this species (Table 1).

Sparisoma viride was largely restricted to coral reef habitats where it occurred at a variety of depths (Table 3). It was one of the more abundant scarids in its main habitat.

Typically we found this species feeding in loosely knit aggregations of up to twelve fish of both color phases and a range of sizes, and occasionally in well-defined schools of up to several hundred adults. We saw no behavior that would have indicated permanent territoriality by members of this species.

We frequently observed sexually active terminal phase males, however, temporarily defending territories on the shallow parts of the outer rims of reefs. In some instances, there appeared to be more males than available territories, and the "excess" formed loose inactive groups a little away from the territory holders. This territoriality was temporary and restricted to that part of the day when sexual activity occurred. The timing of sexual activity varied from site to site, being consistently in mid to late afternoon at one regularly visited place, while early morning activity was observed elsewhere. The earliest spawning seen was at 0745 and the latest at 1700. Twenty-one pair spawnings involving territorial terminal phase males and smaller females were noted. Although we saw no indications of successful sneaking or streaking by initial phase males, or any group spawning, I. Downs (pers. comm.) on one occasion saw several pair spawnings that each involved a (presumed) initial phase male. Sexually active terminal phase males often chased initial phase males.

Spawning occurred in both major seasons and probably throughout the year (Table 4). All females were not constantly producing eggs, since we collected both active and inactive females in the same sample on numerous occasions.

Sparisoma aurofrenatum.—Randall (1968), Böhlke and Chaplin (1968), and Chaplin and Scott (1972) each provide color illustrations of the two adult color phases of this species which shows full, strong sexual dichromatism (Figure 6). We found no indications that terminal phase males could temporarily lose their color elements and revert to the initial pattern. The color phase ratio was one of the least strongly biased towards initial phase (Table 1). There was very little within-population overlap in the size ranges of the two color phases, as indicated by our field observations and collections. Only one instance of overlap, of 2 mm SL, occurred in eight samples totalling 25 terminal and 56 initial phase fishes.

Sparisoma aurofrenatum is another of the scarids that Reinboth (1968) found to be protogynous. Our data show that it is monandric (Figure 6). Males were too rare in the initial phase to allow us to determine accurately whether they were restricted to any particular size classes. Four secondary males with transitional gonads were found, all terminal phase individuals (119–169 mm SL). The testes of initial phase males were much heavier, both absolutely and relatively, than those of terminal phase fish (Table 2). Although the color phase ratio was one of the more equable among the scarids, the rarity of males in the initial phase resulted in the sex ratio being moderately biased towards females (Table 1). We were unable to determine exact size at female maturity. It occurs at lengths less than 90 mm SL.

Sparisoma aurofrenatum was restricted to coral reef areas and their immediate surroundings and occurred throughout the depth range of that habitat. It was one of the more abundant species that we studied (Table 3).

There were strong indications that almost all terminal phase males of this species were permanently territorial. We never observed these males in aggregations or schools, and whenever we saw two together they were almost invariably interacting agonistically. At common borders, fights between terminal phase males were regularly seen and these males appeared to be distributed evenly throughout their habitat. With initial phase fish, the situation was less clear, but it appeared that a harem of a few females of varying sizes lived within the permanent territory of a larger terminal phase male. This system is similar to that described by Buckman and Ogden (1973) for *Scarus croicensis*. We certainly never saw schools of initial phase fish or more than about six individuals together in a small area.

Spawning apparently took place within the permanent territories of the terminal phase males. Sexually active terminal phase males were observed coursing actively about their territories on the edges of reefs from midmorning until early afternoon. We noted 26 pair spawnings involving such males

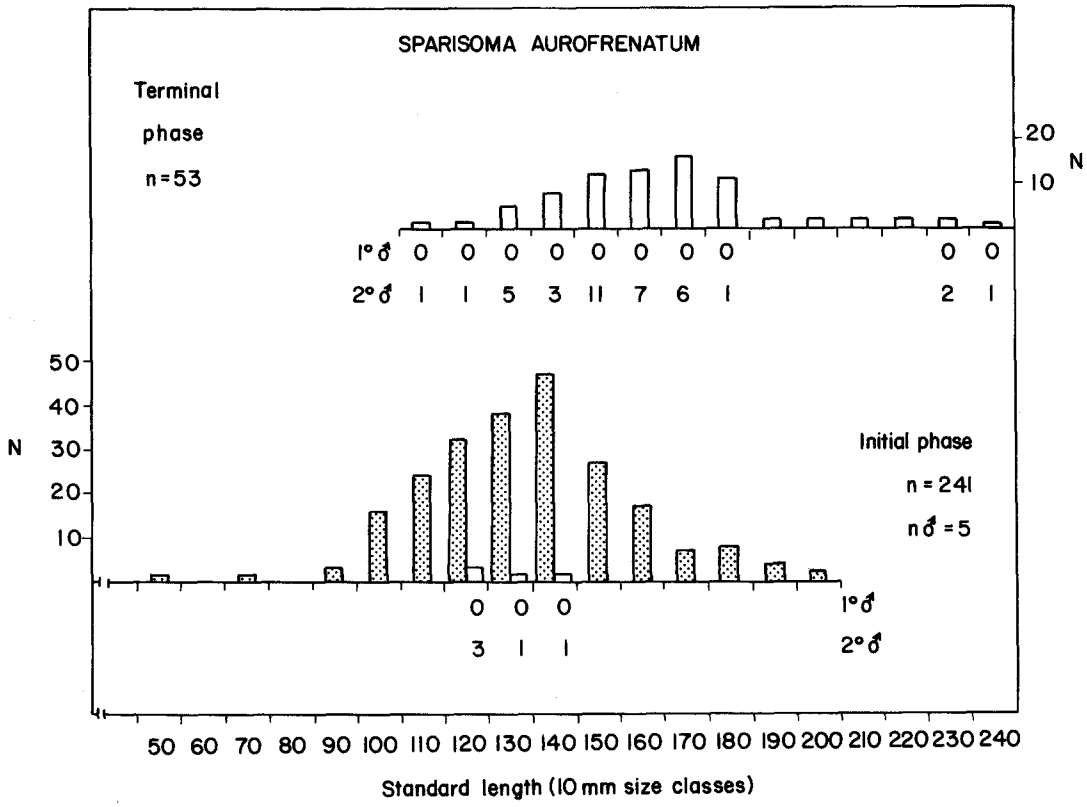

FIGURE 6.—Pattern of sexuality in *Sparisoma aurofrenatum* (for explanation of format, see Figure 1).

and smaller females, with no indications of attempted participation in them by any other males.

This species was found to be breeding in most months of the year (Table 4) and probably does so throughout both main seasons. Females with ovaries in various states of activity were taken in each of our collections.

Sparisoma radians.—Randall (1968) provides color illustrations of the two color phases of this species. Although it is fully sexually dichromatic, we encounter the same terminological problem as experienced with *Sparisoma chrysopterum*: initial phase fishes grow to the same size as terminal phase males, perhaps even larger than them (see Figures 7, 8; in the two samples collected at Galeta Point and San Blas the size range of terminal phase individuals is completely contained in the size range of the initial phase). For the same reasons as given for *Sparisoma chrysopterum,* however, we retain the color pattern classification. Although terminal phase males evidence temporary fading of their brighter color elements, thus strongly resembling initial phase fish, the two can be distinguished on close inspection. Terminal phase males also have more heavily built heads than most initial phase fish. The color phase ratio, based on two large trawl collections, and supported by field observations, was quite equable (Table 1). These two collections also showed a very high degree of intrapopulational overlap in the size ranges of the color phases (Figure 8).

