

Sexual Patterns in the Labroid
Fishes of the Western Caribbean, I:
The Wrasses (Labridae)

ROBERT R. WARNER
and
D. ROSS ROBERTSON

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ABSTRACT

Warner, Robert R., and D. Ross Robertson. Sexual Patterns in the Labroid Fishes of the Western Caribbean, I: The Wrasses (Labridae). *Smithsonian Contributions to Zoology*, number 254, 27 pages, 11 figures, 7 tables, 1978.—We report here on the results of a two year investigation into the interactions of sex change, coloration, and mating behavior in nine Caribbean wrasses (*Bodianus rufus*, *Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. pictus*, *H. poeyi*, *H. radiatus*, *Clepticus parrae*, and *Thalassoma bifasciatum*). For each species, we outline (1) the distribution of sexual types according to size and coloration, (2) the testis weights of different types of males, (3) characteristic habitat and relative abundance, (4) the social and mating system, and (5) breeding seasonality. In all dichromatic labrid species, sex change from female to male appears to precede a change of coloration into the bright terminal phase. Two wrasses (*B. rufus* and *C. parrae*) that lack non-sex-changed (primary) males have mating systems in which terminal phase males can effectively control the spawning of the females. Other labrid species have lek-type mating systems, within which small primary males interfere in the spawnings of large terminal males. This activity is reflected in the high testis weight of these small males, who face sperm competition in mating. There is a general correlation between population density (measured by relative abundance) and frequency of primary males.

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Sexual Patterns in the Labroid Fishes of the Western Caribbean, I: The Wrasses (Labridae)

*Robert R. Warner
and D. Ross Robertson*

Introduction

Fishes are exceptional among the vertebrates in that many of them change sex during their adult lives (Atz, 1964; Reinboth, 1970; Warner, in press). The change can either be from female to male (protogyny) or the reverse (protandry). In the few protogynous species whose social systems have been studied in detail, the females mate chiefly with larger, older males (Robertson, 1972; Robertson and Choat, 1974; Warner, Robertson, and Leigh, 1975). This factor of strong sexual selection often leads to sexual dimorphism, with males developing specialized structures and colorations for combat and display.

Intense sexual selection also creates large differences in the age-specific fecundity patterns between males and females and this leads to selection for sex change. These differences are to the reproductive advantage of individuals that change sex at a certain time, e.g., females that change into males when they become large enough to compete success-

fully for females (Robertson and Choat, 1974; Warner, 1975a). They are thus the right sex at the right size. Many of the protogynous species also contain small males that are colored like females and that employ a mixture of mating strategies different from those of the large, brightly colored, and often territorial males (Warner, Robertson, and Leigh, 1975).

The interrelation of mating system, sex change, and sexual dichromatism can be exceedingly complex. Labroid fishes (including the wrasses, family Labridae, and parrotfishes, family Scaridae), most of which are protogynous, present a good example of the wide diversity of sex and coloration patterns that can exist. Most labroids are found in the shallow, warm seas of the tropics. They tend to mate the year round, in specific areas. Thus the details of their life histories and behavior can be easily observed by a diver.

Since the pioneering work on protogyny in tropical and subtropical labroids by Reinboth (1957, 1962, 1967, 1968, 1970, 1973), there have been two major efforts at systematically examining the sexual patterns of a series of labroid species. Choat (1969) studied a large number of western Pacific (Great Barrier Reef) wrasses and parrotfishes (published in part in Choat and Robertson, 1975). Roede

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(1972) detailed sex and coloration in seven Caribbean labrids, but did not distinguish between primary and secondary (sex-changed) males (terminology detailed below).

In this paper and the one following (Robertson and Warner, 1978) * we describe the patterns of sex, coloration, and mating behavior for most of the Caribbean labroids. We have done this in part to test our ideas on (1) how sexual selection can act as a cause for sex change, and (2) how non-sex-changing males can coexist with sequential hermaphrodites. Basically we expect few small males in species where low effective population density allows large, dominant males to control most of the spawning (for details of these arguments, see Warner, Robertson, and Leigh, 1975). We have found some consistent patterns among the species that lend support to our expectations, but there are several species with apparent anomalies and unexpected distributions of sex and coloration. We have offered explanations for many of these anomalies and modified our hypotheses accordingly. Others remain a mystery to us and stand as suggestions for future research in tropical marine biology.

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* Order of authorship was determined by the flip of a coin.

Materials and Methods

SPECIES STUDIED.—We were able to obtain enough specimens to examine in reasonable detail the following eight shallow-water species: *Bodianus rufus*, *Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. pictus*, *H. poeyi*, *Clepticus parrac*, and *Thalassoma bifasciatum*. An interesting but less complete sample of *Halichoeres radiatus* was also collected. Of the remaining six shallow-water species listed by Randall (1968), we very infrequently observed *Lachnolaimus maximus*, *Doratonotus megalepis*, *Hemipteronotus splendens*, and *H. martinicensis*.

STUDY AREA.—All specimens were collected and all observations made on the reefs in the Archipiélago de San Blas off the Caribbean coast of Panama. Within this general area our operations were restricted to the western limits of the archipelago, i.e., to no more than 50 kilometers east of the Peninsula de San Blas.

COLLECTING.—Collecting and field observations were spread throughout the year during both the wet and dry seasons (see Glynn, 1972) from March 1974 to May 1975.

In many species of labrids, periods of sexual activity are characterized by mass migrations of individuals to particular sites on reefs, where they assemble in sex-specific groups. Therefore we did not make collections at such times in order to increase the chances of random sampling with respect to sex in each size class. Specimens of *Halichoeres bivittatus* and *Thalassoma bifasciatum* were collected in a lift net as figured in Roede (1972). These and the other small species were also collected using a small, multipronged spear in a simplified Hawaiian sling. Large *Bodianus rufus* and *Clepticus parrac* were taken with a small multipronged speargun.

TERMINOLOGY.—The profusion of color patterns and sexual types that occur among the labroid fishes has been a source of problems both to taxonomists and ichthyologists in general. Closely related species are often morphologically very similar, except in their color patterns. Although it has long been known that some species in each family are sexually dichromatic (Longley, 1914; Lönnberg and Gustavson, 1937; Longley and Hildebrand, 1941) a realization of just how common intraspecific polychromatism is in these groups really only began about twenty years ago. At that time investigators began

to examine population structures, to experiment with inductions of sex and color phase changes, and to make field observations on social groupings and spawning activity (Brock and Yamaguchi, 1954; Randall, 1955, 1963; Bacci and Razzauti, 1958; Strasburg and Hiatt, 1957; Winn and Bardach, 1957, 1960; Schultz, 1958; Sordi, 1962; Randall and Randall, 1963).

Because interest in the reproductive biology of the wrasses and parrotfishes has expanded rapidly, and the number of people engaged in research on it has grown, a variety of synonyms for the different color phases, sexual types, and mating behaviors has come into use. This has begun to complicate communication so that standardization of terms seems necessary. We discuss the terms used in these papers below, and summarize our definitions in Appendix 1.

Coloration: Within many labroid species there exist several distinct, relatively permanent color patterns. Individuals may also exhibit rapid, temporary, and sometimes radical color changes. In this study we are interested primarily in examining the distribution of different color patterns with respect to sex and size in each species. In labroids there is often a recognizable dichotomy in the color patterns shown by adult fishes, with a predictable change from one pattern to the other as the animal ages. Some of the terms that have been used in the past for the juvenile and adult color phases are shown in Appendix 2. We follow the scheme used previously (Randall, 1968; Reinboth, 1973, 1975; Warner, Robertson, and Leigh, 1975) in referring to the pattern shown by the smallest adults as the initial pattern and that shown by the largest adult males as the terminal pattern. Fishes with these patterns are then in the initial and terminal color phases. When immature individuals show coloration different from that of small adults, it is termed the juvenile color pattern. To some extent, this is a convenient oversimplification, since variability often exists, particularly in the initial pattern (see Roede, 1972). Also for convenience, we classified individuals in the process of changing color as being in terminal phase. We support the continued use of juvenile, initial adult, and terminal adult for the three possible basic phases for the following reasons: (1) they are simple and etymologically self-explanatory; (2) they are functional since they refer to major, distinct phases in the animal's life history (further

splitting seems of less obvious value); and (3) they are in common usage.

The terms sexual dichromatism and monochromatism have long been used in the same manner as we will use them here. In monochromatic species, females are capable of developing all the same patterns as males. In dichromatic species, females cannot do so, and all the fishes of one color phase are definitely known to be males. Two types of dichromatism can be distinguished on the basis of whether or not the terminal pattern has any color elements that the initial pattern does not have: with full dichromatism some of the elements are present only in the terminal pattern, whereas with partial dichromatism the same elements are common to both patterns, but some are much more strongly developed in the terminal pattern. Dichromatic species can also be divided into two different categories depending on the permanence of the terminal coloration: in temporarily dichromatic species, terminal phase fish can revert to the initial pattern, whereas they cannot do so in permanently dichromatic species.

Sexuality: Reinboth's work on protogyny in the labroid fishes (Reinboth, 1957, 1962, 1967, 1968) led to his discovery that, ontogenetically, there were two types of males, those born as such (primary males) and those resulting from sex changes in females (secondary males). The data herein, however, and that of Choat and Robertson (1975) on parrotfishes indicate the need for making a further distinction between those hermaphroditic males that function as females before they change sex (post-maturational secondary males) and those that "change" before they have matured as females (pre-maturational secondary males). Harrington (1971) termed the latter false male gonochores.

If a species contains both primary and secondary males, it is diandric (Reinboth, 1967). When the only males present are secondary, it is monandric. In species that have both secondary and primary males, the proportion that are of the latter type varies considerably (Choat and Robertson, 1975, and data herein). The existence of non-sex-changing females contributes added complexity. We term these primary females, to distinguish them from hermaphroditic females, and to show that they are analogous to primary males. At least one species of wrasse appears not to be hermaphroditic (Diener, 1976).

Mating Patterns: We outline the structure of

the social and mating systems of many of the species, based on field observations. A broad distinction may be made between species that mate in leks and those that mate in harems. Leks are formed when males tend to concentrate at traditional sites, each defending a small area against the intrusions of other males. Females also gather at this area and generally spawn with one of the competing males. Territoriality is temporary in lekking species, lasting only for the duration of the spawning period.

