

The Social and Mating Systems of Two Labrid Fishes, *Halichoeres maculipinna* and *H. garnoti*, off the Caribbean Coast of Panama

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Abstract

Large males of both species are territorial, particularly when spawning. Small *Halichoeres maculipinna* (but not *H. garnoti*) are territorial towards equal sized conspecifics, but not towards dissimilar sized conspecifics or any individuals of an abundant congener. Territoriality of small *H. maculipinna* may be related to the process of sex-change rather than defense of food. Both sexes of both species, but particularly *H. maculipinna*, migrate from feeding areas to spawning sites at the edges of reefs at specific times of day. In the two species a large male spawns both with females that live in his feeding area and with many others. Differences in the mating system of *H. maculipinna* in Panama and Florida seem related to habitat differences at those sites. The relative spatial distributions of feeding and spawning sites may affect (a) whether a female spawns with a large male with whom she feeds, and (b) the ability of large males to monopolize mates at the expense of small males. The spawning success of small males seems to depend on whether large males can penalize their participation in spawning rather than on the ability of small males to predict the occurrence of (and then interfere in) spawnings by large males. In both species, the male-specific color pattern is most intensely exhibited by large males during sexual interactions and tends to be lost when they are being aggressive towards conspecifics. The evolutionary development of such a color pattern in labroid fishes seems to be a response to intersexual rather than intrasexual interactions.

Introduction

Aspects of the reproductive biology of the labroid fishes which have received considerable attention from evolutionary biologists include the adaptive significance of, and relationships between: (1) protogynous herma-

phroditism and the occurrence and coexistence of various sexual phenotypes, (2) differently structured social and mating systems, and (3) the existence of distinct, sex-specific color phases (Robertson, 1972; Buckman and Ogden, 1973; Potts, 1974; Robertson, 1974; Robertson and Choat, 1974; Choat and Robertson, 1975; Barlow, 1975; Moyer and Shepard, 1975; Warner, 1975a, b; Warner, *et al.*, 1975; Meyer, 1977; Olla and Samet, 1977; Robertson and Hoffman, 1977; Warner and Downs, 1977; Robertson and Warner, 1978; Dipper and Pullin, 1979; Nakazono, 1979; Pottle and Green, 1979a, b; Warner and Hoffman, 1980). Recently, on the basis of a study in Florida of the behavior of two wrasses, *Halichoeres maculipinna* and *H. garnoti*, Thresher (1979) criticised some of the observations and hypotheses of Robertson and Hoffman (1977) and Warner and Robertson (1978) on (a) the structure of those species mating systems, (b) the factors that determine the structure of the mating systems and the mating success of males of different social classes, and (c) the adaptive significance of labroid sexual dichromatism. The purpose of this paper is to describe the mating systems of *H. maculipinna* and *H. garnoti* in Panama, to compare them to those in Florida, and to attempt to reconcile the Floridian and Panamanian data.

Materials and Methods

Observations were made on reefs situated on the shallow extension of San Blas Point, at the eastern end of the Archipiélago de San Blas, Panama (Lat. 9°32'N, Long. 79°4'N). Throughout this paper the study sites there are referred to as Panama and Thresher's study site as Florida.

Data on *Halichoeres maculipinna* were collected on two small patch reefs (80–130 m in largest dimension) which rose from depths of 1.5 to 6 m to within 0.5 m of the surface at low tide. Surrounding areas were covered

with seagrass. Most of the edges of both reefs were composed of *Agaricia* sp. coral and were almost vertical. The top of each reef consisted of pitted coralline rock with scattered small patches of *Millepora* spp. hydrocorals and *Agaricia* spp. On top of one reef there was a small patch of densely growing macroalgae (*Sargassum* and *Turbinaria* species). Most *H. maculipinna* had their feeding areas on the tops of the reefs.

Data on *Halichoeres garnoti* were collected from three sites. One was the patch reefs described above. The second site was at a depth of 5 to 7 m at one end of a 0.5-km-long patch reef. The habitat there was composed of scattered corals (mainly massive types), large gorgonians, and sponges on a sand substrate. On the deeper side of this area a slope composed mainly of *Agaricia* spp. coral graded off into sand at about 25 m depth. The third site (Achutupu, Chichime Keys, 10 km east of San Blas Point) was similar to the second in habitat composition, and ranged in depth from 4 to 12 m. It merged into a sand bottom on its deep side.

General descriptions of the biology, morphology and color patterns of *Halichoeres maculipinna* and *H. garnoti* are found in Randal (1967, 1968), Böhlke and Chaplin (1968), Roede (1972), Warner and Robertson (1977) and Thresher (1979). Among many wrasses two types of males can be found: "Primary Males", which apparently are born as males, and "Secondary Males", which are derived by sex change from females (Reinboth, 1967). Many labroids start their adult lives in an "Initial Color Phase" (IP), then undergo a radical change into the "Terminal Color Phase" (TP), in which they end their lives. Sexually dichromatic species contain both color phases; females and (if they occur) small males belong to the IP, while large males belong to the TP. Sexually monochromatic species have only an IP (Robertson and Hoffman, 1977). In *H. maculipinna*, which is sexually dichromatic, IP and TP males may be either primary or secondary (Warner and Robertson, 1978). *H. garnoti* is also sexually dichromatic (Thresher, 1979), but all Panamanian males of this species are secondary (Warner and Robertson, 1978).

TP males of both *Halichoeres maculipinna* and *Halichoeres garnoti* have the capability of switching between maximum intensity TP colors and the IP pattern (Robertson and Hoffman, 1977; Thresher, 1979). Their increasing intensity of development of the TP color pattern from the IP pattern was scored as follows.

Halichoeres maculipinna. Stage 0: Usually the fish is of a uniformly pale grey-green with faint pink lines on the face and fins. There is sometimes a dark stripe along the midline of each side. Stage 3: The midregion of the fish's side is dark grey-brown anteriorly and mid-grey posteriorly. The lower half of the body is white anteriorly and pale grey posteriorly. Various pink lines of the face, fins and body and a black patch above the anus are very well defined. A yellow stripe runs along the anterior two-thirds of the body immediately above that spot. There is a large blackish spot at the leading edge of the dorsal fin.

Halichoeres garnoti. Stage 0: The body is fairly uniformly pale grey, with a slight yellow cast. Stage 3: The head is bright yellow with a dark grey line along the lower half of the cheek. A thick black bar at the middle of the body joins a broad black stripe that runs along the top of the back half of the body, extends onto the dorsal fin, and covers most of the tail. The body is white behind this bar, with a bluish cast (see Randall, 1968, Fig. 230).

Observations were made between 07:00 and 17:00 hrs. Individuals of both species were caught with lift nets and tagged with subcutaneous injections of acrylic paint (see Thresher, 1979). Maps were made of the spatial distributions of tagged fish of both color phases over periods of up to 10 d, using observation periods of 0.25 to 3 h. Members of both color phases were divided into three size classes - large, medium and small - which represented the upper, middle, and lower thirds of the size (weight) range of individuals living on the study reefs. I recorded the colors of TP males at the beginning of agonistic and sexual interactions, and any color changes that occurred during those interactions. An interaction was considered to have started when the subject TP male obviously began responding behaviorally to the other fish. The times at which spawnings occurred were noted and the location of the feeding areas of individual females relative to the feeding area of the TP male with whom each spawned was determined.