Since, in our large sample covering both color phases, all the males that we examined proved to be secondary, *Sparisoma radians* is monadric. The few initial phase males encountered were all among the smaller size classes of that phase (20–60 mm SL). Only two males with transitional gonads were obtained, both in the largest size class of initial phase males (both 63 mm SL). Four small males without fully developed terminal colors were also taken. Although the gonads of terminal phase males were slightly heavier than those of initial phase males,

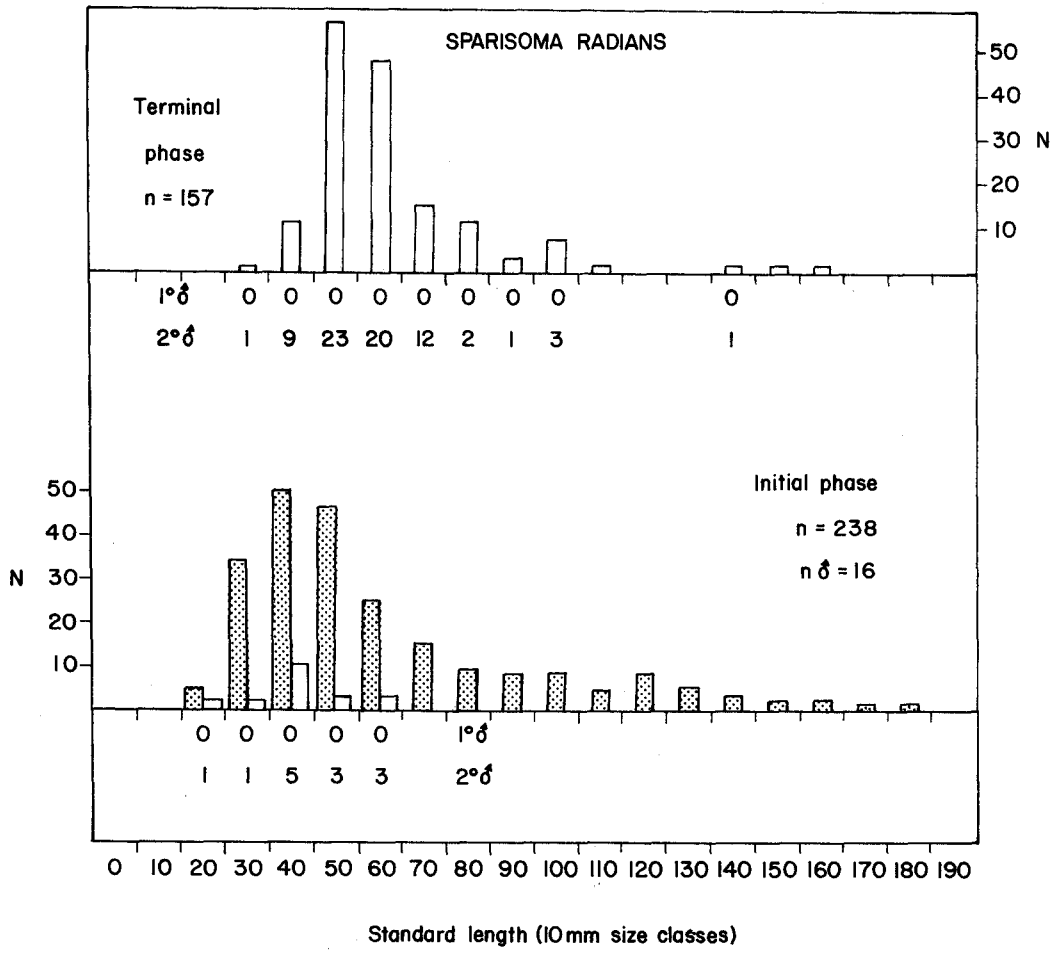

FIGURE 7.—Pattern of sexuality in *Sparisoma radians* (for explanation of format, see Figure 1).

they comprised much less of the total body weight (Table 2). They did weigh more, relative to the fish's body weight, however, than the gonads of terminal phase males of any other scarids we examined. Because of the very low color phase ratio, the sex ratio was less strongly biased towards females than in any of the other scarid species (Table 1). Mature females were found among the smallest individuals collected.

Sparisoma radians was essentially restricted to shallow beds of dense turtle grass and *Sargassum,* although it also extended into the interfaces between these and hard reef areas. Overall, it was one of the most abundant species (Table 3). Although we have no specific data, it is our impression that this species tended to form permanent aggregations, even within large areas of apparently uniform habitat.

There were strong indications that some, at least, of the terminal phase males were permanently territorial, since we repeatedly observed defense of small ($\bar{x}$ = 7 m^2, n = 13) areas in the same sites throughout the day. In the same localities, initial phase fish and less brightly colored nonterritorial terminal phase fish moved about singly or in small schools of up to twenty individuals, and were harrassed by the territorial males. It also appeared that some of the initial phase individuals remained for a long time in small groups within the territories of larger terminal phase males.

Sexual activity was observed in midafternoons, most frequently along the sloping outer edges of

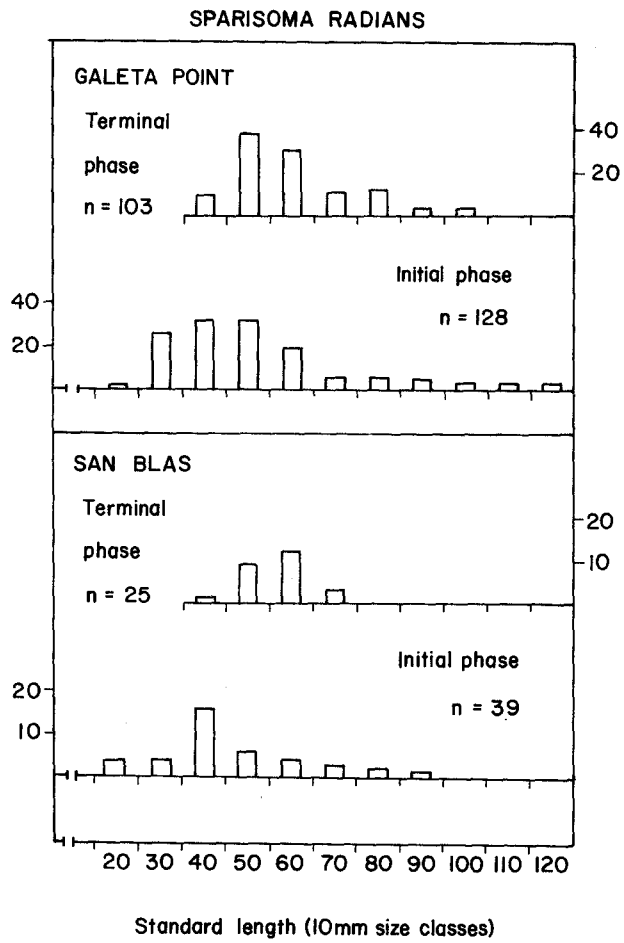

FIGURE 8.—Size range overlap between initial and terminal phase *Sparisoma radians* within two local populations; initial phase individuals include both males and females.

grass beds, where the species was found at other times. At such times, territorial terminal phase males became brighter colored and more strongly territorial. There was a general influx into the spawning ground by females, which were often followed by small groups of initial phase males and nonterritorial terminal phase males. Territorial males pair spawned with these females. The other two classes of males group spawned with the females. Often, males of both color phases were in one spawning aggregation. Pair spawnings of territorial males were commonly participated in by one or more other males of either or both color phases. This occurred in 35 of 62 spawnings observed. Territorial males also commonly interfered in the pair spawnings of neighboring territory holders. They would occasionally join in group spawnings, although they often tried initially to disrupt them. For example, we watched the spawning activity of three territorial males over three days on one spawning ground. The three males pair spawned a total of 29 times, and in 16 of these spawnings suffered interference by other males. These same three males group spawned three times, and six times they interfered in neighbor's pair spawnings.

Sparisoma atomarium.—Superficially, this species strongly resembles its congener *Sparisoma radians*: both are small, cryptically colored fish of similar shape that live in association with turtle grass beds. None of the three recent works that describe and figure parrotfishes (Randall, 1968; Böhlke and Chaplin, 1968; Chaplin and Scott, 1972) illustrate or even adequately describe the color patterns of *S. atomarium*. For this reason, we show the main characteristics by which these two sibling species can be distinguished in the field (see Figure 9). Close observation is often needed before decisions can be made.

Sparisoma atomarium is fully sexually dichromatic. Terminal phase males can evidence alteration of the intensity of their colors, but evidently do not revert even temporarily to the initial color pattern. The color phase ratio was the second most strongly biased toward the initial phase when compared to that of all other species we examined (Table 1). There was also very little overlap in the size ranges of the two color phases within any population. In eight separate population collections, totalling 27 terminal phase and 78 initial phase fishes, there were only three instances of overlap, none of more than 4 mm SL.

Sparisoma atomarium is monandric, since no primary males were found in the moderate sample of males examined (Figure 10). Males were also rare in the initial phase, and apparently restricted to the upper end of the size range of that phase. No males with transitional gonads were collected. The sample size of initial phase males was too small to allow determination of whether the size of the gonads of such males differed significantly from those of terminal phase males (Table 2). The sex ratio was more strongly biased towards females than in any other species (Table 1), because both terminal phase and initial phase males were scarce. Mature females occurred in the smallest size classes that we collected.