Males maintaining harems are permanently territorial. Their territories contain a group of females with whom the dominant male mates almost exclusively. More complete descriptions of a harem species can be found in Robertson (1972) and of a lekking species in Warner, Robertson, and Leigh (1975). We generally make distinctions between pair spawning, where a single male mates with a single female, and group spawning, where a number of males fertilize the eggs of one female. This latter type of spawning is often characteristic of small, initial phase males. These small males may also remain close to the territory of a larger male and individually steal spawnings with females who are waiting to spawn with larger males (sneaking), or join the large male and the female at the climax of spawning (streaking; see Warner, Robertson, and Leigh, 1975).

DETERMINATION OF POPULATION PARAMETERS.— We present data on the degree of sexual dichromatism of each species and on the relationship of the color phases to sex and size. Using data gathered both from collections of specimens and from field observations, we also measure the degree of overlap in the size ranges of the initial and terminal phases in the dichromatic species. The ratio of the number of initial phase fish to terminal phase fish was estimated by counts made outside spawning periods. Some bias probably arises as a result of the terminal phase being characteristically more strikingly colored, and thus being more visible to the observer.

The sex of specimens could often be determined macroscopically, by observing the release of gametes, color and general appearance of the gonad, and, in unripe females, by the presence of maturing eggs. The sex of inactive specimens was determined histologically. Primary and secondary males in each species were differentiated histologically using cri-

teria laid down by Reinboth (1962). For each species, we were able to determine (1) if both primary and secondary males were present in a species (diandry), or only secondary males (monandry), (2) the size/frequency distribution of both types in terminal and initial color phases, and (3) the distribution in the population of secondary males in the process of sex change.

Ripe individuals were defined as those emitting gametes when stimulated with a little finger pressure on the belly, active females as those with vitellogenic oocytes, and inactive females as those with only previtellogenic oocytes. Secondary males whose gonads contained many previtellogenic oocytes or degenerating oocytes were classed as transitional.

In other labroid fishes there are radical differences in the sizes of the testes of males in different color phases (Robertson and Choat, 1974; Choat and Robertson, 1975). Therefore, the testis weight of males in the various labrids was considered in relation to the color phase and sexual derivation of the male.

Breeding seasonality was determined from observations on spawning in different months and collections of ripe females at various times. The adult sex ratio of each species was estimated from a combination of the sex ratio of individuals in each color phase and the color phase ratio (for a similar technique, see Warner, 1975b).

Small populations of *Thalassoma bifasciatum* differ greatly from large populations in two ways: (1) in the proportion of initial phase fish that are males, and (2) in the color phase ratio (and hence the sex ratio) (Warner, Robertson, and Leigh, 1975). Only relatively large populations of the other diandric species were sampled.

We also provide quantitative information on the types of habitats in which we encountered each species. The relative abundance of each species was estimated by making counts in a series of 10 minute swims in a series of habitats and at different depth profiles, in a number of different sites. These habitats, which include the majority of the substrate types we encountered, were (1) shallow (<5m depth) *Sargassum* beds (large dense stands up to 50 cm thick), (2) turtle grass beds (large, dense stands of *Thalassia*) in water <5 m deep, and (3) hard reef areas of coral or coralline rock, including sand bottoms thickly dotted with coral growths. In this

latter habitat a series of sampling runs were made on each of the following depth profiles: <3 m, 3–6 m, 6–9 m, 9–12 m, 12–15 m, 15–18 m.

Results

Bodianus rufus.—There are no indications that this species exhibits sexual dichromatism, either from the work of other researchers (e.g., Feddern, 1963; Randall, 1968; Böhlke and Chaplin, 1968) or from our own observations. We found both sexes in a single color phase (Figure 1) and never saw males develop a distinctly different color pattern, even when they became sexually active.

This species is almost certainly monandric, since males were found only at the upper end of the size range and all males examined histologically were secondary (Figure 1). Two males with transitional gonads were found, both of them quite small for their sex (170 and 185 mm SL). Female sexual maturity is attained at about 100 mm SL. We obtained no information on the sex ratio in this species, although limited observations by S. Hoffman indicate that it is strongly biased towards females (Table 1). The males had disproportionately small gonads relative to males of other species (Table 2).

Bodianus rufus was relatively uncommon and occurred at a variety of depths on hard reef substrates (Table 3). We found it associated with sites of marked structural complexity, on the outer rims of reefs. Adults usually occurred singly or occasionally in very transient aggregations of up to six individuals of various sizes. We never saw them forming schools or feeding in coordinated groups. This suggested to us that *B. rufus* had a social system similar to that of the labrid *Labroides dimidiatus*, which forms permanent harem groups composed of a single male and several smaller females (Robertson, 1972). Such has since been found to be the case (S. Hoffman, pers. comm.).

The mating systems of these two species are also essentially the same. In both, spawning occurs only within the social group. We have observed pair spawning in *B. rufus* in the very late afternoon.

Our data on breeding seasonality are too incomplete to show anything beyond the fact that breeding occurred in both wet and dry seasons (Table 4). Apparently females do not continuously produce eggs, since we often collected inactive, active, and ripe females from the same location on the same day.

Halichoeres bivittatus.—The different color pat-

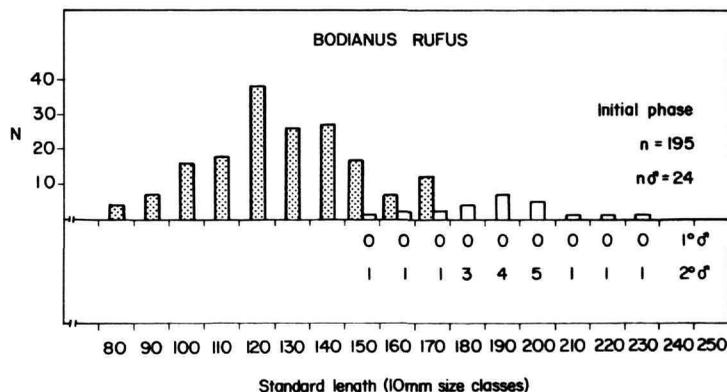


FIGURE 1.—Pattern of sexuality in *Bodianus rufus*: size/frequency bar graph of our sample, with indication of sexual ontogeny of a number of the males in each size class (n = sample size in specified color phase; 1° ♂ = primary males; 2° ♂ = secondary males; stippled bars = females; white bars = males; 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; lengths were measured to the nearest mm; placement in size classes follows the pattern of all fishes 10–19 mm SL belonging in the 10 mm size class).

terns shown by individuals of various sizes have been described by Roede (1972) (see also Randall, 1968; Böhlke and Chaplin, 1968; and Chaplin and Scott, 1972). *Halichoeres bivittatus* is judged to be sexually dichromatic since (1) the largest adults have a color pattern very different from that of smaller ones, and (2) individuals with this terminal color pattern most strongly developed were invariably males. The situation, however, is far from simple, as was also found by Reinboth (1975) and Roede (1972). There is no distinct cutoff point between the two phases (i.e., the division indicated in Figure 2 is rather arbitrary, based on degrees of brightness in colors of large specimens). Also, the color pattern of the largest females contains all the elements of the terminal phase (as was also found by Roede, 1972). The dichromatism is therefore only partial. With increasing size of the terminal phase males, colors tend to become brighter, but the colors of all such males fade when they are sexually inactive. The distinctions between the two phases then became much less obvious. We made many of the decisions regarding color phase when a specimen was dead, since coloration was typically

easier to distinguish at that time.

Our estimates of the color phase ratio and degree of color phase overlap are limited by this lack of discrete dichromatism. However, the color phase ratio appears quite heavily biased towards the initial phase (Table 1). Terminal phase males tended to be much larger than initial phase fish. Within each local population, there was little overlap in the size ranges of the two color phases: in one sample of 32 initial phase and 11 terminal phase fish there was only a 5 mm overlap in the standard length ranges. Because the size of transformation differs from one population to another, Figure 2 shows more overlap than actually exists on a single reef.

Both primary and secondary males were found in this species (Figure 2; see also Reinboth, 1975, and Roede, 1972). Also, primary males were present in relatively high and similar proportions in both color phases (Figure 2; Table 5). The few secondary males in the initial phase occurred only among the largest size classes (Figure 2). Only one secondary male with a transitional testis was collected (71 mm SL). Since the smallest females we collected were

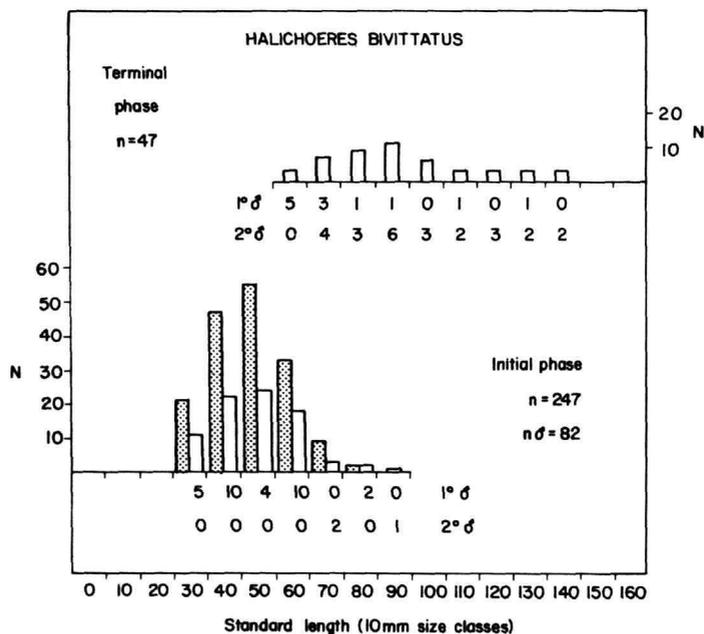


FIGURE 2.—Pattern of sexuality in *Halichoeres bivittatus* (for explanation of format, see Figure 1).

sexually active, we were unable to determine the size at maturity.

While the testes of both primary and secondary terminal phase males were somewhat heavier than those of initial phase males, there were no significant differences in the weights relative to body weights (Table 2). In terms of the entire population sampled, however, there was considerable variation in these relative weights, and a graph of the relationship between fish length and relative testis weight (Figure 3) shows that the small males, regardless of their origin or color phase, had relatively larger testes.