The data presented here are based on 145 h of observation on *Halichoeres maculipinna* and 165 h on *H. garnoti*.

The diets of *Halichoeres maculipinna* and most common of its congeners with which it shared space (*H. bivittatus*) were analyzed. Space-sharing *H. maculipinna* and *H. bivittatus* were speared and the relative abundance of different items in the stomach of each was determined. The items in each stomach were subjectively ranked in abundance and assigned a value from 5 (for the most abundant) to 1. The values for each item from all fish were then summed and a cumulative rank assigned to each item according to its total score.

Results

Halichoeres maculipinna. Some large, sexually inactive TP males fed throughout areas that overlapped extensively with those of other large TP males; others did not share their feeding areas with other large TP males (Fig. 1). Large TP males defended their feeding areas against neighbours of equal size whose areas did not overlap with theirs. When the areas of two large males overlapped the larger fish aggressively dominated (i.e., chased and displaced) the smaller one. The outer borders of the feeding ranges of small TP males usually coincided with those of the large males (Fig. 1). Small and medium TP males defended their feeding ranges against equal sized TP males living in the feeding area of the same or neighbouring large males.

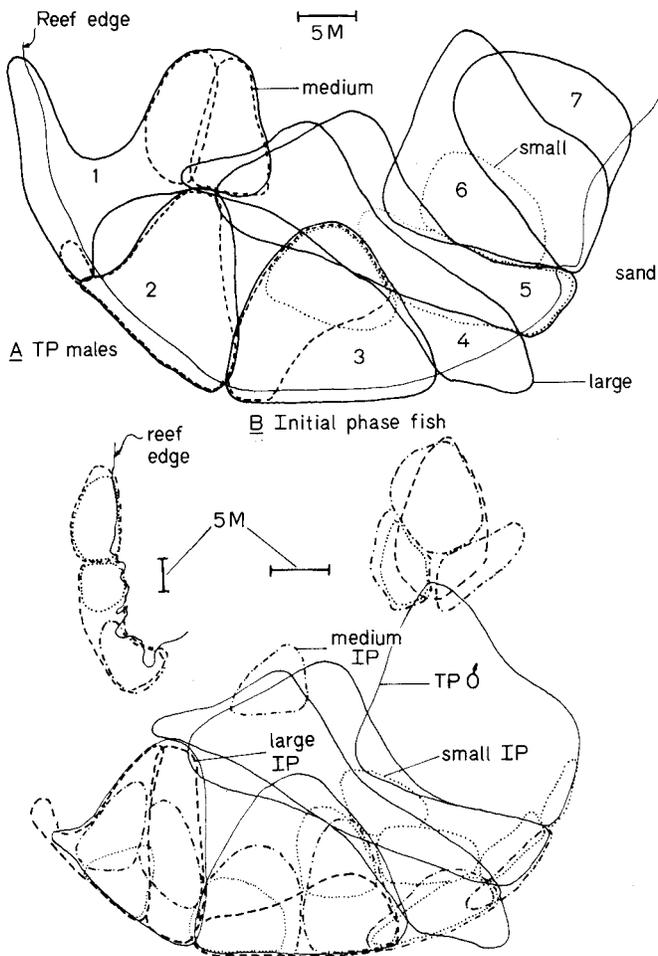


Fig. 1. *Halichoeres maculipinna*. Feeding areas. Each outline represents ≥ 30 min observation on each of ≥ 3 d. Not all IP fish resident in the study area are shown in Fig. 1B

When sexually active (see below), large TP males restricted their activities to the immediate vicinity of their spawning areas. They vigorously defended those areas against TP males of all sizes, including small TP males that normally fed there at other times. Large TP males whose feeding areas overlapped extensively occupied separate spawning areas (Fig. 2).

IP fish typically moved about singly, although small transient groups of 2 to 3 fish formed occasionally. Of 104 IP fish that were examined in four surveys on the study reefs, 80.8% were moving about and feeding by themselves (i.e., there were no other IP fish within 1 m of them), and 15.4% were moving and feeding within 1 m of an IP conspecific, but the two fish were acting independently. Only 3.8% were moving and feeding jointly with a conspecific; but they continued to do so for less than 30 s after the observation began. The feeding areas of any two IP fish typically overlapped if there was a noticeable (to the observer) difference in their sizes (Fig. 1-b). The larger of the two dominated the smaller in any of the low intensity interactions that determined priority of access to food. IP fish of all sizes defended their feeding areas against equal sized conspecifics and the feeding areas of equal sized fish usually did not overlap (Fig. 1-b). The feeding areas of some IP fish were inside the feeding areas of TP males, while others lived outside TP males' areas. When IP fish lived inside TP males' territories the outer boundaries of their feeding areas tended to coincide with the outer boundary of the feeding area of the large TP male in whose area they lived (Fig. 1-b).

On the study reefs, and other similar areas nearby, *Halichoeres maculipinna* was outnumbered by the bottom-feeding congener *H. bivittatus* at ratios of 1.2-4.2:1 ($n = 6$ sites, 33-335 fish per site). No territorial interactions between these two species were observed. There were no significant differences in the diets of small and large IP *H. maculipinna* (Table 1). While the diets of *H. bivittatus* and *H. maculipinna* were marginally different, they were very similar, as many items were well represented in the stomachs of both species (Table 1).

Sexually inactive males usually displayed little of their TP colors when moving about their feeding areas, but occasionally exhibited them without an obvious stimulus. On each of 16 medium and large TP males, 50 observations were made at 10 s intervals. These males displayed "Stage 0" colors on a mean of 44.1 (SE = 1.2) of the observations, "Stage 1" on a mean of 5.3 (SE = 1.1) observations, and "Stage 2" on a mean of 0.7 (SE = 0.2) observations. "Stage 2" colors were only developed by these males when they were interacting with IP fish. When chasing IP fish or displacing them from food TP males exhibited various colors, but tended to have moder-

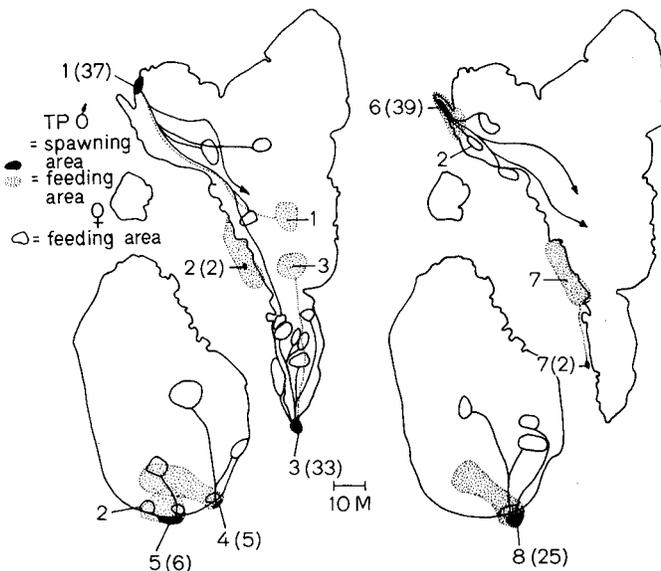


Fig. 2. *Halichoeres maculipinna*. Feeding and spawning sites. TP males; a (b) next to each spawning site = identification number of male (number of spawnings by that male in that area). Females: line with arrow = path taken by female that was lost to sight in surf; 2 next to a female feeding area indicates 2 females used that area. A line connects a female's spawning and feeding areas