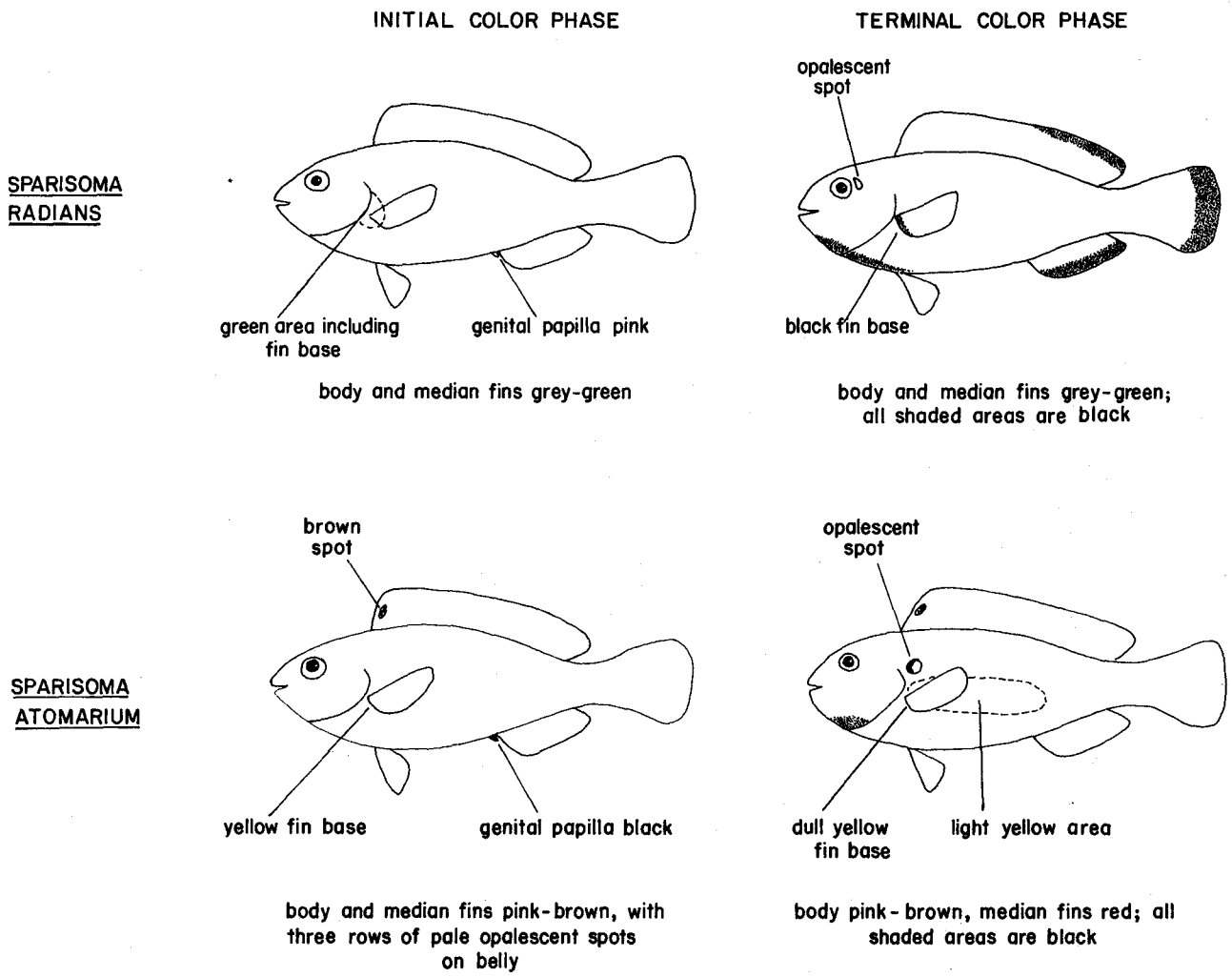

FIGURE 9.—Distinguishing coloration of *Sparisoma radians* and *S. atomarium*.

Although *Sparisoma atomarium* was found in dense turtle grass beds, where it mingled with *S. radians,* we more often encountered it in the interfaces between grass and coral reef substrates, where *S. radians* was much less common. Overall it was one of the least abundant species (Table 3).

The social system of this species in many respects closely resembles that of *Sparisoma aurofrenatum.* The site attachment and numerous agonistic interactions of the solitary terminal phase males suggested permanent territoriality. Small groups of females appeared to restrict their movement to within the territories of these larger males. In areas of dense turtle grass stands, where the species reached its highest densities, we also saw small feeding schools of up to twenty subadult and small adult intial phase fish. Our collections showed that these were all females.

The mating system of *S. atomarium* resembles that of *S. aurofrenatum*: terminal phase males spawn with the females resident in their permanent territories. Sixty-eight pair spawnings by such territorial males and "their" females were noted, all in midafternoons. We also observed one pair spawning by a known initial phase male with a female that had been responding to an actively courting terminal phase male. We never saw any behavior that suggested that group spawning was likely to occur.

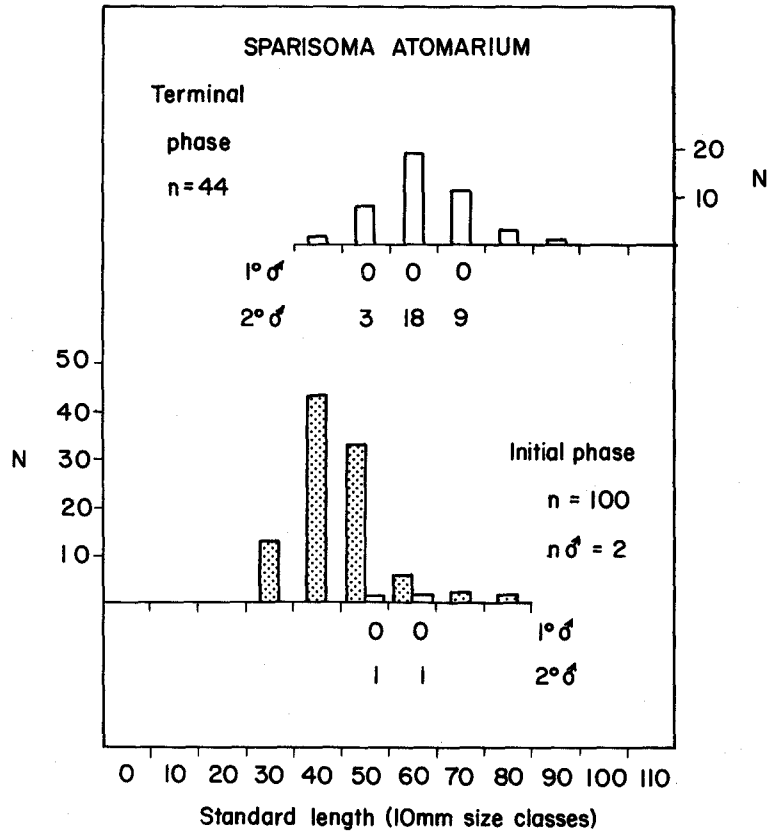

FIGURE 10.—Pattern of sexuality in *Sparisoma atomarium* (for explanation of format, see Figure 1).

This species spawned throughout the wet season and during much of the dry, probably throughout the year (Table 4). Not all females, however, were continuously producing eggs.

Scarus vetula.—*Scarus vetula* is fully sexually dichromatic, with no indication that terminal phase males can temporarily lose their characteristic colors. Randall (1968), Böhlke and Chaplin (1968), and especially Chaplin and Scott (1972) provide color illustrations of the two phases. Initial phase fish were about four times as common as terminal phase fish (Table 1). The few data we have show the within-site overlap in the size ranges of the two phases to be low (two overlaps, one of 2.4 cm SL, in five collections of six terminal and 24 initial phase fish). We occasionally saw, but could not catch, smaller terminal phase fish.

This species is diandric (Figure 11). Although primary males were quite rare, we found them in both color phases. No secondary males with transitional testes were collected and no secondary males were found in the initial phase. Although we obtained only a small sample of initial phase males, their testes were much heavier than those of terminal phase males (Table 2). The single terminal phase primary male's testis was the same size as those of secondary males. The sex ratio was moderately biased towards females, mainly due to the rarity of initial phase males (Table 1). No mature females smaller than 140 mm SL were collected.

This species was limited to fairly shallow coral reef habitats (Table 3). Typically, we found it along the exposed edges of reefs with heavy sculpturing and many physical complexities. Even in this habitat it was one of the least abundant scarids.