The sex ratio was quite equable (Table 1), principally due to the large complement of males in the initial phase.

Although we found this species in a great variety of habitats, it reached its greatest densities in the dense stands of *Sargassum* that capped the tops of many reefs. It was largely limited to these shallow

habitats (<5 m), where it was the most abundant labrid (Table 3).

We saw no indication of permanent territoriality by individuals of any size or sex class. Outside periods of sexual activity, fish of widely varying sizes and from both color phases commonly formed transient, loosely knit aggregations of up to forty individuals. The overall impression was one of independent movement of individuals at most times of the day, with opportunistic scrambles for food.

The mating system of large populations of this species resembles that of large *Thalassoma bifasciatum* populations (see Warner, Robertson, and Leigh, 1975). Breeding was restricted to several hours in the midafternoon and was concentrated around the periphery of reefs in shallow water. The greatest activity occurred in areas where the species was abundant at other times. In these spawning grounds, terminal phase males defended temporary territories in which they pair spawned with single females. Group spawning occurred commonly in and around terminal phase fishes' territories. These groups consisted mainly of initial phase fish, but occasionally a terminal phase individual would join as well. Initial phase males also interfered in the pair-spawning activities of the territorial males, behaving in similar fashion to that described for *T. bifasciatum* by Warner, Robertson, and Leigh (1975). We never observed, however, the aggregates of hundreds or thousands of initial phase fish that were common with *T. bifasciatum*; the initial phase aggregates in *H. bivittatus* typically numbered about twenty fish.

Halichoeres bivittatus evidently spawned throughout the year (Table 4). Not all females, however, were continuously active: we often obtained both active and inactive females in the same sample. Some sketchy evidence suggests that active and inactive females tended to be in different parts of the same reef. In collections made outside spawning periods, few of the females collected from the center of reefs were ripe, while many of those caught near the edges of reefs were. Possibly there are cycles of movement of females from one area to another corresponding to cycles of their gonadal activity. It should also be noted that while collections from reef center and reef edge contained both sexes, for practical reasons we were unable to determine sex ratios in the reef-center samples. Our overall estimate of the sex ratio may then be biased.

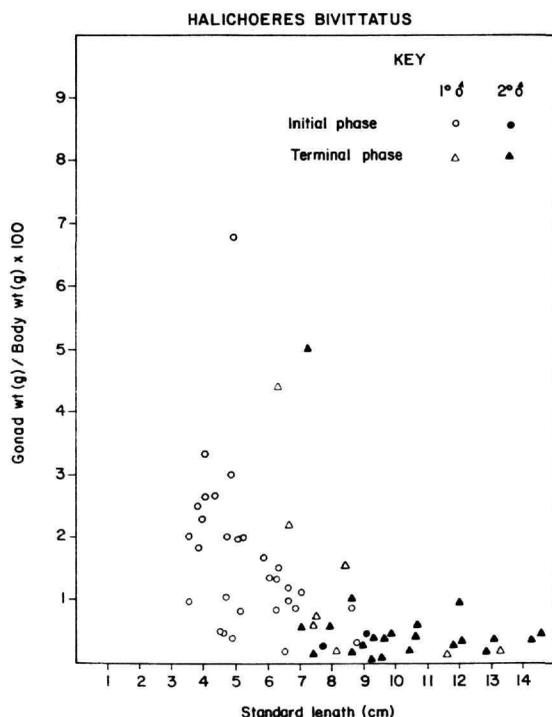


FIGURE 3.—Gonad weights (shown as percent of body weight) for various sizes of male *Halichoeres bivittatus*.

Halichoeres radiatus.—Since the largest adults have a color pattern very different from that of small ones (see Randall, 1968; Chaplin and Scott, 1972), this species is probably sexually dichromatic. Whether such dichromatism might be partial or full is not clear; we saw complete intergradation between the two patterns. Because of their extreme shyness, terminal phase fishes could not be collected for sex determination. Whether such fish retained these terminal colors permanently or were capable of temporarily losing them is also not known. Terminal phase fish were rarer and larger than initial phase fish.

Reinboth (1975) found that this species was hermaphroditic. Although only secondary males were present in the sample we obtained (Figure 4), our sample sizes are too small to show whether the species is monandric or diandric. The smallest mature female we collected was 160 mm SL. Secondary males were present in the initial phase and began appearing in the population at sizes smaller than that of the smallest mature female (Figure 4). The smallest secondary male collected did not have transitional gonads. The males collected all had small testes, relative to their body weight (Table 2). We were unable to determine the sex-ratio.

Halichoeres radiatus was largely restricted to areas of coral cover, where it was found at all depths sampled (Table 3).

Individuals were normally seen moving about singly. However, on several occasions in midafternoon we observed an intensely colored terminal

phase fish moving actively about a loosely knit group of about six initial phase fish. Beyond this probable example of premating behavior, we have no information on spawning or breeding seasonality in this rather secretive species.

Halichoeres garnoti.—Roede (1972) has described in detail the range of color patterns shown by this species (see also Randall, 1968; and Chaplin and Scott, 1972). Although both an initial and a terminal phase exists, and all terminal phase fish we collected were males (see Figure 3), sexual dichromatism is only partial. The distribution pattern of coloration types is similar to that of *H. bivittatus*. An element of doubt remains as to whether or not this species is really dichromatic. Our results and those of Reinboth (1973) tend to show that it is, but Roede (1972) reported finding large females showing the terminal color pattern. Both large initial phase and terminal phase fish were capable of completely losing the characteristic angled black bar on the body temporarily, which complicated both our attempts to obtain field estimates of color phase ratios and to resolve the question of the degree of dichromatism. Death colors were often used to assess the color phase of a specimen. The color phase ratio was moderately biased toward the initial phase (Table 1), and there was little if any overlap in the size ranges of the two phases within a population: in each of 10 samples (totalling 23 terminal and 86 initial phase fish), there were no overlaps.

Halichoeres garnoti is evidently monandric. All males we examined histologically were secondary,

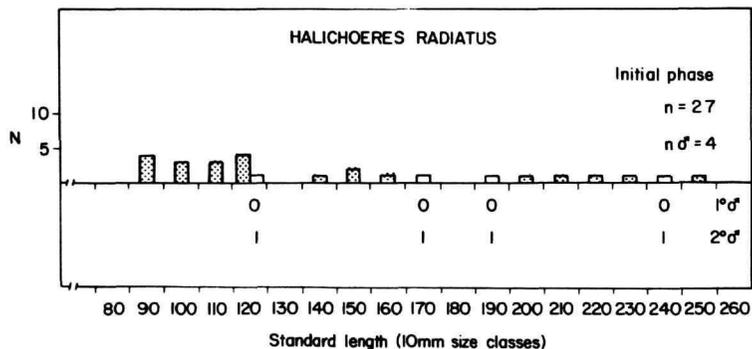


FIGURE 4.—Pattern of sexuality in *Halichoeres radiatus* (for explanation of format, see Figure 1).

and we found no males among the smaller size classes (Figure 5). Both Reinboth's (1975) and Roede's (1972) results agree with this. The few initial phase males collected were all relatively large (Figure 5). Most of them (5 of 6 examined) had transitional gonads. The smallest females we obtained were already sexually active.

Relative to body weight, the gonads of males of both color phases were small when compared to other species; those of terminal phase fish were both absolutely and relatively larger than those of initial males (Table 2). The sex ratio was moderately biased in favor of females (Table 1), mainly because of the paucity of males in the initial phase.

This species occurred in reef areas containing much sand dotted with scattered coral growths. As Table 3 shows, it was restricted to areas containing hard corals and occurred most commonly in the deeper parts of such areas.

Terminal phase males did not appear to be permanently territorial; however, the small aggregations that formed at baits typically contained only one highly colored terminal phase fish, the largest individual present. This suggests either some exclusion of other large males from an area by a resident terminal phase male, or some effect of dominance relationships on the display of ter-

minal phase colors.

Pair spawnings between a large brightly colored terminal phase fish and a smaller initial phase individual were seen on several occasions in the same habitat where the species was usually found. Such sexually active males appeared to be scattered about singly in this habitat rather than clumped at any particular sites.

We collected ripe females in both wet and dry seasons, and saw terminal males displaying sexually throughout the year (Table 4). Beyond this, we have no information on breeding seasonality. Females at all stages of oogenic activity were often collected in the same sample.

Halichoeres maculipinna.—Detailed descriptions of *H. maculipinna*'s color patterns are given by Roede (1972) and good color illustrations by Randall (1968) and Chaplin and Scott (1972). The species shows full sexual dichromatism since all terminal phase fish collected were males (Figure 6) and the terminal pattern contains several elements not present in the initial pattern. However, the terminal phase males can temporarily lose the elements characteristic of their phase. This species also possesses a juvenile color pattern, some elements of which are retained by small adults. Death colors were often used in determining the color phase of collected specimens.

The color phase ratio was strongly biased towards the initial phase (Table 1), but this can be considered as only an approximation due to the lack of a permanent terminal pattern. The few data we have show a small degree of intrapopulation overlap in the size ranges of the two phases. The phases overlapped in two of three collections comprising 19 terminal phase and 59 initial phase fish, but by less than 1 cm SL in each case.

Although Reinboth (1975) suggested, on the basis of a rather small sample, that *H. maculipinna* was monandric, our data show otherwise. Both primary and secondary males were present in both color phases (Figure 6). The proportion of primary males in the two color phases differed in our samples with comparatively more in the terminal phase (Table 5). Secondary males were found throughout the initial phase size range, including some well below the smallest sizes of terminal phase fish. They also formed a large proportion (0.41) of the initial phase male population (Figure 6). Of these seven secondary initial phase males, the three which

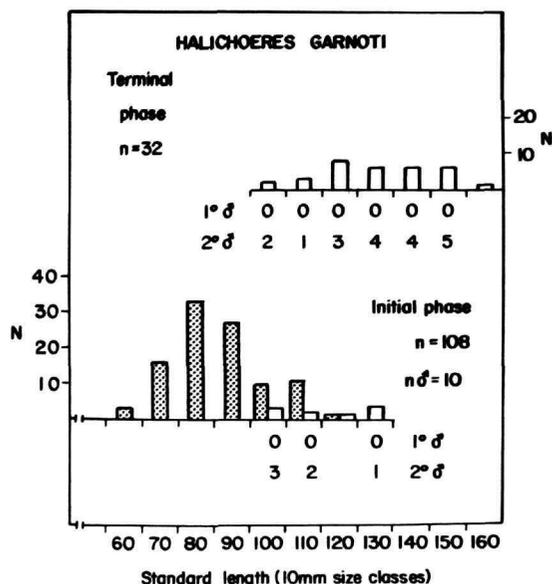


FIGURE 5.—Pattern of sexuality in *Halichoeres garnoti* (for explanation of format, see Figure 1).