Table 1. Ranked abundance of items found in the stomachs of two *Halichoeres* species

Item	Abundance Rank ¹			
	<i>H. maculipinna</i>		<i>H. bivittatus</i>	
	Small fish	Large fish	Total	
Amphipods	2	1	1	6
Polychaetes	1	3	2	3
Crustacean fragments ²	3	2	3	1
Shrimp	4	6	4	4
Gastropods	6	4	5	2
Eggs	7	5	6	7
Copepods	5	7	7	—
Unidentifiable	— ³	8	8	5
Echinoids	—	—	—	8
Crabs	—	—	—	8
<i>n</i> fish	14	15	29	19
Size range (mm SL).	43–60	62–96	43–96	53–99

¹ 1 = most abundant item; see Materials and Methods for calculation

² Appeared to be amphipod and shrimp fragments

³ Not present

Spearman rank correlation coefficient: small and large *H. maculipinna* $r_s = 0.864$, $P < 0.01$; *H. maculipinna* and *H. bivittatus* $r_s = 0.636$, $0.05 < P < 0.10$

Table 2 *Halichoeres maculipinna*. Color exhibited by aggressive terminal phase males

Receiver of TP male's aggression	Color stage ¹ fish exhibits at start of interaction	Number of interactions observed							
		During spawning periods				Outside spawning periods			
		Color stage ¹ fish changes to during interaction							
		0	1	2	3	0	1	2	3
Conspecific Terminal Phase Male	0	95/21 ²	—	—	—	40/6	—	—	—
	1	14/9	45/7	—	—	2/—	—	—	—
	2	3/2	6/6	1/—	—	—	—	—	—
	3	1/—	43/11	4/—	—	—	—	—	—
Initial Phase Conspecific	0	—/30	—	—	—	—/8	—	—	—
	1	—/6	—/20	—	—	—	—/5	—	—
	2	—/8	—/5	—/5	—	—	—	—/34	—
	3	—/11	—/42	—/32	—/5	—	—	—	—/12

¹ 0 to 3 represents increasing intensity of development of TP colors

² a/b : a = interactions in which both participants were aggressive; b = interactions in which only one TP male was aggressive. Observations were made on 34 TP males

ately intensely developed TP colors (Table 2). Males often showed little or no TP colors when they attacked and chased IP fish during spawning periods, and any colors showing at the start of the attack tended to fade during the attack (Table 2).

Both sexually active and, especially, sexually inactive males showed very little tendency to develop TP colors intensely when attacking or chasing other TP males (Table 2). Males tended to lose their TP colors during

the course of the attack on or fight with another TP male. Defeated or submissive males invariably lost whatever TP colors they had at the start of an encounter with a more dominant TP male.

TP male colors were noted during three parts of the sequence of events that led up to spawning: (1) when the male approached a female and moved rapidly round her while spreading his median fins, particularly the colored anterior part of the dorsal fin; (2) when the male

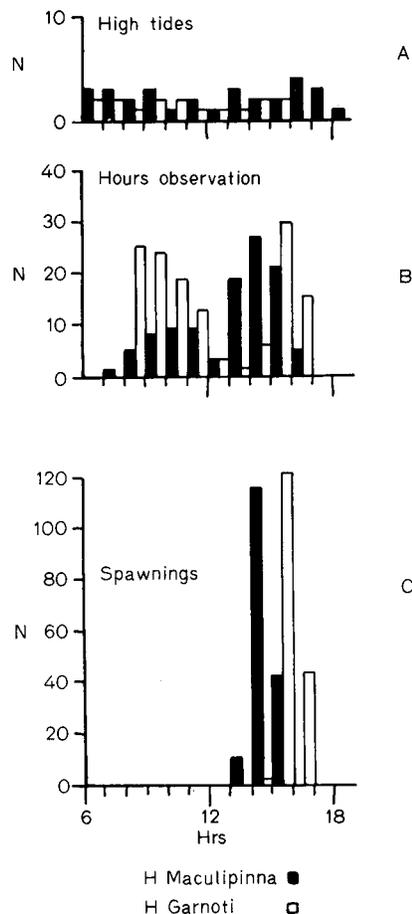


Fig. 3. Diel spawning activity of two *Halichoeres* species. (A) Number of days on which high tide occurred during a particular hour of day when spawning was observed in the afternoon. (B) Number of hours observation during each hour of the day. (C) Number of spawnings observed during each hour of the day

looped (rushed rapidly up and down in the water column in a manner similar to the spawning act); and (3) as the male and female prepared to take off in the spawning rush. Males had "Stage 3" colors in 83.5% of 659 approaches, "Stage 2" in 11.6% and "Stage 1" in 4.9% of them. They invariably had "Stage 3" colors when looping ($n = 204$) and preparing to spawn ($n = 221$).

Finally, small TP males that were resident in the feeding areas of large TP males were occasionally seen making courtship approaches to IP fish. The TP colors of those small males were not as intensely developed as those of similarly behaving large TP males.

Spawning by *Halichoeres maculipinna* occurred only between 13:00 and 15:30 hrs (Fig. 3). There was no evident correlation between the timing of spawning activity and the tides, as spawnings were observed on days when the high tide occurred between 06:00 and 18:00 hrs (Fig. 3). Spawning also occurred on 4 d when there was no high tide during daylight hours.

All spawnings observed by myself and by Warner and Robertson (1978) took place at the outer edges of reefs.

Seven of the 10 large TP males that were studied in detail had spawning areas within their feeding areas (males 4, 5, 6, 8 in Fig. 2, whose spawning areas are shown; and males 1, 6, and 7 in Fig. 1, whose spawning areas are not shown). The others migrated to spawning areas as far as 75 m from their feeding areas (males 1, 2, and 7 in Fig. 2). The spawning area of each of those 10 TP males was at the outer edge of the reef. The three TP males which migrated away from their feeding areas established spawning territories in areas in which no other TP males had feeding areas and there were no *Halichoeres maculipinna* feeding areas at all in the spawning area of one of those three. The males that migrated had feeding areas located either near the center of the reef or where a larger male had a combined feeding/spawning area at the reef edge. Nonmigratory males had feeding areas that incorporated a section of reef edge that was not occupied by a larger fish.

Only large TP males were observed to spawn. During spawning periods, some small TP males were seen actively courting females (and developing TP colors while doing so), but others were sexually inactive. The number of spawnings per day by a large TP male ranged from 5 to 20 (mean = 13; $n = 9$ fish, 15 d). Small males interfered as streakers (Warner and Robertson, 1978) in 4.1% of a total of 369 pair spawnings by large TP males. I saw no group spawning by IP males in the present study area or clustering which Warner and Robertson (1978) observed to lead into group spawning on large reefs with large populations.