We never saw any indication of long-term school formation by any individuals. Initial phase fish were found dispersed singly throughout the habitat or in small, transient groups of up to half a dozen fish of different sizes. Terminal phase males, which

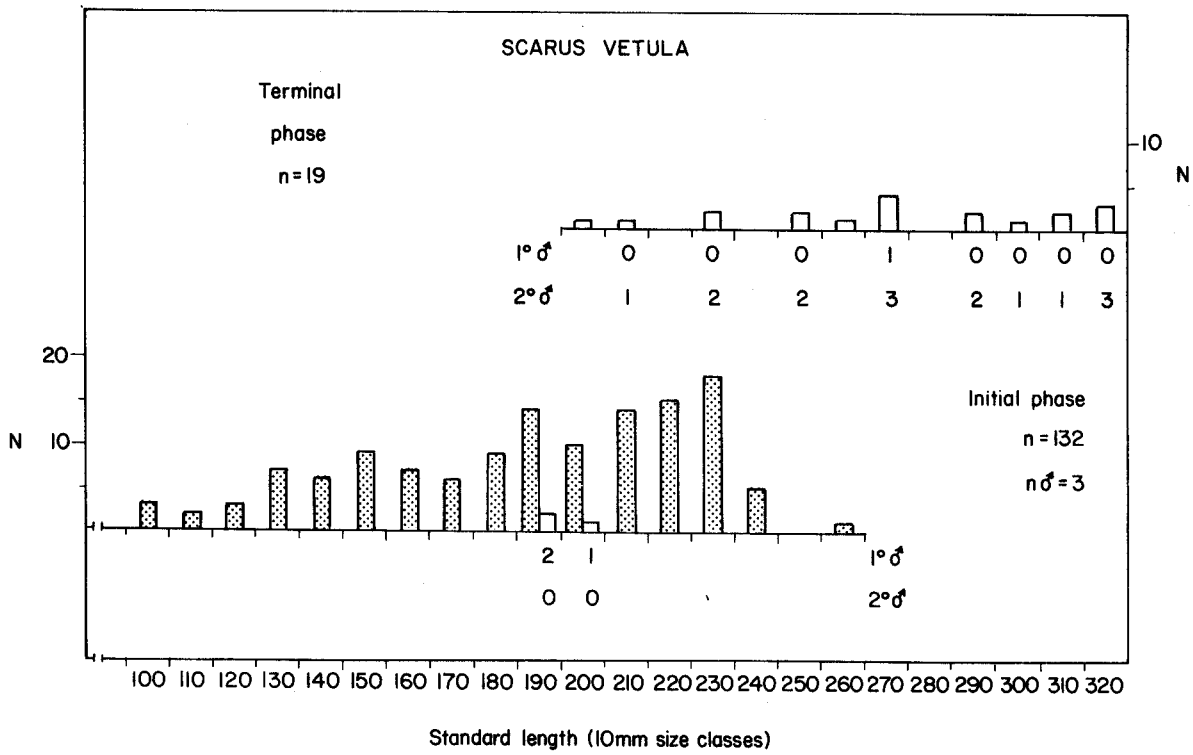

FIGURE 11.—Pattern of sexuality in *Scarus vetula* (for explanation of format, see Figure 1).

usually occured singly, often engaged in aggressive interactions that strongly resembled border encounters between neighboring territory holders. Thus it appears that large terminal phase males hold permanent territories, within which a small group (3–4) of smaller females lived. Winn and Bardach (1960) have made a similar suggestion. We also observed smaller, nonterritorial terminal phase males on the peripheries of territories.

We never observed sexual activity by *S. vetula,* although Randall and Randall (1963) report seeing a terminal phase male pair spawn. The data are too sparse (Table 4) to make any statements about the seasonality of its breeding.

Scarus croicensis.—This common and widespread species has been the subject of research on behavioral ecology and sexuality more than any other parrotfish, in the Caribbean or elsewhere (Randall and Randall, 1963; Ogden and Buckman, 1973; Buckman and Ogden, 1973; Barlow, 1975; Robertson et al., 1976; Warner and Downs, 1977). Although we have dealt with this species in detail elsewhere, a synopsis is presented here and new information added where relevant.

A major problem confronts our efforts to examine certain population parameters in this species: the existence of a complex social system with significant variation in the composition of the different social classes. Ogden and Buckman (1973) first described these distinct behavioral classes. Warner and Downs (1977) expanded on that work by making detailed examination of the composition of each social class in terms of its age and sexual type. Because the social classes do differ greatly in composition, it is difficult to sample the population for such things as sex ratio without knowing the proportion of the population that each social class represents. This we have been unable to do, and therefore our estimates of initial phase male proportions (Table 5) and sex ratio (Table 1) must be considered rough approximations.

Scarus croicensis is fully and strongly sexually dichromatic, with no evidence that terminal phase males are capable of temporarily losing their characteristic color pattern. Under certain conditions, however, their bright colors can effectively be masked and become very dull. Randall (1968), Böhlke and Chaplin (1968), and Chaplin and Scott

(1972) all contain color illustrations of the two phases. The color phase ratio was moderately biased towards the initial phase (Table 1). At several sites, within-site overlap in the size ranges of the two phases was very low. A few short observations on individually recognizable fish indicate that natural changeovers from the initial to the terminal coloration can essentially be completed in as little as 10 days.

Scarus croicensis is diandric (Figure 12), with a high proportion of primary males in both color phases. Because of differences in the composition of social classes, we do not know whether the proportion of such males is significantly different in each phase. Only one secondary male was found among all the initial phase fish collected; this was a relatively large fish (100 mm SL) with transitional gonads. Two other males with transitional gonads were also collected; both were in the process of changing color phase also. The testes of primary initial phase males weighed much more, both absolutely and relatively, than those of primary or secondary terminal phase males (Table 2; see also Warner and Downs, 1977, fig. 4). No mature females smaller than 40 mm SL were collected.

This species was common throughout the coral reef areas that we sampled as well as the interfaces of coral reefs and turtle grass beds or sand areas. Overall, it was the most abundant scarid encountered (Table 3).

Three distinct social classes were recognized by Ogden and Buckman (1973): (1) territorial groups, composed of a terminal phase male and several

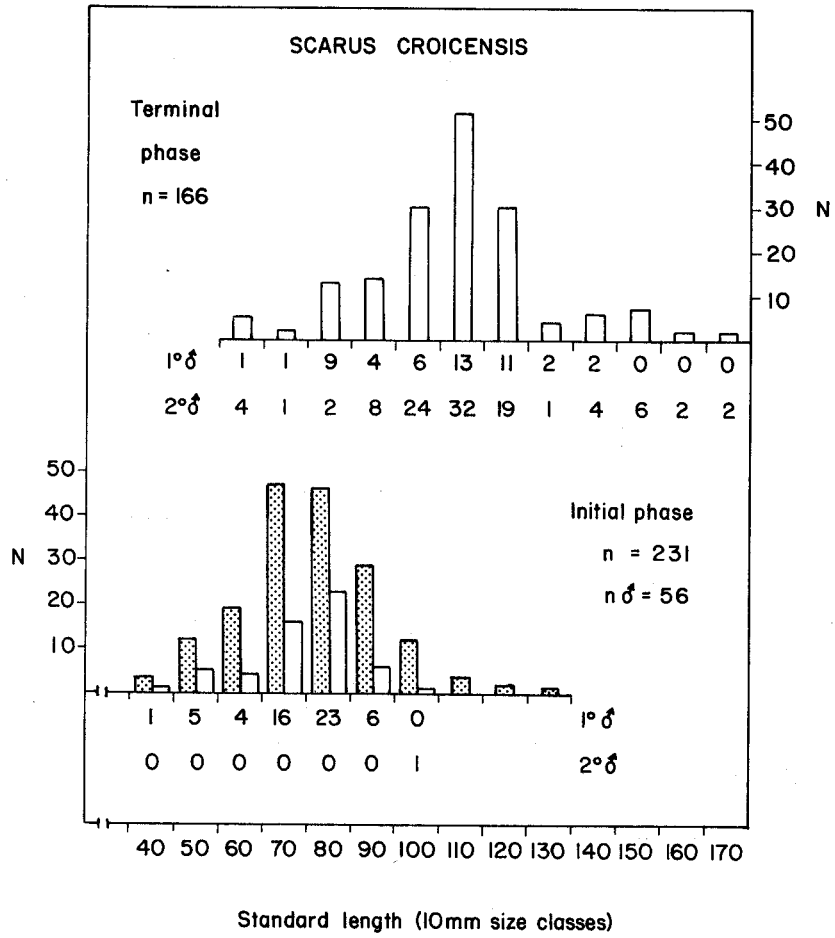

FIGURE 12.—Pattern of sexuality in *Scarus croicensis* (for explanation of format, see Figure 1).

females, all of which defend a common area (although Ogden and Buckman noted a few males among the territorial initial phase fish they collected, all 119 initial phase fish that we collected from harem groups were females); (2) foraging groups or feeding schools composed of hundreds of fishes of both color phases, and containing many initial phase primary males; (3) small stationary groups, with a composition similar to that of foraging groups. Evidently, there is also considerable movement of individuals between these classes.