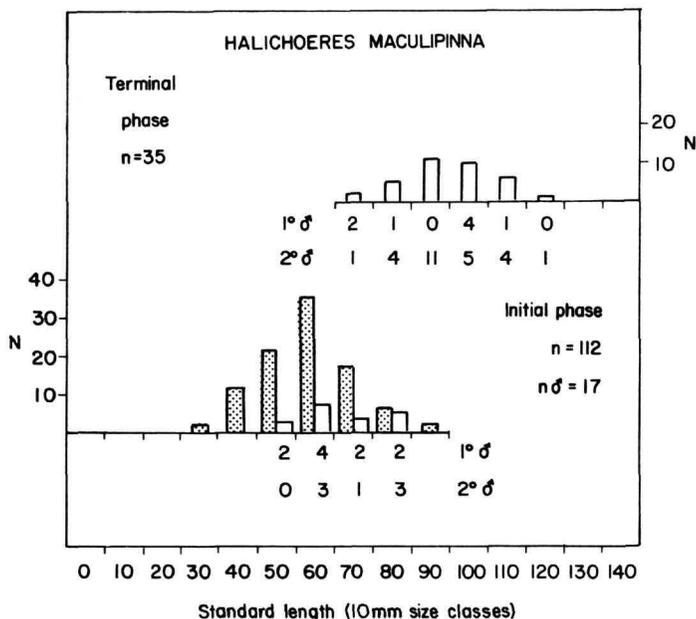


FIGURE 6.—Pattern of sexuality of *Halichoeres maculipinna* (for explanation of format, see Figure 1).

we examined had transitional testes. The gonads of initial phase primary males tended to make up a higher proportion of body weight than those of either primary or secondary terminal phase males (Table 2). Although the three initial phase secondary males examined had small testes, the sample is too small to determine whether or not the gonads of such males are consistently smaller than those of primary males in the same color phase. The sex ratio was not strongly biased towards females (Table 1). The smallest females in our sample were already sexually active.

This species was most abundant in shallow *Sargassum* beds on the tops of reefs, but was also common on and adjacent to hard reef substrates. In the *Sargassum* it was the second most abundant labrid, reaching densities there higher than those of any species other than *H. bivittatus* (Table 3).

We detected no indications of strong permanent territoriality by members of either color phase. Their movements overlapped each other, without recognizable defense of specific areas. Feeding aggregations of up to a dozen or so individuals readily formed at baits.

Sexually active, intensely colored terminal phase

males were regularly observed in midafternoon along the shallow outer rims of reefs. There they defended temporary reproductive territories within which they spawned singly with females that approached them. Such territorial males were widely scattered rather than being clustered in discrete areas. Initial phase males participated as streakers in six of 168 pair spawnings observed. In four cases, initial phase males induced pair spawnings with females that were responding to a courting terminal phase male in the immediate vicinity. We have observed group spawning involving small aggregations of less than twenty initial phase individuals on three occasions, on two large reefs containing many *H. maculipinna*.

The species as a whole bred throughout the year (Table 4), although not all mature females were continuously active, since we often collected both active and inactive specimens in the same sample.

Halichoeres pictus.—Good descriptions and figures of the color phase of this species are contained in Randall (1968) and Böhlke and Chaplin (1968). Our data show that it is sexually dichromatic. This dichromatism is full, strongly expressed, and permanent. Fading of most of the diagnostic color

elements however, was observed in sexually inactive terminal phase males. The color phase ratio was strongly biased towards the initial phase (Table 1). The degree of intrapopulation overlap in the size ranges of the two phases, as shown by the few data we have, was quite low. In two collections (10 terminal and 44 initial phase fish) there was one overlap, of only 2 mm SL.

Both color phases of *H. pictus* contained primary and secondary males (Figure 7). The terminal phase also contained significantly more primary males than did the initial phase (Table 5). One secondary male (93 mm SL) with transitional gonads was collected; it did not have fully developed terminal colors. Initial phase primary males had relatively heavier testes than those of primary or secondary terminal phase males (Table 2). The few secondary initial phase males had relatively large testes. The sex ratio was moderately biased towards females (Table 1), mainly because of the paucity of initial phase males. We were unable to determine size at maturity.

We observed *H. pictus* only on the outer faces of reefs, typically at shallow depths on slopes that faced deep open water. It was one of the least common labrids, both overall and within its typi-

cal habitat (Table 3). This species was usually clumped in small aggregations of up to forty individuals of both color phases. There were no indications of permanent territoriality within such groups and the fish fed quietly together in mid-water.

We have little significant information on this species' mating system. We noted a few pair spawnings involving an intensely colored terminal phase male and a smaller female, and some aggressiveness between such sexually active males.

Halichoeres pictus bred during both wet and dry seasons (Table 4) and probably continuously throughout the year. As with other labrids, not all females were continuously producing eggs.

Halichoeres poeyi.—Although two color phases are distinguishable in this species (see Randall, 1968), the patterns of these intergrade smoothly, particularly with respect to body color elements. Our delimitation of these phases was therefore based largely on tail colors, with terminal phase fish having three convergent pink tail lines as figured in Chaplin and Scott (1972: pl. 16: fig. 2). Terminal phase fish were all males (Figure 8), and the larger they were, the more strongly developed were their characteristic colors. Sexual dichromatism in this species is thus full by definition, but rather subtle. Death colors were often used when making decisions about a specimen's color phase. The color phase ratio was moderately biased towards the

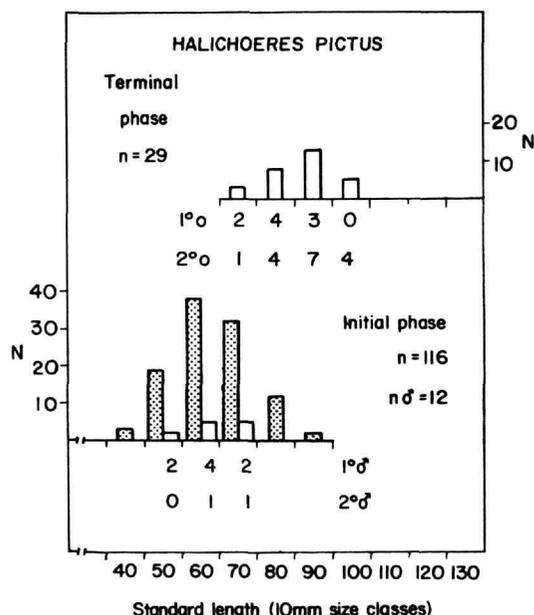


FIGURE 7.—Pattern of sexuality in *Halichoeres pictus* (for explanation of format, see Figure 1).

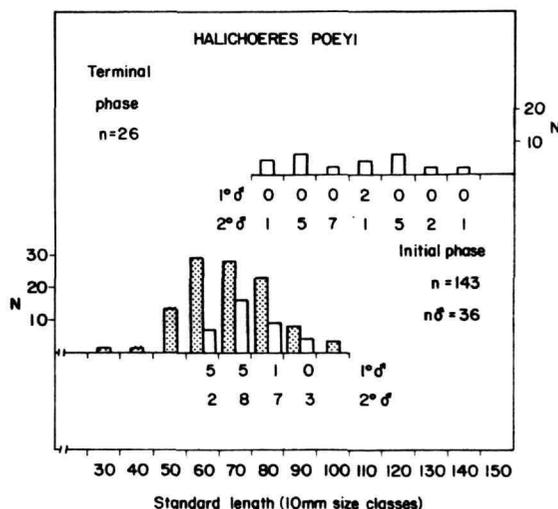


FIGURE 8.—Pattern of sexuality in *Halichoeres poeyi* (for explanation of format, see Figure 1).

initial phase (Table 1). There was little within-site overlap in the size ranges of the two color phases. In a total of six collections (of 15 terminal phase and 82 initial phase fish), there were three overlaps, all of less than 1 cm SL.

Primary and secondary males were present in both color phases of *H. poeyi* (Figure 8) and primary males were about equally represented in both (Table 5). Secondary males occurred in all size classes of initial phase males, and included fish much smaller than the smallest terminal phase males. Males (mostly secondary) constituted quite a large proportion (0.25) of the initial phase. A high proportion (0.45) of the initial phase secondary males had transitional gonads. These were concentrated in the larger size classes (70–100 mm SL). Gonad weights in this species (Table 2) were too variable to indicate any clear relationship between them and color phase. We collected no immature individuals.

As a result of the combination of a moderately biased color phase ratio and an abundance of initial phase males, the sex ratio was not strongly biased towards females (Table 1).

H. poeyi was restricted chiefly to turtlegrass and shallow sessile *Sargassum* beds; in the latter it was one of the more abundant species (Table 3).

No members of either color phase showed any signs of being permanently territorial. Individuals overlapped broadly in their movement, and none appeared to defend discrete areas. Small feeding aggregations of individuals of both color phases would rapidly form at baits.

Sexual activity occurred in midafternoon around the edges of reefs in the species' normal habitat. Terminal phase males became intensely colored, defended territories, and pair spawned with females. No spawning by initial phase males was noted, but we spent very little time observing this species.

Our data show that breeding occurred in both wet and dry seasons (Table 4). As usual, not all females were continuously producing eggs. There were more ripe fish taken from the edges of reefs than from the centers of reefs, a situation similar to that described for *H. bivittatus*.

Clepticus parrae.—Neither Randall (1968) nor Böhlke and Chaplin (1968) adequately described coloration in this species. We have found that it is fully sexually dichromatic. The bodies of terminal phase males are dark blue, an orange area covers

the caudal peduncle and extends down above the anal fin and along the belly, and the tail is light purple. Sexually active terminal phase males develop these and other color elements much more strongly (Robertson and Hoffman, in press). Initial phase fish have uniformly light blue bodies and fins, with no orange markings.