Twenty-five females were followed for 20 to 90 min after they had spawned (with six TP males). Each travelled from the spawning site to a feeding area and fed quietly there for the rest of the observation period. Another three females were lost to sight in surf after they had travelled well away from the spawning site (Fig. 2). Four of those 25 females were tagged individuals, and each went to its normal feeding area after spawning. The feeding areas of five females were in the feeding area of the TP male with which they spawned. The other 23 females had feeding areas up to 60 m outside the feeding area of the TP male with which they spawned (Fig. 2). *Halichoeres garnoti*. Large TP males roamed over large feeding areas when sexually inactive (Figs. 4a and 5). In study area No. 3, the feeding areas of five such males overlapped extensively, except around the spawning area of each (Fig. 5c). The feeding areas of these TP males overlapped completely with those of smaller TP males (Figs. 4a and 5). There were extensive overlaps in the feeding areas of those smaller males, regardless of the size of the fish (Figs. 4a and 5b). The large TP males were generally tolerant of smaller resident TP males, occasionally displacing them from food or slowly chasing them for short distances. The borders of the feeding areas of TP males that shared substrate usually did not coincide (Fig. 4).

During daily periods of sexual activity, each large TP male restricted its movements to the vicinity of its spawning site(s). These males also became obviously territorial at such times, vigorously defending the vicinity

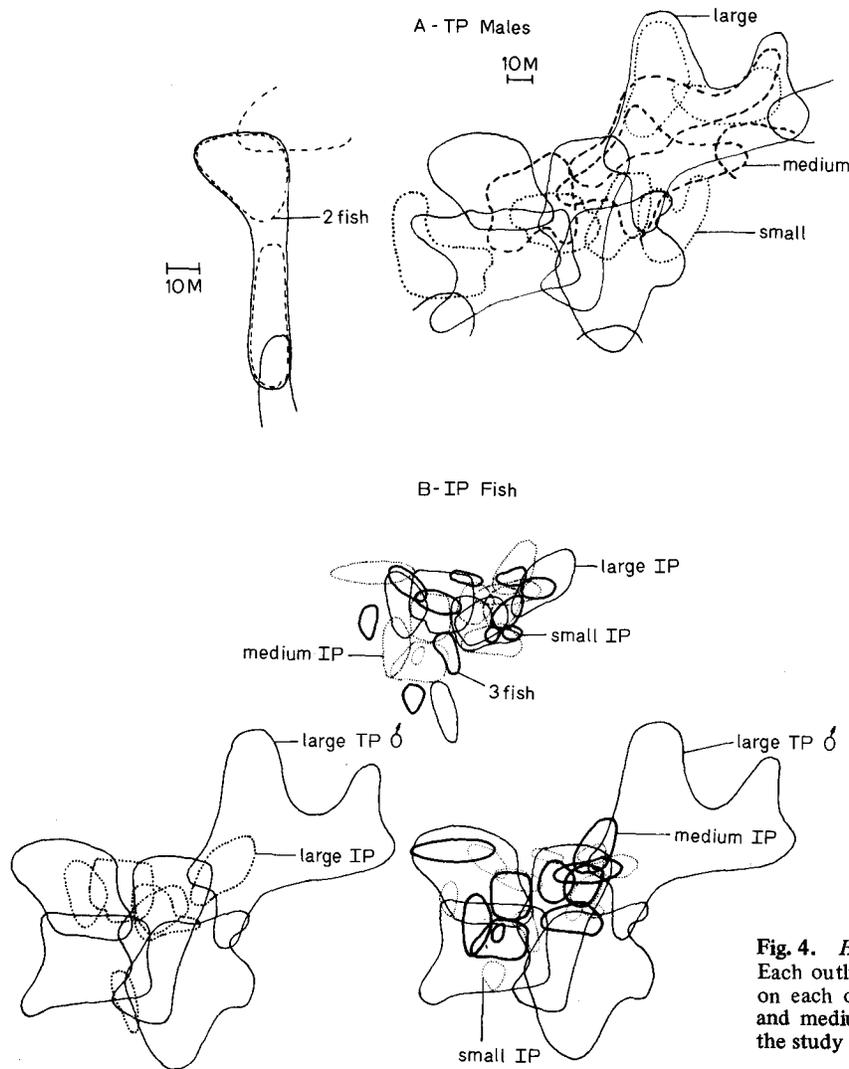


Fig. 4. *Halichoeres garnoti*. Feeding areas. Each outline represents ≥ 30 min observation on each of ≥ 3 d. Not all IP fish and small and medium TP males that were resident in the study area are shown

of their spawning areas against each other and against smaller TP males, including those that were resident in those areas at other times.

The feeding areas of IP fish overlapped extensively and haphazardly with those of IP conspecifics of all sizes and of TP males (Figs. 4 and 5). I saw no tendency towards IP territoriality such as was evident in *Halichoeres maculipinna*. Agonistic interactions between IP *H. garnoti* consisted of one fish chasing a smaller fish away from a food source.

Sexually inactive males usually showed little or nothing of their TP colors when roaming about and feeding. Occasionally they brightened to Stage 1 or Stage 2 without any apparent stimulus. They invariably lost whatever TP colors they had when they approached the edges of their feeding areas. When rushing at and chasing IP fish those males displayed a range of colors, including moderately intense TP colors (Table 3). Sexually active males displayed TP colors at the start of such interactions more often than did sexually inactive males. During the

course of those interactions TP colors of sexually active males often faded (Table 3).

Sexually inactive males exhibited a range of colors when being aggressive to other TP males, though they usually showed little TP coloration and did not develop it to maximum intensity. Also, during the course of the interaction they often faded whatever TP colors they had initially (Table 3). Sexually active males normally displayed medium- to high-intensity TP colors initially when attacking other TP males but often faded during the interaction (Table 3). This fading occurred when only one TP male was being aggressive as well as when two were mutually aggressive. Defeated or submissive males invariably lost any TP colors they might have had at the start of an interaction.

Sexually active males displayed Stage 2 and Stage 3 colors more or less continuously as they cruised rapidly and continuously 1 to 1.5 m above the substrate in the vicinity of their spawning sites. The courtship and spawning sequence is essentially the same in *Halichoeres*