Permanently territorial terminal phase males pair spawned in their territories, with the females of their groups and with other females that wandered past. We often saw group spawnings by small clusters of initial phase males, as well as satellite males of both color phases participating in the pair spawnings of territorial terminal phase males. We also noted a few pair spawnings by initial phase males. The initial phase male aggregations in which group spawnings occurred were small and not found as commonly as were those of some other labroids (see Warner and Robertson, 1978). Considerable amounts of aggression were directed at such male aggregations by the territorial terminal phase males. Spawning occurred between midday and late afternoon, on the outer edges of reefs. Whether some terminal phase males set up temporary spawning territories only for the duration of a spawning period is not clear, although Barlow (1975) made such an observation elsewhere in the Caribbean.

Breeding took place throughout the year (Table 4), although not all females were continuously producing ripe eggs over that period.

Scarus taeniopterus.—The two color phases of this species, which strongly resemble those of *Scarus croicensis,* have been well described (see Randall, 1968; Böhlke and Chaplin, 1968; Chaplin and Scott, 1972). It is fully sexually dichromatic, as far as we can tell, and terminal phase males do not appear to be capable of temporary reversion to the initial coloration. Reinboth (1968) showed that this species was protogynous. We collected few individuals of this species, which was rare in our study area. The six terminal phase males that we did collect, (215–265 mm SL) were secondary, and had small testes (Table 2). The 10 initial phase fish (173–200 mm SL) were all females. This was too small a sample to determine if the species is monandric or diandric.

Our only observations of *S. taeniopterus* occurred on a few occasions in 5–15 meters of water on the outer slopes of reefs with heavy coral growth. The fish were observed singly, with each terminal phase male overlapping several females in its range of movement. This indicates that a harem system may exist, similar to that of *S. croicensis.*

Discussion

General Life History Patterns.—In Warner and Robertson (1978), we have discussed how we construct life history patterns from the structure of our samples. In that paper is given further information on the assumptions involved in this procedure and the sample structures that we considered would indicate a particular pattern.

The patterns of sex and coloration among the Caribbean parrotfish are obviously complex. Are there any instructive generalizations that we might draw from the results given above?

Two major differences on the subfamily level are apparent, as well as several minor ones. First, primary males are present in the Scarinae and absent in the Sparisomatinae (which includes *Cryptotomus* and *Sparisoma*). There are enough similarities between the subfamilies in terms of small male distribution, behavior, and gonad weight to indicate that the small secondary males of the sparisomatines function much as do the small primary males in the scarinines. The only scarinine species in which primary males are known to be absent is an Indo-Pacific species, *Scarus niger.* It is sexually monochromatic, while the other eight species dealt with in detail by Choat and Robertson (1975) are both dichromatic and diandric.

Secondly, prematurational sex change appears common in the Sparisomatinae. Although individuals that change sex before maturity spend their adult lives as males, and are thus functionally analogous to primary males, their gonads are definitely derived from ovaries. This suggests there has been a development of secondary gonochorism in these species, which may have lost their primary males in the evolutionary past. Very small secondary males are found in three species of *Sparisoma* (*S. rubripinne, S. chrysopterum,* and *S. viride*) and probably occur in several others.

This consistent pattern of primary male scarinines versus early sex-changed sparisomatines apparently does not hold outside the Caribbean. Choat and Robertson (1975) found prematurationally sex-changed males in four of the nine Indo-Pacific scarinine species they examined in detail.

The Caribbean scarinines have a common, straightforward life history pattern. All females appear to change sex if they live long enough; sex change usually occurs over a small size range, and is accompanied by color change. Primary males change from initial to terminal coloration within this same small size range (however, see Choat and Robertson, 1975, for other scarinine patterns).

In contrast, the sparisomatinines show a bewildering array of patterns, often within a single species. In species that have temporarily territorial males, there are broad size overlaps in both sex and color phases. Some females do not appear to change sex at all. This was common in *Sparisoma chrysopterum* and *S. radians,* and may also occur in *S. viride* and *S. rubripinne.* The latter species may also have males that retain initial coloration through to maximum size.

Sparisoma aurofrenatum and *S. atomarium,* the most strictly haremic species, show a pattern of sex change reminiscent of that of the scarinines. All females probably change sex, there are few initial phase males, and the size differential between initial and terminal phase fishes is usually quite distinct. Further on, we discuss the reasons for this consistent pattern in haremic species.

Testis Size in Relation to Spawning Strategies.—In Warner and Robertson (1978) we have discussed the hypothesis proposed by Robertson and Choat (1974) and Choat and Robertson (1975) to account for consistent, and often radical, differences in the size of the gonads of the males of the two color phases of certain dichromatic labroids. The hypothesis states that since males of the two phases have different spawning strategies (group spawning and other multimale forms by initial phase males, and single-male spawnings by terminal phase males), selection has favored the development of larger testes in initial phase males. In a spawning involving more than one male, increased sperm production gives an individual male a greater share of the fertilization of the eggs of the female(s) present in the group.

In the Caribbean scarids, the same pattern of gonad weight differences exists as in the labrids. Small testes were present in the terminal phase males of all species except *Sparisoma radians.* All initial phase males had large testes relative to body weight. This was particularly marked in *Sparisoma rubripinne, S. viride, S. aurofrenatum, Scarus vetula* and *S. croicensis.*

Overall, these data agree with what we know of the spawning patterns of the individual scarid species. We have observed pair spawning by the terminal phase males of all species except *Scarus taeniopterus.* Group spawning by the initial phase males of *Sparisoma rubripinne* and *Scarus croicensis* is also known to occur.

The pattern in *Sparisoma radians* also offers support for the hypothesis. In this species, both initial and terminal phase males (territorials included) commonly participate in multimale spawnings and both have large testes. The testes of terminal phase males of this species are relatively smaller than those of conspecific initial phase males, but relatively larger than those of terminal phase males of the other species we examined. This agrees with the observation that in *S. radians,* the terminal phase males are involved in multimale spawnings far more commonly than are terminal phase males of other species.

Sparisoma rubripinne presents a particularly striking pattern in regard to differences in testis size: the testes of initial phase males increase in size dramatically after 200 mm SL (Figure 3). The reason for this increase remains obscure. Warner and Downs (1977) have considered the interactions between the expenditures of energy on growth and gamete production in different sexual identities of *Scarus croicensis.* Primary males appear to channel more energy into growth than hermaphrodites of the same age. This may enable them to bypass a relatively unproductive "small male" phase and become larger, terminal phase males more quickly. Perhaps an analogous situation exists within the small initial phase males of *Sp. rubripinne:* energy is channeled into growth until a reproductively profitable size is reached, and only then is energy devoted to increasing gonad size. Such rapid increases in gonad weight did not occur in the other

labroid species we studied, which points out the need for a thorough study of the social and mating system of this species.

One final point deserves mention: in all the parrotfish we studied, both sex-changed males and primary males had large testes while in the initial phase, and relatively small testes while in the terminal phase. In other words, testicular ontogeny has little or no effect on testis size. This we also found to be true in the wrasses (Warner and Robertson, 1978).

Social Systems, Mating Systems, and the Success of Different Mating Strategies.—*Perspective:* In the first of these two papers (Warner and Robertson, 1978), we examined the sexuality of nine labrids in the light of our previous discussions of the evolution of protogyny and the coexistence of different sexual genotypes (Warner, Robertson, and Leigh, 1975; Warner, 1975a; Robertson and Choat, 1974; Choat and Robertson, 1975). We wanted to see if there was any necessity to discard, modify, or expand these ideas. Apart from two species for which sufficient information was not available (unfortunately so, since the structure of their populations promises to be quite different from those of the other species), only one, *Clepticus parrae,* did not fit easily into the expected general pattern. We discussed how *C. parrae*'s atypical pattern of sexuality might be related to its atypical (for a labrid) ecology and spawning behavior. How do the scarids fit into the predicted patterns?