The color phase ratio was relatively weakly biased toward the initial phase (= females) (Table 1) and from the few data we obtained there appeared to be little overlap in the size ranges of the two color phases within a population: of the two overlaps in five collections (eight terminal and 44 initial phase individuals) the largest was 1.2 cm SL. We observed little indication of greater overlaps.

Clepticus parrae is evidently monandric. All terminal phase males examined histologically were secondary and no initial phase males were detected (Figure 9). No males with transitional gonads were collected. The sex ratio was moderately biased in favor of females, due mainly to the absence of males in the initial phase. We were unable to determine size at maturity, since all fishes we collected were sexually active.

We invariably found *Clepticus parrae* moving in open water well off the edges of reefs, particularly where these faced deep channels or open water.

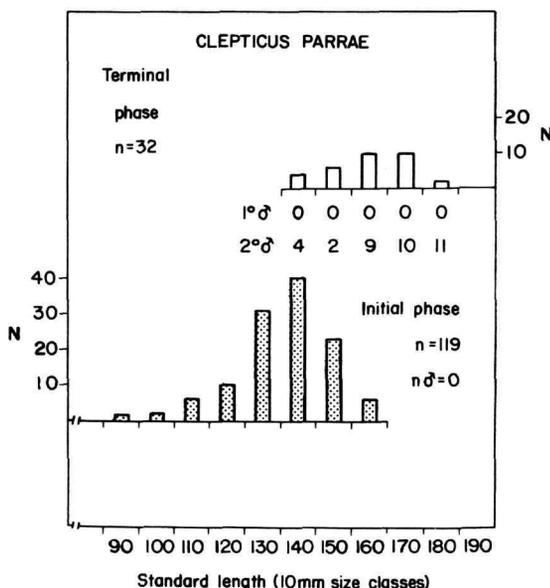


FIGURE 9.—Pattern of sexuality in *Clepticus parrae* (for explanation of format, see Figure 1).

Because of this tendency to move off into open water, we have not included it in our relative abundance estimates. In certain areas, however, it was quite common.

We often observed it in large schools containing hundreds, or even thousands, of fishes of both color phases. There were no indications of any permanent territoriality by any of these. They ranged over large distances, feeding together.

The spawnings we observed in this species occurred at the edges of reefs. Periods of sexual activity lasted for several hours each day, from midafternoon onwards. Strongly colored terminal phase males would pair spawn with smaller females. Robertson and Hoffman (in press) describe pair spawning in this species, which differs radically from any other known labroid pattern. There were no signs of any streaking by other males during pair spawnings. We did observe however, that single terminal phase males would approach courting pairs and attempt to supplant the paired male. These approaches led to vigorous male-male fights, with the intruder usually being driven off. In two cases, a male larger than the paired one succeeded in displacing it and spawned with the female involved.

Clepticus parrae spawned the year round (Table 4). As with other species, not all females were continuously active. With this species in particular there were strong suggestions of cycles of reproductive activity at the population level. At one regularly and frequently visited spawning site, we observed activity on some days but none on others.

Thalassoma bifasciatum.—We have dealt with this species elsewhere (Warner, Robertson, and Leigh, 1975). Here we recapitulate and add relevant material.

Thalassoma bifasciatum is fully sexually dichromatic, with the dichromatism being the strongest and most permanent of any of the Caribbean labrids. Terminal phase males have not evidenced any capability of temporarily reverting to the initial coloration.

The color phase ratio varies considerably from population to population, being most strongly biased towards the initial phase in large populations (data from a large population are given in Table 1). The degree of overlap in the size ranges of the two phases within populations was quite small (Figure 10).

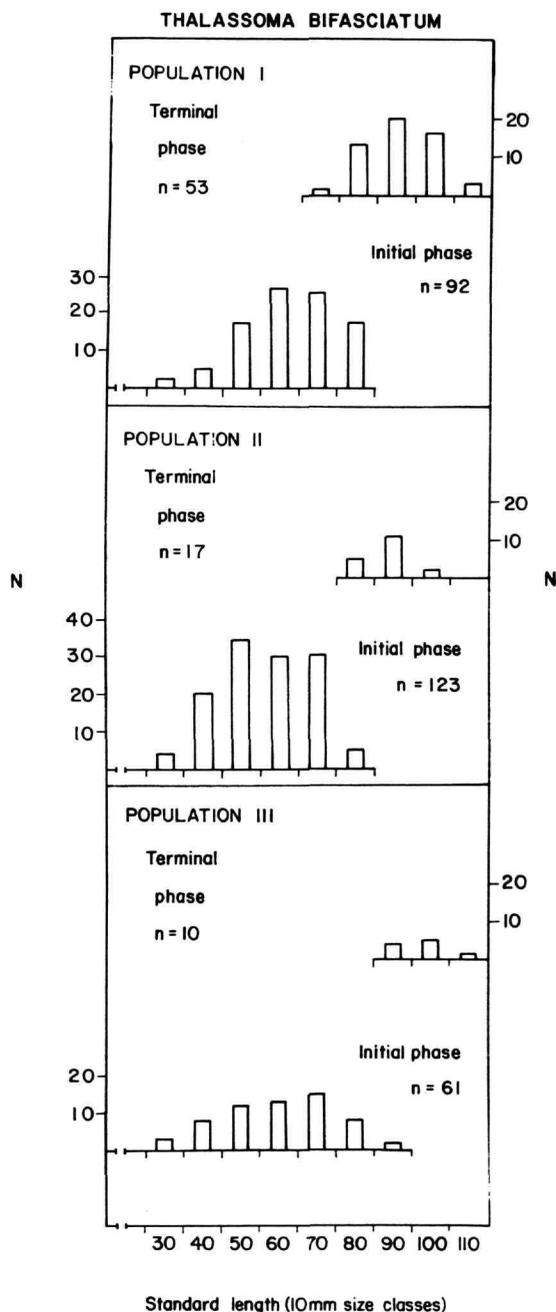


FIGURE 10.—Size/frequency bar graphs for collections of *Thalassoma bifasciatum* from three localities, showing color phase overlap.

The species is diandric, with both male types being present in both color phases (Figure 11; see also Reinboth, 1973). However, primary males were less common (in both color phases) in small populations than in large ones (Warner, Robertson, and Leigh, 1975). Overall, they were equally abundant in the two phases in each type of population (Table

5). The few secondary males present in the initial phase were found in the largest size classes (Table 6). A substantial proportion of such males had transitional testes. Initial phase males had gonads relatively heavier than those of terminal phase males (Table 2). Initial phase primary males had the heaviest testes (in absolute terms) of all male

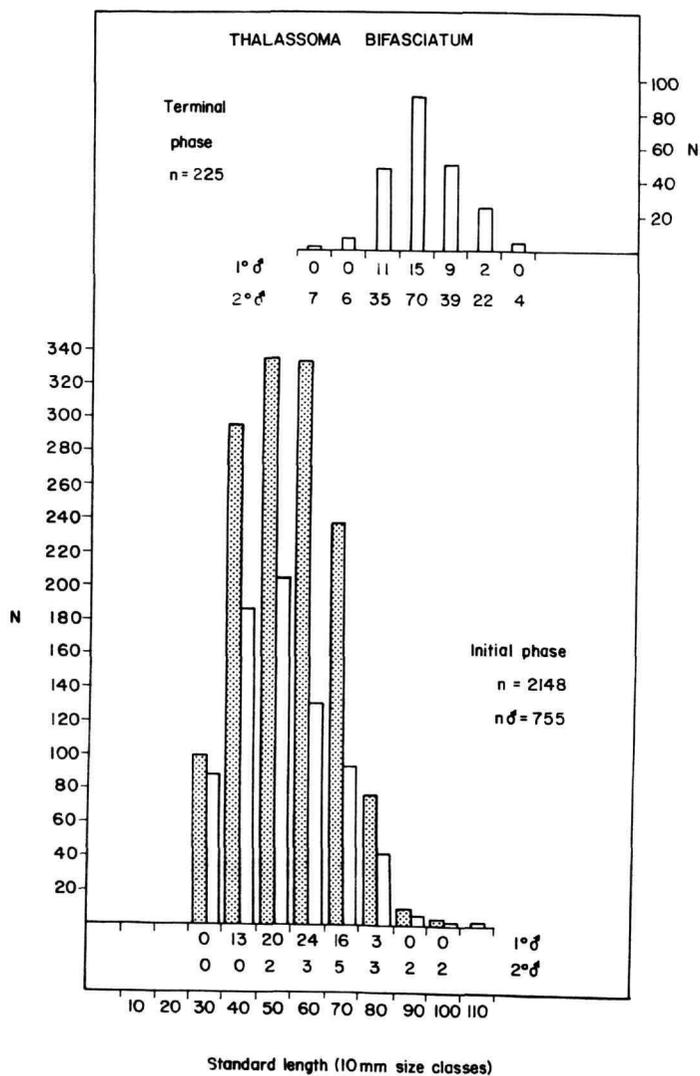


FIGURE 11.—Pattern of sexuality in *Thalassoma bifasciatum* (for explanation of format, see Figure 1).

types, although they were among the smallest in body size.

The sex ratio varied considerably between populations and depended upon both variations in the color phase ratios and the abundance of males in the initial phase. Thus, although there were comparatively many more terminal phase males in small populations than in large ones, the sex ratios in small populations were more strongly biased toward females (see Warner, Robertson, and Leigh, 1975).

Thalassoma bifasciatum was associated mainly with coral reef areas, particularly around the periphery of reefs. It also extended into adjacent areas that were sparsely provided with solid shelter. Both in its main habitat and in general, it was one of the more abundant species (Table 3).

This species often formed aggregations of hundreds or thousands of individuals of both color phases. These actively fed on plankton at the edges of reefs. Similar aggregations formed readily at baits. Observations on tagged fishes of both color phases showed that they had home ranges that overlapped greatly and there was no well defined permanent territoriality.

The mating system of large populations of this species resembled that of lek-forming birds. In the middle of each day temporary concentrations of territorial terminal phase males formed at certain sites where they pair spawned with females that visited them. Group spawning was common, as was streaking and sneaking by initial phase males (see data in Warner, Robertson, and Leigh, 1975).