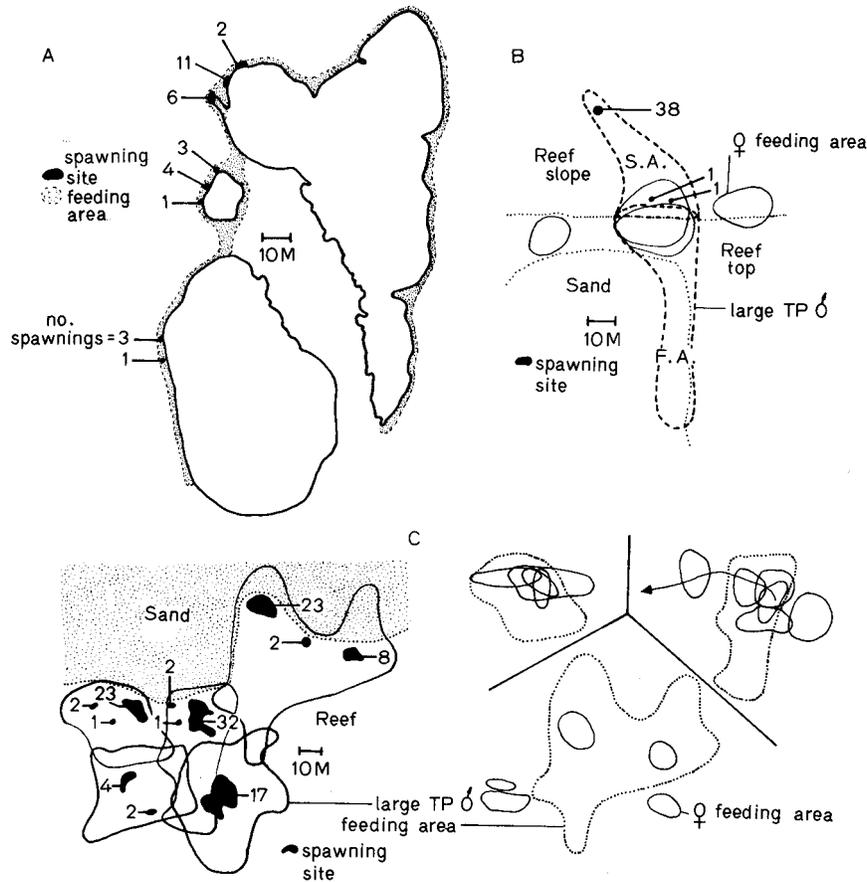


Fig. 5. *Halichoeres garnoti*. Feeding and spawning sites. The location of large TP males' spawning sites in relation to their feeding areas and of each female's feeding area in relation to the feeding area of the male that she spawned with are shown (A) Study area 1. (B) Study area 2: SA = area in which the male moved during the spawning period, FA = same male's feeding area. (C) Study area 3: line with arrow refers to female that left the study area after spawning

Table 3. *Halichoeres garnoti*. Color exhibited by aggressive terminal phase males

Receiver of TP male's aggression	Color stage ¹ fish exhibits at start of interaction	Number of interactions observed							
		During spawning periods				Outside spawning periods			
		Color stage ¹ fish changes to during interaction							
		0	1	2	3	0	1	2	3
Conspecific terminal phase male	0	-/3 ²	-	-	-	-/10	-	-	-
	1	-	2/-	-	-	-	-/25	-	-
	2	-	-	4/2	-	-/1	-/4	-/7	-
	3	2/7	-/6	2/5	-/13	-	-	-	-
Initial phase conspecific	0	-/1	-	-	-	-/13	-	-	-
	1	-	-/4	-	-	-	-/8	-	-
	2	-/1	-/1	-/1	-	-	-	-/30	-
	3	-/1	-/6	-	-/8	-	-	-	-

¹ See 'Materials and Methods' for description of color stages; 0 to 3 represents increasing intensity of development of TP colors

² a/b : a = interactions in which both participants were being aggressive; b = interactions in which only one TP male was being aggressive

Observations were made on 7 TP males

garnoti as in *H. maculipinna*. The colors of males of *H. garnoti* were noted at the same three parts of the courtship and spawning sequence as for *H. maculipinna* males. They showed Stage 3 colors during 80% of 275 courtship approaches and Stage 2 in the remainder. They invariably developed Stage 3 colors when looping ($n = 184$) and at the start of spawning rushes ($n = 166$).

The peak of spawning activity by *Halichoeres garnoti* occurred about 1 h later than that of *H. maculipinna*, and spawnings occurred only between 14:00 and 17:00 hrs, regardless of the time of the high tide (Fig. 3).

The spatial distribution of spawning sites of large males relative to their feeding areas was different in each study area. In study area No. 1, the male spawned inside his feeding area at three different sites scattered along the lee side of the double patch reef (Fig. 5a). In study area No. 2, the male had a highly circumscribed spawning area that was well outside his feeding area (Fig. 5b). No TP *Halichoeres garnoti* had a feeding area at that male's spawning area. Each of the five larger males in study area No. 3 spawned within his feeding area (Fig. 5). Each of the three males whose feeding area included a section of the deep edge of the reef had a spawning site very near that edge of reef. The other two males, which had feeding areas in the center of the reef, spawned near the center of their respective feeding areas (Fig. 5c). Each of these five males spawned in a restricted part of its feeding area rather than throughout that area (Fig. 5). The number of spawnings per day by a large TP male ranged from 2 to 17 (mean = 9.1; $n = 6$ fish, 16 d). I saw no signs of attempted interference in the pair spawnings of large males by any other males. Medium and small TP males were not seen to spawn or be sexually active.

Each of 20 females, including six tagged fish, were followed for 30 to 90 min after they had spawned with four large males. Twelve of those females had feeding areas that were inside the feeding area of the TP male with whom they spawned. The feeding areas of another seven females were from 5 to 20 m outside the feeding area of the male with which they spawned, while one female travelled over 150 m away from the spawning site (Fig. 5b, c).

Discussion

The Daily Timing of Spawning

Tropical reef fishes that have planktonic eggs, including labrids and scarids, often have distinct tidal rhythms of spawning activity (Randall, 1961; Reinboth, 1973; Choat and Robertson, 1975; Johannes, 1978). In Panama, neither *Halichoeres maculipinna* and *H. garnoti* nor other sympatric labroids (Warner and Robertson, 1978; Robertson and Warner, 1978) have such rhythms. Robertson and Hoffman (1977) attributed this to a lack of strong, predictable tidal currents in the study area. The tidal range is small in San Blas and often there are surface currents generated by wind. In Florida, *H.*

maculipinna, *H. garnoti*, and other wrasses do have a tidal spawning rhythm (Thresher, 1979). The maximum tidal range at Florida is almost twice that at the San Blas site (U.S. Department of Commerce Tide Tables) and tidal currents are strong and predictable at the Florida site (A. A. Myrberg, Jr., personal communication). Thus the tides may determine the timing of spawning by a particular species at one site but not elsewhere in its geographic range.

Intraspecific Spatial Relations of the Two Species of *Halichoeres*

Warner and Robertson (1978) saw no indication of strong permanent territoriality by TP males of *Halichoeres maculipinna* and noted movements of TP males to temporary spawning territories at the edges of reefs. I have now found that some males are permanently territorial towards one another and have spawning areas within those territories. During spawning periods, large TP males are strongly territorial, and attempt to exclude all TP males from their spawning areas, which are much smaller than their feeding areas. At Florida, large TP males are permanently territorial towards each other and spawn within their territories (Thresher, 1979). They share their territories with smaller subordinate TP males which also defend the shared area against neighboring TP males of all sizes. Large TP males evidently do not exclude smaller resident TP males from their territories during spawning periods. Thresher indicated that subordinate TP males which live in the territory of the same large male are not territorial towards each other. In Panama, such subordinate males share feeding areas if they are of dissimilar sizes but are mutually territorial if they are of equal sizes.

The spatial relations of IP fish are quite different in Panama and Florida. The "herds" of up to 40 nonterritorial fish that move and feed as groups in Florida are not seen in Panama. In Panama, relations between IP fish resemble those between TP males; dissimilarly sized fish share feeding areas while equal-sized fish are mutually territorial. In addition, the borders of the feeding areas of IP fish often coincide with the borders of large TP males' territories. Thresher's (1979) data (Fig. 1, p 164) show IP herds moving between the territories of adjacent large TP males in Florida.

The few observations made by Warner and Robertson (1978) on *Halichoeres garnoti* in Panama did not indicate strong permanent territoriality by members of either color phase. My new observations show that large TP males are overtly territorial when sexually active. They also seem to be weakly territorial towards each other outside spawning periods because they do little feeding in each others' spawning areas then. In Florida, TP males have very large, broadly overlapping home ranges. They are nonterritorial, even when spawning, and spawn anywhere in their home ranges (Thresher, 1979). Perhaps this lack of territoriality reflects an inability of males to defend very large areas economically, while the more dis-

crete spawning areas that are seen in Panama are readily defensible.