Protogyny is likely to evolve in species in which sexual selection is acting (Warner, Robertson, and Leigh, 1975). We have argued that dichotomous male mating strategies are possible when strong sexual selection and sex change have led to an abundance of females relative to the number of terminal phase males. Territorial terminal phase males pair spawn with females, and initial phase males employ several mating strategies that depend on interfering with the pair spawning of these territorial males. They may move unnoticed into territories and steal pair spawnings or participate in them as streakers. When present in large numbers, they often intercept females enroute to a territorial male and induce them to group spawn. Larger populations can have more skewed color phase ratios than small populations of the same species (Warner, Robertson, and Leigh, 1975). The relatively greater numbers of females present in such large populations lead to greater opportunities for successful meddling by initial phase males. Accordingly, initial phase males are common in large populations and rare in small ones (Warner, Robertson, and Leigh, 1975).

Robertson and Choat (1974) and Choat and Robertson (1975) also examined the effect of interspecific differences in the structure of social and mating systems on the ability of territorial males to reduce the level of interference by nonterritorial males in their spawning. They suggested that in species in which males hold only temporary reproductive territories the anonymity of the individual may facilitate an interference strategy. In species with strictly haremic social systems, in which males are permanently territorial, harem males could indentify potential intruders and effectively eliminate the possibility of spawning interference. Few or no small males would be expected in such species.

Haremic Species: Among the Carribbean scarids, there do not appear to be any species that combine sexual monochromatism, monandry, and strictly haremic social and mating systems. In species with these features (e.g., the labrid *Labroides dimidiatus,* see Robertson and Choat, 1974) the male mates only with the females of his permanent harem. All members of the population live in such harems, and there is no evidence of any males employing a strategy of interference in the spawning activities of territorial males. Most of the scarids we examined (*Sparisoma aurofrenatum, S. radians, S. atomarium,* the three *Scarus* species, and possibly *Cryptotomus roseus*) apparently do form harem groups. However, they are dichromatic and initial phase males are present that have been shown (in some species) to interfere in the spawning of terminal phase males.

Choat and Robertson (1975) relate the sexual monochromatism of species of the *Labroides dimidiatus* type to the pattern of virtually all mating being within a permanent group: there is, therefore, no selection for a distinctive color pattern that serves to attract females during spawning periods. Robertson and Hoffman (in press) amplify this argument.

In *Scarus croicensis,* where the populations are quite dense, haremic terminal phase males have both intra- and extraharemic matings. Some males also establish temporary spawning territories. This puts a premium on attracting females and could

account for the development of sexual dichromatism in this species.

In *S. croicensis,* harem groups constitute large proportions of the populations we studied. On some reefs, there were also large numbers of nonharemic individuals. They apparently could not hold territories because the number of sites available was limited. These individuals employed an alternative strategy: swamping territory holders (see Robertson, et al., 1976). Individual initial phase males are probably excluded from harems by terminal phase males but can still gain food in the harem's territory by feeding en masse. The large groups also contain unattached females, which form a source of extraharemic matings for the harem male. This situation further facilitates the intrusion of identically colored initial phase males into the harem territory and their interference in spawnings.

Of the remaining harem-forming scarids, *Sparisoma radians* is similar to *Scarus croicensis* in having a large nonharemic segment in the population. Group spawning regularly occurs in both as well. Not surprisingly, there are high proportions of initial phase males in this species. Despite these similarities between *Sparisoma radians* and *Scarus croicensis,* several significant differences exist between them that reflect the interaction of habitat type, social system, and sex change: (1) the size overlap of the two color phases is high in *Sparisoma radians* and low in *Scarus croicensis,* and there is a higher proportion of terminal phase fish in the former than in the latter; (2) females of the non-sex-changing types (primary females) are strongly represented in *Sparisoma radians* but absent in *Scarus croicensis* because females grow to much smaller relative size in the latter species (Figures 7 and 12); (3) haremic terminal phase males of *Scarus croicensis* tend only to pair spawn, while those of *Sparisoma radians* commonly participate in both single and multimale spawnings; (4) finally, while in *Sparisoma radians* there is a class of nonterritorial terminal phase fish that employ the same interference spawning strategy as initial phase males, there is no evidence of such a class in *Scarus croicensis* (some observations suggest that nonterritorial terminal phase males of *Scarus croicensis* may not be breeding: feeding schools of such males have been observed to be indifferent to the spawning activity of nearby territorial terminal phase males). Interference in spawning is greatly facilitated in *Sparisoma radians* by a combination of small territory sizes, abundant sea grass cover and cryptic coloration of the nonterritorial males. This allows nonharemic males to enter or hide very close to a territory, and only a short dash is necessary to join a spawning. The same factors also facilitate the streaking of neighbors' pair spawnings by territorial males. In *Scarus croicensis,* territories are much larger and coral does not provide the same kind of cover.

We have no direct information on the frequencies of group spawning in either species, although neither formed large nonterritorial male aggregations of the *Thalassoma bifasciatum* type (see Warner, Robertson, and Leigh, 1975). We think that the high frequency of multimale spawning in *Sparisoma radians* raises the potential fertility of small males, which means that more such males can exist in the population (Warner, Robertson, and Leigh, 1975). A lack of a pronounced mating hierarchy among the males and high mating success of initial phase males would also explain why the non-sex-changing female morph exists. In the absence of a significant fertility differential between females and males at all sizes, there would be no selection to eliminate non-sex-changing females in favor of sex-changing types (see Warner, 1975a). Even if the reproductive success of large males was higher than that of equivalent sized females, this could be offset by higher mortality rates on such males; i.e., the average lifetime fecundity of a female could equal that of a larger, but shorter-lived male or hermaphrodite. The brighter colors and exposed activity during spawning time of terminal phase males could make them more vulnerable to predation and thus bring about such differential mortality rates.

In other species *(Sparisoma aurofrenatum, Sparisoma atomarium, Scarus vetula,* and probably *Scarus taeniopterus),* there is little or no evidence of the occurrence of nonharemic females and no indications of the occurrence of group spawning. This latter group also contains very few initial phase males (Figures 6, 10, and 11). Although the only spawning interference by initial phase males that we saw was in *Sparisoma atomarium,* the large testis size of initial phase males of *Sparisoma aurofrenatum* and *Scarus vetula* (Table 1) indicate to us that they also use an interference strategy.

We reasoned above that the occurrence of extraharemic matings enables initial phase males to

interfere in harem males' spawnings. For two reasons, we think that extraharemic spawnings are uncommon in *Sparisoma atomarium, Sparisoma aurofrenatum,* and *Scarus vetula:* (1) the nonharemic segment of the population appears quite small and thus few "extra" females are probably available; (2) the equable color phase ratios of *Sparisoma aurofrenatum* and *Scarus vetula* indicate that terminal phase males have only small harems and thus can exert high levels of control over their females. A low frequency of extraharemic matings would reduce the chances for initial phase males to interfere. In species where the harems are characteristically small, the loss of a single spawning is significant to the dominant male, and strong attempts to prevent them would be expected. This further lowers the probability of spawning success for initial phase males. Since the proportion of initial phase males in a population depends on their expected reproductive success (Warner, Robertson, and Leigh, 1975), we would expect few such males in these three species (Table 5). This does not rule out the possibility that elsewhere in their geographic ranges these species could be more abundant, with greater spawning opportunities for initial phase males.

Nonharemic Species: Three of the remaining species, *Cryptotomus roseus, Sparisoma rubripinne* and *Sparisoma viride,* fit the expected general pattern reasonably well. They lack strong harem forming tendencies and have an abundance of initial phase males. Initial phase males have been seen spawning in two of the three species. The abundance of females relative to the number of terminal phase males (Table 1) suggests that suitable conditions for the initial phase male strategy are present. Quite distinct differences occur in the structure of initial phase male populations of *Sparisoma rubripinne* and *Sparisoma viride,* however. Males occur among all size classes of initial phase fish in *Sparisoma rubripinne,* but are restricted to the smaller classes in *Sparisoma viride. (Sparisoma radians* is similar to *Sparisoma viride* in this respect.) Why this is so we cannot say.