Breeding occurred throughout the year (Table 4), although not all females were continuously active.

Discussion

PATTERNS OF POPULATION STRUCTURES AND THEIR RELATIONSHIP TO LIFE HISTORIES.—We assume that our samples reflect the life history patterns found within each species. In deducing the life history patterns from sample structures we made two basic assumptions: (1) The absence of a sex or coloration type above a certain (submaximal) size indicates that by the time individuals of that type have reached that size, they all have moved into another class (i.e., changed sex and/or coloration); and (2) all

individuals are capable of reaching the maximum size.

It is possible, of course, that an individual following a certain pattern invariably dies at a size significantly less than the maximum for the species. Then the absence of a type above a certain size would result from those individuals dying rather than changing into another type. For example, the fact that terminal phase males are found in size classes larger than the maximum for females might be due to all the females having died before they have reached a large size. Alternatively, all females may have changed sex before they reach the maximum size. Histological examination helps to eliminate the possibility of differential mortality by indicating the previous history of the individual. Transitionally colored individuals also aid in establishing the patterns of transformation. The consideration of a combination of sample structure, histology, and transitional individuals can usually show which pattern is present by a process of elimination.

LABRID LIFE HISTORY PATTERNS.—*Diandric Species:* There appears to be one rather common pattern for the development of terminal phase males from individuals that start life as females: sex change is followed rapidly by color change. In each species for which we had reasonable numbers of initial phase secondary males (*Halichoeres bivittatus*, *H. maculipinna*, *H. poeyi*, and *Thalassoma bifasciatum*), a large proportion of those males had transitional gonads. We feel that this indicates rapid transition of secondary males into the terminal phase, with most individuals spending little or no time in the initial phase once their sex change has been initiated. The restriction of secondary males to the upper end of the initial phase's size range in *H. bivittatus* and *T. bifasciatum* supports this idea (Figures 2 and 11; Table 6). Also, Reinboth (1973) pointed out that in his sample of *T. bifasciatum*, no transitionally colored secondary male had transitional gonads, indicating that completion of sex change had occurred before that of color change. On the other hand, Roede (1972) found the great majority of specimens having "intersexual" gonads in this species were transitionally colored or fully terminally colored. Her definition of "intersexual," however, is much broader than our "transitional." In our samples, only *Halichoeres pictus* appeared

to show any synchrony in change of sex and color. Whether this might also occur in the other *Halichoeres* species is not clear, because they lack radical dichromatism.

Additionally, in diandric species, primary and secondary males appear to change coloration within the same size range. This is indicated by the smallness of overlaps in size between the initial and terminal color phases.

Monandric Species: *Bodianus rufus* has the simplest pattern seen in the Caribbean labroids. It is monochromatic, and sex change occurs over a small size range. In the dichromatic *Clepticus parrae*, the two transitionally colored males we collected had fully functional gonads, indicating that sex change probably precedes color change. If *Halichoeres garnoti* is truly sexually dichromatic (see above), its sexual pattern is similar to that of *C. parrae*: sex change followed by rapid color change.

In none of these three monandric species is there any tendency for early sex changes (i.e., prematurational or early postmaturational), which are common in the monandric parrotfishes (see Robertson and Warner, 1978). Our meager sample of *Halichoeres radiatus* indicates, however, that prematurational sex change does occur in this species. Its significance is unknown.

SIGNIFICANCE OF TESTIS SIZE IN RELATION TO REPRODUCTIVE STRATEGIES.—Robertson and Choat (1974) and Choat and Robertson (1975) showed that in some of the dichromatic labroids, initial phase males had much heavier testes relative to body weight than did terminal phase males. They related this to basic differences in the spawning strategies of the two male types. Since initial phase males usually spawn in groups, a selective premium would be placed on possessing a large testis. An individual releasing vast amounts of sperm in each group spawning could increase the proportion of the eggs that he fertilized relative to less productive individuals. Terminal phase males normally spawn singly with a female. Since sperm competition in this case does not come into play, there is no selection for the development of a large gonad.

Data presented by Warner, Robertson, and Leigh (1975) for *Thalassoma bifasciatum* show how strong the dichotomy can be between the spawning patterns of the two male phases. Although there was complete intergradation between the extremes of pair and group spawning, 98.3% of the spawning

acts of initial phase males observed were group spawning, but only 5.4% of terminal phase males' spawnings involved more than one male. In this species we have shown that initial phase males have very much heavier testes, both absolutely and relatively, than do terminal phase males (Table 2; Roede, 1972, especially fig. 21b). This pattern also holds true for some of the other dichromatic labrids that we have examined (*Halichoeres maculipinna* and *H. pictus*). With the weakly dichromatic *H. bivittatus*, the differences in relative gonad weight are between large males and small males rather than strictly between color phases (Figure 3; also see Roede, 1972).

The gonad weights of *H. maculipinna* also correlate with the differences in the observed spawning patterns of the two color phases: terminal phase males engage in pair spawning, while initial phase males interfere in pair spawnings and participate in group spawning. In this species, it seems unlikely that group spawning is the predominant spawning mode of initial phase males. Initial phase fertilization success in interference spawnings would also be increased by the greater sperm production of relatively large testes. We do not know the level of zygote production by small males compared to that of females of equivalent size. If it is much less, initial phase males should be selected against (Warner, Robertson, and Leigh, 1975); however, if those males tended to participate as satellites in pair spawnings involving large females, and fertilized a high proportion of the eggs in such cases, then a relatively small number of spawnings by them could lead to a zygote output equivalent to that of small females. *Halichoeres poeyi* and *H. pictus* may also show a similar relationship between gonad size and spawning pattern.

Robertson and Choat (1974) also extended this hypothesis to cover the situation in the monochromatic labrid *Labroides dimidiatus*. The small testis weight of the males of that species correlates well with the absence of spawning patterns other than pair spawning. Neither the monochromatic *Bodianus rufus* nor the dichromatic *Clepticus parrae* showed any indications of multimale spawnings. The males of both of these species have small testes, whose relative weights are similar to those of the pair spawning males of other labrids (Table 2).

Two further comparisons are instructive.

1. The testes of initial phase *T. bifasciatum* males

are heavier, both absolutely and relatively, than those of the other diandric species (see Table 2). The largest spawning aggregations of initial phase males seen were those of *T. bifasciatum*, in which hundreds or thousands of fish were commonly present. For instance, on one well studied reef, an estimated 15,700 initial phase fish visited the spawning area. The bulk of those were males (65% of a sample of 100; Roede, 1972, obtained 85% males in a similar collection). Actual spawning groups were also large as well. Half of them contained an estimated 6–10 initial phase fish and another third an estimated 11–15 such individuals. This follows our expectations that the largest initial phase male testes should be found in species in which group spawning is most strongly developed.

2. In *T. bifasciatum*, the pattern of large initial phase male testes and small terminal phase male testes holds true for both primary and secondary males. One would expect this if both male types evidenced common spawning strategies relevant to a particular color phase. This suggests that selection can alter the size of the male gonad, and its level of sperm production, regardless of its ontogeny. The small sizes of secondary terminal phase males' gonads are thus not necessarily the result of some intrinsic limitation.

Warner and Downs (1977) examined patterns of growth and longevity in primary males and hermaphrodites of the scarid *Scarus croicensis* and came to the conclusion that primary and secondary males in this species follow different life history strategies: primary males appear to spend a relatively short time in the initial phase by growing rapidly and changing to the terminal phase sooner than the hermaphrodites. They also die much sooner than the hermaphrodites. Perhaps a similar situation exists in *H. maculipinna*: initial phase male sexual activity seems quite limited and there are relatively high proportions of primary males in the terminal phase (similarly in *H. pictus*, see Table 5). This could be the result of relatively rapid growth by primary males. In *T. bifasciatum* and *H. bivittatus*, the proportions of primary males are the same in both color phases. This may indicate a lack of accelerated growth by such males when they have a high degree of spawning success (see data on *T. bifasciatum* in Warner, Robertson, and Leigh, 1975); however, we do not exclude the possibility that complex interactions between differential

growth and mortality rates could produce similar proportions. In one population of *T. bifasciatum* that we studied, the proportion of primary males declined with increasing size in the initial phase, suggesting growth or mortality differences. Sex specific movement and spatial distributions could also lead to bias in the initial phase samples.

MATING SYSTEMS AND THE REPRODUCTIVE SUCCESS OF INITIAL PHASE MALES.—In discussing the evolution of protogyny by natural selection (Warner, Robertson, and Leigh, 1975), we concluded that the presence or absence of dual mating strategies was related to the strength of sexual selection, i.e., to the difference in fertility between females and their selected males. In *T. bifasciatum*, dual male strategies are represented by the spawning behaviors of terminal and initial phase males. Intense sexual selection, when coupled with sex change, leads to high numbers of females relative to terminal phase males in large populations. Management of so many females by the dominant males is difficult, a situation that allows initial phase males to be successful in group and interference spawning. In small populations, sex ratios are more equable and terminal phase males should be better able to control the entire spawning area. This would create much less favorable conditions for initial phase males and thus for primary males. We believe it is for this reason that primary males are common in large populations and rare in small ones (Warner, Robertson, and Leigh, 1975).

The coexistence of nonhermaphrodites (primary males) and sex changers in the same species was explained as a form of frequency dependent selection. When initial phase males are rare, they would be favored relative to hermaphrodites, but would be at a disadvantage when they are so common that their average fertility was reduced below that of females. A balance would be struck if the fertility of initial phase males was equal to that of similar sized females, which we showed could occur in large populations. Robertson and Choat (1974) and Choat and Robertson (1975) suggested how this argument might apply to interspecific comparisons. They considered two radically different types of species: those that live in permanent, territorial, harem groups, and those in which there is only periodic territoriality by large males during periods of reproduction. In the former type, a male mates regularly, and almost exclusively, with the females

of his group, whom he probably knows individually; while in the latter each temporarily territorial male competes freely for any female during the spawning period. A lack of free competition for mates in the harem type enables territorial males to virtually eliminate the possibility of breeding by small males. They can be recognized and prevented from spawning, and excluded from the social group. Because of low spawning success relative to hermaphrodites during the early part of their lives, primary males should not be able to maintain themselves in the population of such a species (see also Warner 1975a). This fits with the observation that harem species are monandric and have no small males.