In both Panama and Florida, the feeding areas of IP fish of various sizes overlap haphazardly and are not defended. Similarly the feeding areas of large TP males overlap those of smaller TP males and IP fish in a disorganized manner.

The territoriality of large TP males of both *Halichoeres* species most probably is related to mate sequestering. Such a function cannot be ascribed to the territoriality of IP *H. maculipinna* in Panama. Many reef fishes have significant overlaps in their diets (Hiatt and Strasburg, 1960; Randall, 1967, Hobson, 1974). It is common to find such species defending feeding territories against conspecifics and a broad range of other fishes that eat the same general types of foods but do not necessarily eat the same amounts of the same things as the territory owners (Low, 1971; Robertson *et al.*, 1976; Ebersole, 1977; Sale, 1977; Thresher, 1977; Robertson *et al.*, 1979; Mahoney, 1981). Therefore, it is highly unlikely that the territoriality of IP *H. maculipinna* serves a food defense function because they share feeding areas with fishes that commonly eat many of the same foods - smaller conspecifics and *H. bivittatus*.

Various workers have observed and speculated on the significance of intraspecific territoriality of IP individuals of other labroids (Buckman and Odgen, 1973; Robertson 1974; Pottle and Green, 1979b). The latter two sets of authors suggested that defense of food is not the primary function of female territoriality in their study species. In *Labroides dimidiatus*, female territoriality is evidently functionally related to both the process of sex change and defense of food. A female rises through the ranks of her social group, to eventually change sex. Females of a group resist the efforts of strange females to join the group, probably because they represent a threat to the resident females' position in the hierarchy and may affect resident females' ability ultimately to change sex (Robertson, 1974; Robertson and Hoffman, 1977). The parrotfish that Buckman and Odgen (1973) studied, *Scarus iserti* (= *croicensis*, Randall and Nelson, 1979) is protogynous (Robertson and Warner, 1978). No published information appears to exist on the presence or absence of sex change in the wrasse that Pottle and Green (1979b) studied. The territoriality of females of those two species and of IP *Halichoeres maculipinna* may be functionally related to the process of sex change in the general manner it is in *L. dimidiatus* (see also Buckman and Odgen, 1973). However, IP *H. maculipinna* are not territorial in Florida, and females of *H. garnoti* are not territorial in either Panama or Florida. Investigation of the life history pathways that IP fish follow to become large TP males and of ecological factors that favor or preclude territoriality may show why IP fish are not invariably territorial. Variation in the population density of IP *H. maculipinna* may determine whether territories can be economically defended in only certain areas. Differences in feeding strategies and predator pressures may favor herd formation by IP *H. maculipinna* in some areas, while at other sites they can move about indepen-

dently, and are then capable of being territorial. However, the densities of IP *H. garnoti* in Panama did not appear to be either too low or too high for territories to be economically defended and those fishes do not form "herds". Yet they were nonterritorial.

Variability in Mating System Structure in the Two *Halichoeres* Species

Thresher (1979) maintains that *Halichoeres maculipinna* in Florida, has a mating system of the same structure as that of the labrid *Labroides dimidiatus*, although quantitative data are lacking. *L. dimidiatus* has a "strictly harem" mating system (Robertson and Hoffman, 1977) because a male invariably spawns inside his permanent territory, and over 95% of his spawnings ($n > 400$ spawnings, 16 males) are with females that are resident in his territory (Robertson, 1974). *H. maculipinna* does not have a strictly harem mating system in Panama; only 19% of the females that the subject TP males spawned with were resident in the respective male's territories. The TP males have spawning territories at the edges of reefs, at locations that sometimes are well away from their feeding areas. Many fish in Panama, live on the very shallow tops of reefs. They migrate to spawn at the edges of reefs, where eggs probably have the best chance of being rapidly carried away from reef-based predators (Randall and Randall, 1963; Warner *et al.*, 1975). The Florida site is a section of a large area of deeper reef that is subject to distinct tidal currents. Females there may typically spawn with the TP male in whose territory they live because locations that are suitable for spawning sites are abundant throughout the general area. Thus there are distinct differences in the structure of mating system of *H. maculipinna* in San Blas and Florida.

Warner and Robertson (1978) suggested that *Halichoeres garnoti* might have a harem mating system, because it shared certain population characteristics with known harem species. Although quantitative data are lacking, *H. garnoti* does not appear to have a harem mating system in Florida (Thresher, 1979). The data presented here show that it does not have such a mating system in Panama; 40% of the females that the subject males spawned with were not resident in those male's feeding areas. Females often left the feeding area of one large male and mated elsewhere with another male, and their feeding areas often overlapped those of two large males.

Mating Systems and the Spatial Distributions of Spawning and Feeding Sites

Because females of many labroid species regularly migrate away from feeding areas that they share with large and small males to specific spawning grounds, the selection of a high quality site to release eggs must be of great importance. The relative distributions of spawning and feeding sites may determine (1) whether a female will

spawn with a large male with which she shares a feeding area rather than another large male, and (2) the ability of large males to monopolize mates at the expense of small males.

Both *Halichoeres maculipinna* and *H. garnoti* have spawning migrations in Panama, although such behavior is less pronounced in *H. garnoti*. This difference between the two species is the result of their feeding in different habitats; most *H. maculipinna* feed away from preferred spawning sites, while *H. garnoti* feed where the spawning sites are found. As a result, TP males of *H. maculipinna* are more likely to mate with females that live outside their feeding areas than are males of *H. garnoti*. In Florida the two species share a habitat that contains both feeding and spawning sites, and females of *H. maculipinna*, at least, apparently have a strong tendency to spawn with the TP male with which they share a feeding area.

Males of *Labroides dimidiatus* may be able to maintain high fidelity in their harem females by controlling a female's access to food, which appears to be a limiting resource. When large males lack this option because food either is not limiting or not controllable, nonharem mating systems may develop (Robertson, 1974; Robertson and Hoffman, 1977). Thresher (1979) attributed harem formation by *Halichoeres maculipinna* in Florida to a different mechanism: when females are sedentary a male may be able to form a harem merely by defending a group of them against other males (female defense polygyny - Emlen and Oring, 1977).

When feeding and spawning areas coincide, one strong factor that favors female mobility is eliminated and the potential for such female-defense exists. Sometimes this might be the basis for harem formation. First, the known harem species characteristically feed in habitats where spawning sites occur (Robertson, 1974; Warner and Robertson, 1978). Further, harem formation appears common in those parts of the populations of various Caribbean scarids that feed around the edges of reefs, i.e., where spawning sites also occur (see Robertson and Warner, 1978).

However, one important labroid characteristic, sex change, requires that a general application of a "female defense polygyny" hypothesis to harem formation in labroid fishes be treated with caution. Robertson and Hoffman (1977) argued that males of *Labroides dimidiatus* could penalize female infidelity by being able to affect a female's chances of changing sex, and thereby ultimately achieving maximum spawning success, because a female expelled from one group would have difficulty joining another. A male may be able to control females in this manner regardless of whether he can control access to limiting resources such as food. To fully understand harem formation as a male mating strategy we need to determine (a) the life history paths females can take to ultimately change sex, because the existence of more than one path may affect whether a male can penalize infidelity, and (b) the spawning strategies open to males, as sometimes they may be obliged to form harems in circumstances in which female fidelity is low. If a species

feeds in habitats where only very low-quality spawning sites exist, the disadvantage of not making a spawning migration could be prohibitive. In such a situation, harem female fidelity could be reduced or harem formation precluded. Perhaps this is the reason that males of *Halichoeres maculipinna* do not form high fidelity harems in Panama, even if they can control the ability of females to change sex.