The remaining species, *Sparisoma chrysopterum,* shows a great deal of similarity to *Sparisoma radians* in (1) having the highest proportions of terminal phase males; (2) having large intrapopulational size overlaps of the color phases; and (3) apparently having primary females. However, the pattern in *Sparisoma chrysopterum* is not as easily explained. The abundance of terminal phase males and pronounced size overlap of the two phases suggest that average fertility differentials between terminal phase males and females are probably small. There is no indication that multimale spawning is the predominant mode in *Sparisoma chrysopterum,* even though it is not haremic. It is a large species that does not spawn in small territories in dense grass beds like *Sparisoma radians.* Thus conditions highly favorable to interference in pair spawnings are absent. Interference seems unlikely as a factor diminishing the strength of a mating hierarchy of terminal phase males. A thorough study of the mating system of this species is sorely needed.

Additional Factors: In Warner and Robertson (1978) we showed that the labrids with lek-type mating systems and large dense populations had the highest proportions of males in the initial phase. We reasoned that this resulted from a mating system based on strong sexual selection. In sex-changing species, this tends to bias the sex ratio heavily towards females and promotes the development of an alternative (interference) spawning strategy (see Warner, Robertson, and Leigh, 1975).

The connection between high population levels and lek-type mating systems is not as strongly developed in the parrotfishes, probably because of a more stable and predictable food supply (see below). Also, actual population densities are probably a less reliable indicator of relative ability to form leks in the parrotfishes than in the wrasses. Labrid species tend to be uniformly smaller in size than most parrotfishes, and so abundance measures may correlate well with the number of individuals that gather for spawning. But the large parrotfish species (such as *Sparisoma rubripinne* and *Sparisoma viride)* would be able to move much larger distances than small species such as *Sparisoma radians* or *Sparisoma atomarium.* This could explain the poor correlation between population density and frequency of initial phase males among the scarids (Table 5).

The mating system, however, remains as a fairly dependable predictor of initial phase male success. All species that have strongly developed haremic mating systems have very low proportions of initial phase males (Table 5). Large, mobile species that lack permanent territoriality tend to have many

initial phase males (e.g., *Sparisoma viride, Sparisoma rubripinne).* In *Scarus croicensis,* population density may play a major role. Territoriality is observed in both males and females (Buckman and Ogden, 1973), but population density is high enough that many individuals are not site attached and feed in large schools, swamping the territory owners (Robertson et al, 1976). Females from these schools participate in spawnings with territorial males, and this facilitates interference spawning by initial phase males (described in greater detail above).

Throughout these two discussions of labroid sexuality we have borne in mind the very real possibility that numerous sexual types can continue to coexist within a single species because different types are successful in different habitats. Consider, for example, the situation in the labrid *Thalassoma bifasciatum,* which we described in detail elsewhere (Warner, Robertson, and Leigh, 1975; Warner and Robertson, 1978). Terminal phase males are successful in small populations and initial phase males have greater success in large populations. Planktonic larval dispersal continually redistributes all types to all habitats, and a polymorphism of sexual types could be maintained from a mosaic of local population effects. The composition of sexual types in a sample population may reflect the overall composition of populations within the area of larval dispersal, rather than a local selective equilibrium. Thus we should not necessarily expect significant reproductive success of a particular sexual type in a local population chosen at random.

This may be the explanation for the confusing patterns of such species as *Sparisoma chrysopterum* and *Sparisoma rubripinne.* Rather than seeking a selective advantage for initial phase males in low density populations, perhaps we should look elsewhere in the Caribbean for locales that support larger numbers of the species in question. At such sites initial phase male success may compensate for failures elsewhere.

Social control of sex change has been demonstrated in two species of labrids, *Labroides dimidiatus* (Robertson, 1972), and *Thalassoma bifasciatum* (see Warner, Robertson, and Leigh, 1975; D. R. Robertson, unpublished data). In the latter, a color phase change often accompanies sex change. We have no reason to doubt that the timing of sex and/or color change is not controlled externally, with social factors playing a major part, in many of the species that we have dealt with here. In a strictly haremic species, such as *L. dimidiatus,* the cue that triggers female's sex change is simple and clear: the death of the harem male releases the largest female from his aggressive domination (Robertson, 1972). In species in which social relationships are not so precisely defined, however, factors leading to sex and color change are probably more complex. It is quite possible that the large size overlap in sex and coloration types in some species is evidence of a lack of precise and effective mechanism relating cues to actual sex change. If fecundity differentials between males and females are not large, as may well be the case in species such as *Sparisoma radians,* the decline in reproductive output due to an imprecisely timed sex change would be smaller than in a species with a larger fecundity differential. Size range overlaps should therefore be relatively large in species of the former type. In the more strongly haremic species, the penalties are probably more severe for imprecise timing because of the ability of harem males to control outside males. It is in this type of species that sex and color phase size range overlaps should be small. Examples include *Sparisoma aurofrenatum, Sparisoma atomarium, Scarus vetula,* and *Scarus croicensis.*

One final point deserves mention. We have spoken of the social and mating system in each species as the primary factor shaping the patterns of sexuality. Although social systems are certainly the proximate cause of those patterns, social systems are in turn controlled by the distribution in space and time of the basic resources of food and shelter. We believe that this is reflected in a major difference between the scarids and labrids: dichromatic, haremic species are much more common among the parrotfishes. Scarids are herbivores and labrids carnivores. Benthic algal resources may be more predictably available over a small area than benthic invertebrates or plankton. This would both encourage the defense of algal resources by a parrotfish and enable it to provide itself with an assured supply of food in an area of defendable size (see Schoener, 1968). Permanent feeding territoriality may thus have permitted the development of haremic systems (Robertson and Hoffman, in press). Investigations of the relationships between basic

resources and social structure are badly needed, and provide an opportunity for further research.

As our appreciation of the complexity of the reproductive biology of this group expands so does the realization that a continuum of types probably exists between the extreme states of whatever attribute we care to examine (e.g., spawning patterns). In addition to classifying species in terms of the sexual types present, we suggest that they should also be categorized as to (1) whether or not they are sexually dichromatic, and (2) whether males are present in both color phases of a dichromatic species. This is necessary because males in each phase are employing radically different spawning strategies. In Table 6, we show the range of sexual types found thus far in the labroid fishes. Although it is useful to have reasonably precise terminology that facilitates distinguishing major trends, we feel that there is little value in much greater proliferation of verbiage. We suggest that the terms should be kept to a practical minimum and be as straightforward and self-explanatory as possible. Thought and discussion should be given to the evolutionary sources and functions of the types of variations encountered rather than mere classification of them.

In these two papers we have briefly surveyed many species; the depth of our understanding of them is limited by a lack of comprehensive information. More detailed studies will undoubtedly alter our perspective, but we think it is likely that the comprehensive (and often highly speculative) arguments that we have proposed will stand in substance. They have been supported by the comparative tests to which we subjected them. The exceptions have proved especially instructive in pointing out the conditions under which various mating systems can operate, and in turn what life history patterns can result. We have become particularly aware of the complexity of alternative solutions that are potentially available.

Appendix

Tables

TABLE 1.—Color phase ratios and estimated adult sex ratios of nine species of Caribbean scarids (color phase data obtained by tallying the coloration of individuals encountered in a series of 10 minute swims in suitable habitats; overall sex ratio calculated from color phase ratio and initial phase sex ratio, the latter data from our collections)

Species	Number of counts	Total number of individuals from all counts	Color phase ratio Terminal phase:initial phase	Sex ratio ♂:♀
Cryptotomus roseus	10	182	1:7.3	1:3.3
Sparisoma rubripinne	27	989	1:4.0	1:1.4
Sparisoma chrysopterum	40	924	1:2.1	1:1.7
Sparisoma viride	20	1109	1:4.4	1:2.4
Sparisoma aurofrenatum	31	1147	1:3.1	1:2.8
Sparisoma radians	3	295	1:1.3	1:1.04
Sparisoma atomarium	8	355	1:6.9	1:5.7
Scarus vetula	12	284	1:3.7	1:3.3
Scarus croicensis	21	7371	1:5.9	1:4.5

TABLE 2.—Testes weights of 10 species of Caribbean parrotfishes, individuals classified according to coloration and sexual ontogeny (the mean and its 95% confidence interval shown for both absolute testes weights and testes weights relative to body weight; this relative weight may be read as percent of body weight; all secondary males used in this tabulation showed posttransitional gonads)