In species in which males held only temporary spawning territories the anonymity of the initial phase males should facilitate their interference with the spawning activities of territorial males. The ability of terminal phase males to exclude them outside spawning periods would also be negligible. In this type of species, small males could attain a much higher level of success than they could in species of the harem type. When these small males grow large, they can then assume the dominant male behavior and coloration.

How does our data on the Caribbean labrids relate to these hypotheses? Essentially, each species can act as a test of the ideas, indicating where modifications or expansions might be needed.

First, the relationship between social and mating system types and the presence or absence of primary males holds fairly well: *Bodianus rufus*, which has an harem system, is monandric, with no evidence of any small males. Of the remaining species for which we have fairly comprehensive information, most have nonharem social systems, primary males are present, and in many instances there is evidence of initial phase male spawning activity.

Halichoeres garnoti and *Clepticus parrae* are the only anomalous cases. We need more information to resolve the situation in *H. garnoti*. It is the only established monandric *Halichoeres* species, and it contains no small secondary males such as exist in nonharem, monandric parrotfishes (Robertson and Warner, 1978). These facts suggest that *H. garnoti* may have a social and mating system of the harem type. A thorough study of the reproductive behavior of this exceptional *Halichoeres* is needed.

Clepticus parrae is atypical for the Caribbean labrids in several important ways. (1) It is the only

truly schooling, open water species and is the least reliant on coral for shelter; accordingly, its morphology differs greatly from that of the other species (see Davis and Birdsong, 1973). (2) It is both dichromatic and monandric, with no indications of any existence of small initial phase males. (3) The combination of this pattern of color and sex change with the nonharem social and mating system of this species appears to contradict the ideas of initial phase male (and thus primary male) spawning success that we have presented. There are data dealing with the finer details of the mating system, however, that may resolve this apparent conflict.

Spawning in *C. parrae* is unlike that in the other species that we have observed. Terminal phase *C. parrae* do not wait in small defended areas for females to visit them but roam actively about in overlapping manner over large distances. Robertson and Hoffman (in press) have described the mating pattern in detail, contrasted it to that of *T. bifasciatum* and discussed the adaptive significance of the differences. In *C. parrae*, females seem to require long term tactile stimulation from a persistent male to induce spawning, and the spawning sequence requires a high degree of coordination and continuing physical contact between the pair. Spawning thus requires considerable time and effort by the male to induce participation by the female. In *T. bifasciatum*, the terminal phase male puts much less effort into each spawning. Courtships are often very abbreviated, and reliance is placed on visual displays rather than on tactile stimulation, which is usually not needed. In contrast to the situation in *C. parrae*, the spawning rush can be much more easily triggered in females of *T. bifasciatum*; thus, the courtship and spawning sequence is much more open to manipulation by initial phase males. Because the females of *C. parrae* appear to respond only to concerted and persistent tactile stimulation of single males, interference spawning (group spawning and sneaking) that rely on manipulation of the female's ready susceptibility to casual tactile stimulation are probably not viable propositions in that species. Streaking, the only spawning pattern of an initial phase male that does not involve tactile stimulation by him, could be a significant means of fertilization by an initial phase male in *C. parrae*. In *T. bifasciatum*, however, streaking contributes very little to initial phase males' spawning success: only 4.4% of pair spawnings were

streaked ($n = 40$ spawning periods) and only one of 364 spawning acts by 15 initial phase males was a streaking. We see no reason why *C. parrae* males should be less effective at aggressively inhibiting streaking than terminal phase *T. bifasciatum*.

In addition, *C. parrae* has the most equable color phase ratio (= sex ratio) of any of the labrids considered here. This, combined with the long time span involved in each spawning, means that each terminal phase male probably has relatively few successful spawnings per day. A loss of a single spawning would then represent a major diminution in a male's daily reproductive output and vigorous defense of each female is to be expected. Thus the conditions necessary for initial phase males to achieve spawning success are certainly not present in *C. parrae*.

We have reasoned that dominant males that succeed in minimizing the participation of other males in spawning activities maximize their own spawning success. Let us now examine in greater detail how, in species such as *T. bifasciatum*, initial phase males attempt to frustrate such activity and what factors lead to their success or failure in doing so.

In species like *T. bifasciatum* the anonymity of the initial phase male reduces the ability of terminal phase males to discriminate against them. Initial phase males in *T. bifasciatum* gain their spawnings in a variety of ways and anonymity probably plays a varying role in this, depending on their relative abundance in the population. When initial phase males are rare, their resemblance to females (suggested as being mimetic by Choat and Robertson, 1975) increases their chances of penetrating a terminal phase male's territory and sneaking or streaking his spawnings.

Labroids may be able to detect sex other than by visual means. Randall and Randall (1963) suggested that males of one of the scarids might be detecting the sex of females chemically. Our observations of *T. bifasciatum* and other labroids strongly suggest that terminal phase males can distinguish between females and initial phase males by following initial phase fish and closely inspecting their vents. We have repeatedly seen such behavior lead to a terminal phase male aggressively chasing a known initial phase male. Terminal phase males do not always succeed in such a detection, however. Rarely, initial phase males carry the mimicry a step further: we have observed known initial phase males going

through the basic female motions of spawning with a terminal phase male. Once this led to the initial phase male sneaking a spawning with a waiting female immediately afterwards.

With increasing abundance, the chances of all initial phase males successfully employing the "mimicry" strategy would decline. An alternative mode of achieving success is to overwhelm the territorial male by numbers. A large territorial male is able to break up groups of up to about twelve initial phase males, and prevent them from group spawning in his territory. Larger groups can enter such a male's territory quite successfully and the frequency of group spawnings increases with the number of initial phase males present in the spawning area. In the presence of masses of about 50 initial phase males, large territorial terminal phase males become hyperaggressive and chase out all initial phase fish, including females. This, of course, works in the initial phase males' favor, since females then become more available to them. Groups of initial phase males also intercept females on their way to a territorial terminal phase male and can induce group spawning by tactile stimulation.

Group spawning, however, has some definite disadvantages to the participant male. An initial phase male cannot always predict whether it will be adequately rewarded for joining a particular aggregation. There could be too few males to overwhelm the territory owner or too many initial phase males relative to the number of females. Because in the initial phase both sexes are colored alike, initial phase males have the additional problem of distinguishing females, and they often make mistakes. About 50% of group spawnings yield no observable eggs and appear to lack a female participant. This leads to a considerable wastage of the group-spawning male's gametes. Finally, predatory fishes often attack these male aggregations and eat individuals whose attention is concentrated on spawning.

As Warner, Robertson, and Leigh (1975) have shown, initial phase male mating strategies work well in situations where there are many females per terminal phase male. The strategy of overwhelming these males is most liable to pay off in these situations, and proportionately larger numbers of initial phase males can attain spawning success. On larger reefs, there are fewer terminal phase males per female in *T. bifasciatum*: we previously attributed

this solely to the fact that a higher potential fertility of large males leads to more intense sexual selection and hence to a later age of sex change (Warner, Robertson, and Leigh, 1975). Topography, however, plays a part in this phenomenon as well: spawning sites (down-current corners) are limited on any reef, and their number does not increase directly with the size of the reef. If the number of successful terminal phase males is limited by available spawning sites, we might expect there to be fewer terminal phase males per female in large populations on big reefs.

Another factor also acts on large reefs. Initial phase male spawning success is achieved at the expense of terminal phase male success. In situations in which initial phase male success is high, the potential number of successful terminal phase males may be reduced. The result is that fewer initial phase fish change to the terminal phase, there being no reproductive advantage in doing so.

For whatever reason, in large *T. bifasciatum* populations, the color phase ratios are very skewed (Table 1). In these populations, initial phase males reach high proportions (Table 5) and apparently achieve the same zygote production as females (Warner, Robertson, and Leigh, 1975). Primary males may be avoiding small reefs by emigration while very small or by non-random settlement. Fringing, barrier reefs tend to be large and they may also be the first encountered by drifting juveniles preparing for settlement. If primary males tend to settle out on the first reef they encounter, while hermaphrodites wait a longer period, there might tend to be more initial phase males on large fringing reefs.

We think that terminal phase males can effectively reduce initial phase male spawning activity on small reefs in a manner analogous to male activity in harem forming species. In small populations, an initial phase male would have less ability to remain anonymous. A terminal phase male could also directly benefit by detecting and excluding specific initial phase males. This is much less effective on a large reef. Also, because the overall spawning activity of terminal phase males is lower on small reefs due to the presence of fewer females, more time may be available to that male for defense and detection of small males. The only initial phase

male spawning strategy that could seem to work in such situations involves "mimicry." With few females present the swamping technique would provide too little return for effort.

Since population size appears to have such a strong effect within this one species, it might logically be expected to have similar effects in other species that have similar social and mating systems. In Table 7, we summarize the basic abundance and sexual data for the five diandric labrids that we examined. Generally, those species which have large dense populations (measured by relative abundance ranks) also have the strongest representation of initial phase males. *Halichoeres pictus*, which occurs in small isolated clumps, has the fewest such males. This relationship is in general accordance with what we have found within *T. bifasciatum*.

The situation, however, is potentially far more complicated than would be indicated from simple comparisons of initial phase male abundances and population sizes. The social system is probably the most critical factor in determining initial phase male success. We have shown this in the parrotfishes, where we had adequate numbers of harem and nonharem species for comparison (Robertson and Warner, 1978). Harem species tended to have lower proportions of initial phase males.

There are other strategies available to small males, some of which we have already mentioned: avoidance of populations in which reproductive success is liable to be low, and rapid growth to bypass an unfavorable phase. Choat and Robertson (1975) also raise the possibility of differences in age or size at maturity. Each strategy carries with it a certain risk of death, and differential mortality is an important and often overlooked factor in comparisons of reproductive success.

We have presented an overview of the patterns of sexuality in the Caribbean wrasses. More patterns and further discussions can be found in the companion paper on parrotfishes (Robertson and Warner, 1978). Both of these studies provide a general impression of the factors working to shape the life history patterns of tropical reef fishes. There is still a critical need for detailed studies of single species in a series of habitats. Only in this way can we unravel the proximate factors affecting fitness.