The greatest amounts of interference spawning by small males occur when they mass in such numbers that large males cannot exclude them from spawning sites (Warner and Robertson, 1978). Numerous females must visit a large male's spawning site for each small male to be adequately rewarded for such behavior. This condition is most likely to be met in species that have large dense populations and many females per large male (Warner *et al.*, 1975; Warner and Robertson, 1978; Warner and Hoffman, 1980). Small males are absent in *Halichoeres garnoti* but constitute about 15% of the IP fish in *H. maculipinna* in Panama (Warner and Robertson, 1978). On large reefs, large males of the wrasse *Thalassoma bifasciatum* typically spawn about 40 times a day (Warner *et al.*, 1975). Compared to this, large males of *H. garnoti* have a low spawning rate, which can be attributed to a combination of a weakly biased sex ratio, a low population density (Warner and Robertson, 1978), and a lack of extensive spawning migrations to circumscribed spawning grounds. Low spawning rates of large males rules out massed activity as a rewarding spawning strategy for small males in this species. For a male that spawns at a low rate, each spawning has a higher relative value than it does to a male with high absolute success. More strenuous efforts to screen out small males using subterfuge strategies would be advantageous to a male with a low spawning rate and he would have more time to do this than would a male that spawned more frequently. However, it is difficult to understand why subterfuge interference should not offer a small measure of success to small *H. garnoti* males and enable them to persist in the species. Because *H. garnoti* is not organized in small harem groups, a large male would have difficulty in detecting and penalizing small males to the degree that a large male *Labroides dimidiatus* conceivably could. Further, some Caribbean parrotfishes appear to have mating systems that are more similar to that of *L. dimidiatus* than *H. garnoti*, and yet the populations of those parrotfishes do contain a few small males (Robertson and Warner, 1978).

Large males of *Halichoeres maculipinna* in Panama suffer a small amount of interference from small males. In part this may be due to the low spawning rate of large males. In addition, the restriction of a large male's spawning to a small discrete area that females visit a few at a time may make it easier for him to screen out small males attempting subterfuge interference than it would be if he roamed over a large area that contained many ripe and unripe females as well as resident small males. In Florida, large males roam in this manner during spawning periods and, as Thresher (1979) pointed out, small male interference is additionally facilitated by the

formation of herds of IP fish and the occurrence of spawnings in the immediate vicinity of herds. IP male interference in TP males' spawnings is very common in Florida.

Thus, spawning migrations may facilitate mate monopolization by large males when few females visit each male but lead to high spawning success for small males when a large male is visited by many females. There is no reason why we should not see significant differences in small male spawning success in two species with identical population densities if both make spawning migrations, but one moves to more localized spawning grounds than the other. If, as Johannes (1978) indicates, extensive spawning migrations are more prevalent among larger species of reef fishes, then small male success should be less dependent on population density *per se* in the larger migratory species.

Predictability of Large Males' Spawnings and Success of Subterfuge Interference by Small Males

It has been suggested that the success of large male labrids in preventing small males from interfering in their pair spawnings may be an important ultimate determinant of whether or not primary males exist in a species (Robertson and Choat, 1974; Warner *et al.*, 1975; Warner and Hoffman, 1980). Thresher (1979) presented an alternative to this mate monopolization hypothesis to account for the presence of primary males in *Halichoeres maculipinna* and their absence in *H. garnoti* and the wrasse *Clepticus parrae*. He argued that the ability of a small male to predict the occurrence of a large male's spawning determines its ability to join that spawning: in Florida, pair spawnings by TP males of *H. maculipinna* occur next to IP herds that contain both sexes; therefore, small males can predict their occurrence. In *H. garnoti*, a combination of the lack of herd formation and the tendency of TP males to spawn anywhere throughout their large feeding areas makes such prediction too difficult. This latter argument was also extended to *C. parrae*.

My data do not support the spawning predictability hypothesis. First, TP males of *Halichoeres garnoti* do have discrete, regularly used spawning sites in Panama, and, although males of *Clepticus parrae* lack spawning territories, they do have a discrete spawning ground at Robertson and Hoffman's (1977) study area in Panama. Second, even if TP males do not spawn at predictable sites there are a number of simple cues that small males could potentially use, either singly or in combination, to predict the occurrence of spawnings: (1) Spawnings occur at a particular time of day or stage of the tide. (2) A male may be able to detect a gravid female well before courtship begins. Such a female may (inadvertently?) provide visual cues (from her swollen belly and genital region) or chemical cues (from ovarian secretions?). Both IP and TP males of various species of labroids, including *Halichoeres maculipinna*, often closely follow and inspect the belly and vent region of IP conspecifics

during spawning periods (Randall and Randall, 1963; Warner and Robertson, 1978; personal observation). (3) Courtship by TP males is distinctive and conspicuous and there is a time lag between its initiation and the spawning. This lag can be on the order of minutes in both *C. parrae* (Robertson and Hoffman, 1977) and *H. garnoti* (personal observation). (4) Gravid females, including those of *H. garnoti*, often behave in a distinctive manner both before and during courtship by a TP male (Robertson and Hoffman, 1977, personal observation). (5) The movement that the female and large male make together up into the water column to release gametes is quite slow in some species, e.g., *C. parrae* (Robertson and Hoffman, 1977) and the scarid *Cryptotomus roseus* (personal observation).

The Functional Significance of Sexual Dichromatism in Labroid Fishes

Sexual dimorphism in characteristics such as color is often attributed to the effects of sexual selection, which can operate through either intersexual or intrasexual interactions (Darwin, 1871). It has been suggested that sexual dichromatism has developed in labroids in which males compete for females during spawning periods because the display of a distinctive, conspicuous, color pattern enhances the ability of a male to attract a conspecific female's attention and be chosen by her as a mate. Such attraction is particularly important when numerous individuals of different species congregate simultaneously at a common spawning ground, because a male competes with males of both his own and different species for a female's attention (Choat and Robertson, 1975; Robertson and Hoffman, 1977). For example, I have seen TP males of 10 wrasses and parrotfishes courting at the same time in a 500 m² area of reef in San Blas, and as many as 700 sexually active individuals of 28 dichromatic wrasses and parrotfishes at one time in a 500 m² area of reef edge at Palau (western Pacific). Even though females select specific types of sites to spawn at, and males that have fought for and won those sites have high spawning rates because they hold those sites, TP colors may often influence female mate choice because a spawning ground contains a number of good sites and the males that hold them compete to attract females to them.

The labroid TP pattern often comprises two parts, one of simple, high contrast color elements that allows a diver to identify the fish at relative large distances, and another of detailed, subdued colors that a diver can perceive fully only when very close to the fish (less than 1 m in some species). I suggest that the former part of the pattern functions to attract a female's attention at a distance and identify a conspecific male to her. The latter part, or both, has a role in allowing the female to distinguish a sexually active TP male that is in control of a spawning territory (if such territories exist), and to determine the quality of a male that she has approached. There may be systematic variation in the degree to which

males develop TP colors, because larger, more dominant males seem to be those that display the brightest coloration. I also suggest that females choose conspicuously colored, actively moving and displaying males because they reduce the risk of predation on the female by (a) diverting predators' attention away from her, (b) inducing predator attacks before the female is at the most vulnerable point of the spawning sequence, and (c) inducing predator activity that indicates their numbers, presence and location to the female.