Species	Color phase	Primary males			Secondary males		
		n	Gonad weight (g)	GW/BW x 100 (percent)	n	Gonad weight (g)	GW/BW x 100 (percent)
Cryptotomus roseus	initial	0	--	--	12	0.02 ± 0.01	1.15 ± 0.62
	terminal	0	--	--	18	0.02 ± 0.01	0.41 ± 0.14
Sparisoma rubipinne	initial	0	--	--	43	7.97 ± 3.42	1.57 ± 0.56
	terminal	0	--	--	39	0.58 ± 0.15	0.12 ± 0.05
Sparisoma chrysopterum	initial	0	--	--	2	0.25	0.16
	terminal	0	--	--	22	0.24 ± 0.01	0.07 ± 0.02
Sparisoma viride	initial	0	--	--	20	0.71 ± 0.26	0.33 ± 0.09
	terminal	0	--	--	33	0.25 ± 0.10	0.06 ± 0.01
Sparisoma aurofrenatum	initial	0	--	--	5	0.56 ± 0.70	0.67 ± 0.62
	terminal	0	--	--	36	0.14 ± 0.03	0.11 ± 0.02
Sparisoma radians	initial	0	--	--	13	0.10 ± 0.04	3.35 ± 1.25
	terminal	0	--	--	73	0.12 ± 0.05	0.76 ± 0.15
Sparisoma atomarium	initial	0	--	--	2	0.02	0.27
	terminal	0	--	--	32	0.02 ± 0.003	0.20 ± 0.03
Scarus vetula	initial	3	5.21	1.89	0	--	--
	terminal	1	1.33	0.17	16	0.99 ± 0.46	0.11 ± 0.04
Scarus croicensis	initial	35	0.25 ± 0.05	1.63 ± 0.27	0	--	--
	terminal	15	0.09 ± 0.003	0.21 ± 0.10	42	0.08 ± 0.02	0.15 ± 0.03
Scarus taeniopterus	initial	0	--	--	0	--	--
	terminal	0	--	--	6	0.20 ± 0.11	0.05 ± 0.03

TABLE 3.—Relative abundance of 10 species of Caribbean parrotfishes measured by habitat (numbers represent fish seen per 10 minutes by observer swiming along a horizontal transect; these transects were run at the surface for the first two habitats and along a series of depth profiles for the hard reef)

Species	Sessile *Sargassum*	Turtle grass	Hard reef depth profiles (m)					
			≤ 3	3-6	6-9	9-12	12-15	15-18
Scarus croicensis	--	--	33.0	23.6	23.0	26.3	28.8	31.5
Sparisoma radians	31.8	33.6	0.03	0.02	0.03	--	--	--
Sparisoma viride	--	--	8.8	6.3	4.6	5.2	4.4	3.9
Sparisoma aurofrenatum	--	--	4.0	5.5	4.9	4.6	4.4	4.2
Sparisoma rubripinne	5.0	--	3.1	2.4	2.6	2.8	2.7	4.8
Sparisoma chrysopterum	--	5.5	1.2	.03	0.4	--	--	0.1
Sparisoma atomarium	--	4.2	--	--	--	--	--	--
Scarus vetula	--	--	1.7	0.8	1.0	0.1	0.2	--
Cryptotomus roseus	--	2.3	--	--	--	--	--	--
Total sampling runs	5	26	32	29	16	8	4	2
Total sampling minutes	50	260	380	410	205	95	65	85

TABLE 4.—Breeding seasonally in 10 species of Caribbean parrotfishes (+ = male sexual displays observed; + + = spawning and male sexual displays observed, or ripe females collected; nd = no data available)

Species	Dry season				Wet season							
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Cryptotomus roseus	++	++	++	++	++	++	++	++	++	++	++	++
Sparisoma rubripinne	++	++	++	++	++	++	++	++	nd	nd	nd	++
Sparisoma chrysopterum	++	+	++	++	++	++	nd	nd	nd	++	++	+
Sparisoma viride	++	++	++	++	++	++	nd	++	++	++	nd	nd
Sparisoma aurofrenatum	++	++	++	++	++	++	nd	++	++	++	++	++
Sparisoma radians	++	++	++	++	++	++	++	++	++	++	++	++
Sparisoma atomarium	nd	nd	++	++	++	++	++	++	++	++	++	++
Scarus vetula	++	nd	++	nd	nd	nd	nd	nd	nd	nd	nd	nd
Scarus croicensis	++	++	++	++	++	++	++	++	++	++	++	++

TABLE 5.—Rank order of abundance within a common habitat, male proportion of initial color phase, and type of mating system for nine species of Caribbean parrotfishes

Habitat/Species	Rank order of abundance	Male proportion of initial color phase	Prescence of haremic mating system
Turtle grass substrates			
Sparisoma radians	1	.06	partial
Sparisoma chrysopterum	2	.05	absent
Sparisoma atomarium	3	.02	strong
Cryptotomus roseus	4	.10	absent?
Hard reef substrates			
Scarus croicensis	1	.24	partial
Sparisoma viride	2	.13	absent
Sparisoma aurofrenatum	3	.02	strong
Sparisoma rubripinne	4	.21	absent
Scarus vetula	5	.02	strong

TABLE 6.—Summary of major features of sex and coloration found in 37 species of labroid fishes grouped by families (status: T.P. = terminal phase, I.P. = initial phase, 1° = primary, 2° = secondary, Premat = prematurational; occurence: P = present, A = absent, C = common (more than 10% of stated color phase), U = uncommon (less than 10% of stated color phase), ? = data inadequate for firm statement)

Species	T.P.	I.P. 1°♂	I.P. 2°♂	T.P. 1°♂	T.P. 2°♂	Pre-mat 2°♂	1° ♀	Authority
LABRIDAE								
Bodianus rufus	A	A	C	A	A	A	A	Warner and Robertson, 1978
B. diplotaenia	P	A	U	A	C	A	A	S. Hoffman, pers. comm.
Clepticus parrae	P	A	A	A	P	A	A	Warner and Robertson, 1978
Coris julis	P	A	U	C	C	A	P?	Reinboth, 1975
Hemipterinotus novacula	P	A?	A?	A?	C	A	P?	Reinboth, 1975
Halichoeres bivittatus	P	C	U	C	C	A	A	Warner and Robertson, 1978
H. dispilus	P	C	?	P	P	?	?	Reinboth, 1975
H. garnoti	P	A	U	A	C	A	A	Warner and Robertson, 1978
H. maculipinna	P	U	U	C	C	A	A	Warner and Robertson, 1978
H. poecilopterus	P	P	P	A?	C	?	A?	Reinboth, 1975
H. poeyi	P	U	C	U	C	A?	A?	Warner and Robertson, 1978
H. pictus	P	U	U	C	C	A	A	Warner and Robertson, 1978
Labroides dimidiatus	A	A	C	A	A	A	A	Robertson, 1972
Oxyjulis californica	A	C	A	A	A	A	A?	Diener, 1976
Pimelometopon pulchrum	P	A	U	A	C	A	A	Warner, 1975b
Thalassoma bifasciatum	P	C	U	C	C	A	A	Warner and Robertson, 1978
T. cupido	P	P	?	P	P	?	?	K. Meyer, pers. comm.
T. lucasanum	P	P	A	C	C	A	A	Warner and Hoffman, pers. comm.
T. lunare	P	C	A?	P?	C	A	A	Robertson and Choat, 1974
SCARIDAE								
Cryptotomus roseus	P	A	C	A	C	P?	A?	[this paper]
Scarus croicensis	P	C	U	C	C	A	A	[this paper]
S. fasciatus	P	C	A?	C	C	P	A	Choat and Robertson, 1975
S. formosus	P	U	?	U	C	A?	A	Choat and Robertson, 1975
S. forsteri	P	C	?	C	C	P	?	Choat and Robertson, 1975
S. globiceps	P	C	A?	C	C	P	?	Choat and Robertson, 1975
S. lunula	P	U	A	U	C	A?	A?	Choat and Robertson, 1975
S. niger	A	A	P	A	A	A	A	Choat and Robertson, 1975
S. sexvittatus	P	U	A?	U	C	P	A?	Choat and Robertson, 1975
S. sordidus	P	C	A?	U	C	?	A	Choat and Robertson, 1975
S. venosus	P	U	P	?	C	P	A?	Choat and Robertson, 1975
S. vetula	P	U	A	U	C	A	A	[this paper]
Sparisoma atomarium	P	A	U	A	C	A	A?	[this paper]
S. aurofrenatum	P	A	U	A	C	A	A	[this paper]
S. chrysopterum	P	A	U	A	C	P	P	[this paper]
S. radians	P	A	U	A	C	P?	P	[this paper]
S. rubripinne	P	A	C	A	C	P	P?	[this paper]
S. viride	P	A	C	A	C	P	P?	[this paper]

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