Appendix 1

Definition of Terms

(Used herein and in Robertson and Warner, 1978)

COLORATION

juvenile phase. Having a color pattern characteristic of immature individuals.

initial phase. Having a color pattern characteristic of small adult individuals.

terminal phase. Having a color pattern characteristic of the largest males.

sexual monochromatism. Females develop the same color pattern as males.

sexual dichromatism. At least some males (terminal phase) have color patterns different from females (initial phase).

full. Some coloration elements are present only in the terminal pattern.

partial. Initial and terminal patterns differ only in intensity of some color elements.

temporary. Males can revert to initial pattern.

permanent. Males cannot revert to initial pattern.

SEXUALITY

gonochorist. An individual that does not have the genetic capacity to change sex.

protogynous hermaphrodite. An individual that can change sex from female to male.

primary female. A gonochoristic female.

primary male (1° ♂). A gonochoristic male.

secondary male (2° ♂). A male resulting from the sex change of a female protogynous hermaphrodite.

prematurational. Sex change occurs before the female ever functions as an adult.

postmaturational. Sex change occurs after a functional female stage.

diandry. both primary and secondary males present in the same population.

monandry. All males present in a population are secondary.

MATING PATTERNS

leks. Males are territorial during spawning periods only. At such times they tend to aggregate at traditional sites and vie for mating with the females who come to the sites to spawn.

harems. Males are permanently territorial and include within the territory a group of females with whom they mate nearly exclusively.

pair spawning. A single male mating with a single female.

group spawning. A group of males mating with a single female.

sneaking. An initial phase male surreptitiously inducing a female to pair spawn within the territory of a terminal phase male.

streaking. Rushing in to join a male and a female at the climax of pair spawning.

Appendix 2

Terminology Applied to Labroid Color Phases

<i>Authority</i>	<i>Juveniles</i>	<i>Smaller adults</i>	<i>Larger adults</i>
Randall, 1963	-	drab	terminal
Randall, 1968	-	drab	terminal
Rosenblatt and Hobson, 1969	juvenile	"female"	definitive or terminal
Böhlke and Chaplin, 1968	-	-	super male
Roede, 1972	juvenile	first adult	terminal
Reinboth, 1973	-	plain	bright
Ogden and Buckman, 1973	-	striped	terminal
Moyer and Shephard, 1974	-	drab	bright
Robertson and Choat, 1974	juvenile	drab	gaudy
Roede, 1975	juvenile	first adult	terminal
Reinboth, 1975	-	initial	terminal
Barlow, 1975	tiro	mid	term
Choat and Robertson, 1975	juvenile	drab	gaudy
Warner, Robertson, and Leigh, 1975	-	initial	terminal
Warner, 1975b	-	uniform	bicolored
Warner and Downs, 1977	-	initial	terminal

Appendix 3

Tables

TABLE 1.—Color phase ratios and estimated adult sex ratios of eight species of Caribbean wrasses (color phase data tallied in series of counts performed during 10 minute swims in suitable habitats; overall sex ratios calculated from the color phase ratio and the initial phase sex ratio, the latter data from our collections)

Species	Number of counts	Total number of individuals from all counts	Color phase ratio		Sex ratio ♂:♀
			Terminal phase	Initial phase	
<i>Bodianus rufus</i>	--	--	--	--	1:8.5 ^a
<i>Halichoeres bivittatus</i> ..	13	1299	1:6.8	1:1.2	1:1.2
<i>H. garnoti</i>	27	998	1:4.4	1:2.9	1:2.9
<i>H. maculipinna</i>	18	747	1:6.5	1:2.5	1:2.5
<i>H. pictus</i>	11	333	1:6.1	1:3.1	1:3.1
<i>H. poeyi</i>	12	486	1:4.9	1:1.4	1:1.4
<i>Clepticus parrae</i>	12	770	1:3.2	1:3.2	1:3.2
<i>Thalassoma bifasciatum</i> ..	1 ^b	5157	1:135	1:1.2	1:1.2

^aS. Hoffman, unpublished data.

^bCount lasted approximately 20 minutes.

TABLE 2.—Testes weights of nine species of Caribbean wrasses, 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)	GM/BW x 100 (percent)	n	Gonad weight (g)	GM/BW x 100 (percent)
<i>Bodianus rufus</i>	initial	0	--	--	16	0.18 ± 0.08	0.09 ± 0.06
<i>Halichoeres bivittatus</i> ...	initial	27	0.04 ± 0.01	1.69 ± 0.54	2	0.05	0.35
	terminal	11	0.10 ± 0.04	1.21 ± 0.82	23	0.11 ± 0.04	0.59 ± 0.43
<i>H. radiatus</i>	initial	0	--	--	6	0.17 ± 0.20	0.13 ± 0.06
<i>H. garnoti</i>	initial	0	--	--	4	0.03 ± 0.02	0.08 ± 0.06
	terminal	0	--	--	26	0.08 ± 0.02	0.15 ± 0.03
<i>H. maculipinna</i>	initial	9	0.03 ± 0.01	0.66 ± 0.34	3	0.01	0.16
	terminal	7	0.04 ± 0.03	0.25 ± 0.21	27	0.04 ± 0.01	0.16 ± 0.03
<i>H. pictus</i>	initial	8	0.02 ± 0.01	0.54 ± 0.27	2	0.02	0.30
	terminal	10	0.02 ± 0.01	0.16 ± 0.06	14	0.02 ± 0.01	0.13 ± 0.05
<i>H. poeyi</i>	initial	11	0.04 ± 0.02	0.55 ± 0.31	6	0.03 ± 0.04	0.48 ± 0.57
	terminal	2	0.21	0.64	20	0.06 ± 0.02	0.23 ± 0.08
<i>Clepticus parrae</i>	terminal	0	--	--	29	0.16 ± 0.05	0.12 ± 0.03
<i>Thalassoma bifasciatum</i> ...	initial	77	0.12 ± 0.02	2.64 ± 0.42	7	0.15 ± 0.17	2.71 ± 3.94
	terminal	36	0.05 ± 0.02	0.26 ± 0.11	170	0.03 ± 0.01	0.22 ± 0.03

TABLE 3.—Relative abundance of seven species of Caribbean wrasses measured by habitat (numbers represent fish seen per 10 minutes by observer swimming 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 profile (m)					
			≤ 3	3-6	6-9	9-12	12-15	15-18
<i>Halichoeres bivittatus</i>	137.6	139.5	10.7	3.9	6.1	0.5	0.1	0.5
<i>H. maculipinna</i>	84.4	2.1	0.9	0.6	0.1	0.1	--	--
<i>Thalassoma bifasciatum</i>	--	--	31.5	7.3	3.9	2.1	0.4	2.8
<i>H. poeyi</i>	31.2	1.4	1.5	0.5	0.9	0.7	0.4	--
<i>H. garnoti</i>	--	--	4.2	4.2	4.0	9.9	9.9	11.4
<i>Bodianus rufus</i>	--	--	1.3	2.2	1.3	2.7	2.7	3.2
<i>H. radiatus</i>	--	--	0.7	0.6	0.4	0.4	--	0.6
<i>H. pictus</i>	--	--	1.4	--	--	--	--	--
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 seasonality in eight species of Caribbean wrasses (+ = 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
<i>Bodianus rufus</i>	++	nd	++	++	++	++	nd	nd	nd	nd	nd	nd
<i>Halichoeres bivittatus</i>	++	++	++	++	++	++	++	++	++	+	++	++
<i>H. garnoti</i>	+	+	++	++	++	+	+	+	++	+	+	+
<i>H. maculipinna</i>	++	++	++	++	++	++	++	++	++	++	++	++
<i>H. pictus</i>	++	nd	++	++	++	++	++	++	nd	++	nd	nd
<i>H. poeyi</i>	nd	nd	++	++	++	++	nd	nd	nd	nd	++	nd
<i>Clepticus parrae</i>	++	++	++	++	++	++	++	++	++	++	++	++
<i>Thalassoma bifasciatum</i>	++	++	++	++	++	++	++	++	++	++	++	++

TABLE 5.—Distribution of primary males in the two color phases of five diandric Caribbean wrasses (tests for differences in proportions of primary males between initial and terminal coloration by means of the normal statistic $z = \frac{\bar{X}_1 - \bar{X}_2}{\sqrt{\bar{p}(1-\bar{p})(1/N_1 + 1/N_2)}}$, where \bar{X} is the observed proportion, N is the sample size, and $\bar{p} = (N_1\bar{X}_1 + N_2\bar{X}_2)/(N_1 + N_2)$; see Dixon and Massey, 1969:249)

Species	Initial phase		Terminal phase		Test for differences in proportions
	N	Primary male proportion	N	Primary male proportion	
<i>Halichoeres bivittatus</i>	247	0.32	37	0.32	n.s.
<i>H. maculipinna</i>	112	0.09	34	0.24	p < 0.05
<i>H. pictus</i>	116	0.08	25	0.36	p < 0.001
<i>H. poeyi</i>	143	0.09	28	0.07	n.s.
<i>Thalassoma bifasciatum</i>					
Large populations	690	0.22	124	0.21	n.s.
Small populations	167	0.02	69	0.04	n.s.

TABLE 6.—Sexual ontogeny of initial phase males of *Thalassoma bifasciatum* collected from one population (proportion of total of collected individuals in parentheses)

Size class (mm SL)	N	Primary males	Transitional secondary males	Functional secondary males
40-49	14	14	--	--
50-59	15	15	--	--
60-69	17	15	1	1
70-79	15	13	1	1
80-89	4	2	0	2
	65	59 (0.91)	2 (0.03)	4 (0.06)

TABLE 7.—Rank order of abundance within common habitat and male proportion of initial color phase for five species of diandric Caribbean wrasses

Habitat/Species	Rank order of abundance	Male proportion of initial color phase
<u>Sargassum</u> , turtle grass substrates		
<u>Halichoeres bivittatus</u>	1	.33
<u>H. maculipinna</u>	2	.15
<u>H. poeyi</u>	3	.11
Hard reef substrates		
<u>Thalassoma bifasciatum</u>	1	.22
<u>H. bivittatus</u>	2	.33
<u>H. poeyi</u>	3	.11
<u>H. maculipinna</u>	4	.15
<u>H. pictus</u>	5	.10

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