If the hypothesis is correct that the color dimorphism is the result of male-female interactions rather than male-male interactions, then species in which "typically" there is no continuing free competition for mates at spawning grounds should be the least dichromatic species. In addition, if TP males can change color, the TP pattern should be more intensely displayed during sexual interactions than during agonistic interactions, especially those between TP males, because sexual tendencies should be more strongly expressed by a TP male during interaction with an IP fish than during interactions with a TP fish.

Various observations support this hypothesis. First, *Labroides dimidiatus*, which is sexually monochromatic, has a harem mating system in Australia (see above). In Aldabra in the western Indian Ocean, the same apparently holds true; all of 39 spawnings by five males that I saw there were intraharem. Limited data from the monochromatic congener *L. bicolor* indicate that it is harem at Aldabra; all but one of 36 spawnings by four males were intraharem. Further, the monochromatic Caribbean labrid *Bodianus rufus* has a harem mating system in Panama: 95% of 203 pair spawnings by four males were intraharem (S. Hoffman, personal communication).

Second, TP males of many dichromatic labroids do compete for females that migrate to specific spawning areas. These include three wrasses and four parrotfishes from the Caribbean (Barlow, 1975; Warner and Robertson 1978; Robertson and Warner, 1978), and 16 dichromatic wrasses and 12 dichromatic parrotfishes at Palau in the western Pacific (Robertson and Foster, in preparation). One monochromatic or nearly monochromatic scarid, *Scarus niger*, also made such migrations at the Palau site. Choat and Robertson (1975) suggested that elsewhere this species was harem; how much variation there is in the structure of its mating system in different sites is not known. Five dichromatic labrids and one dichromatic scarid from Japan appear not to have strictly harem mating systems (Meyer, 1977; Nakazono, 1979; Yogo *et al.*, 1980); the data are inadequate to determine if *Duymaeria flagellifera* may be an exception. One dichromatic north-temperate wrasse lacks a harem mating system at one site (Pottle and Green, 1979a).

Third, Robertson and Hoffman (1977) observed that TP males of two species of wrasses tend to lose their TP colors during fights with other males.

Thresher (1979) presented four criticisms of this intersexual selection hypothesis:

(1) Sexual monochromatism could have been selected for in *Labroides dimidiatus* despite counterselection for dichromatism through male-male interactions: this species is an obligate cleaner that removes ectoparasites from other fishes. Males might be placed at a disadvantage in gaining food if they displayed a color pattern different from that of females, because of problems with host recognition and preferences. Although Robertson (1974) also proposed this idea, Robertson and Hoffman (1977) favoured the intersexual-selection hypothesis as a more general hypothesis because the cleaner/host-recognition hypothesis does not hold for the harem labrid *Bodianus rufus*. Although juveniles of *B. rufus* often act as cleaners, adults only rarely do so (Randall, 1967, personal observation). Further, many labrids, including *L. dimidiatus* (Robertson, 1974), can make rapid and often radical color changes. If the display of a TP color pattern was important to territory maintenance interactions of male *L. dimidiatus*, I suggest that it would have developed a TP pattern that could be switched on and off at will, and used only in appropriate contexts. Although the host/cleaner-recognition and intersexual-selection hypotheses are not mutually exclusive alternatives, the latter has the most general explanatory potential.

(2) In Florida, *Halichoeres maculipinna* is thought to have a strictly harem mating system. In Panama it does not. The Panamanian data on the mating systems of both *Halichoeres* species support that intersexual-selection hypothesis.

(3) Thresher stated that, contrary to Robertson and Hoffman's (1977) report, TP males of *Halichoeres maculipinna* intensify their TP colors at the start of and during territorial interactions with conspecific TP males. The data presented here on both *Halichoeres* species are consistent with Robertson and Hoffman's statement: Panamanian TP males that are attacking conspecifics characteristically do not develop intense TP colors and also tend to fade such colors during an interaction. However, sexually active TP males are more likely than inactive males to exhibit TP colors when aggressive and in general those males are more likely to exhibit TP colors when attacking IP fish than when attacking TP conspecifics.

Some of the apparent differences in these two reports and differences in the degree to which TP males exhibit TP colors in various social contexts could be explained if a TP male simultaneously makes both sexual and aggressive responses to the same fish, or different responses to different fish. The tendency to display sexual signals would be most strongly and continuously present during spawning periods. Also a TP male would be more likely to respond sexually towards an IP fish, which might be a female, than towards a TP male, which invariably is a sexual competitor. Thus, the idea that TP colors are sexually motivated is not incompatible with the observation that they often are displayed by aggressive males, particularly during spawning periods.

The display of TP colors is related to dominance status among males; the dominant male in a territory is the

male who exhibits those colors most continuously and intensely (Thresher, 1979; personal observation), perhaps to communicate information on his status to a female. Subordinate males of species that can change their colors probably do not normally display such colors because dominant males would penalize such behavior. Subordinate males may also be behaviorally suppressed and incapable of fully developing those colors until they achieve dominant status. Thresher observed that when he removed a dominant TP male *Halichoeres maculipinna*, a number of TP males contested control of his territory. During this contest, those males had intense TP colors. Those males may have displayed such colors because their dominance relations had not stabilized; each was behaving as if it was the dominant male and was advertising that to resident females. Thresher's observations may also have been made during a spawning period.

Thus, the Panamanian data on color changes by TP males support the intersexual-selection hypothesis and the Floridian data are not so inconsistent with it as Thresher (1979) suggested.

(4) Thresher maintains that there is a poor correlation between harem mating systems and sexual monochromatism in various labrids and scarids. However, the papers cited (Moyer and Shepard, 1975; Robertson and Warner, 1978) do not contain the necessary quantitative data. There is increasing evidence of intraspecific variability in mating system structure among the labroid fishes, e.g. *Halichoeres maculipinna*. In the dichromatic scarid *Scarus iserti*, harem formation is merely one of a number of elements of its mating system (Buckman and Ogden, 1973; Ogden and Buckman, 1973; Barlow, 1975; Robertson and Hoffman, 1977; Robertson and Warner, 1978; Colin, 1978). It is necessary, therefore, to gather quantitative data on the degree of variation in mating systems of a species in various habitats and localities. Testing whether a species is invariably harem should be done in large populations living in large areas of a habitat in which one might expect spawning migrations to be advantageous. In such a habitat a female's mobility, and thus her choice of a mate, would not be limited by habitat availability *per se*.

I conclude that, from the existing data, the intersexual-selection hypothesis does account for the development of sexual dichromatism in the labroid fishes. If so, the question then arises, why do males not make extensive use of the TP pattern during agonistic interactions? Perhaps females assess mate quality by different criteria than males use to determine dominance relations. In addition, if the display of TP colors carries a predation risk, then it could be advantageous for a male to divert a predator's attention from the other individual during sexual interactions because it could increase his chance of being chosen by females. However, it could be quite disadvantageous for him to attract and divert such attention during agonistic interactions with other males.

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