Protogynous Hermaphroditism in Fishes of the Family Scaridae

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A. Introduction

The demonstration of sequential hermaphroditism in shallow water marine fishes is no longer a novelty. Initial studies of sequential hermaphroditism served to focus attention on problems relating to sex determination, differentiation and the physiological mechanisms involved in the change of sexual identities. Attempts to clarify the selective advantage of sequential hermaphroditism, which is now recognized as a widespread population phenomenon (Atz, 1964; Reinboth, 1970), have not always kept pace with histological and physiological studies.

This paper is an amplification of arguments previously put forward by Robertson and Choat (1973), concerning the selective advantages associated with a protogynous hermaphroditic sequence in labrid fishes. These arguments were based on the following assumptions. The opportunity to breed is distributed unequally amongst males in a given population, being restricted to larger individuals. Males are promiscuous and capable of fertilizing a large number of females. Under these circumstances there will be a selective advantage for males to be larger than females and protogynous hermaphroditism may evolve. These arguments are largely an extension of the size advantage model of Ghiselin (1969). Implicit in such assumptions is the idea that competition for gametes between individuals will be a powerful moulding force in the evolution of hermaphroditism. This argument accomodates selection at the individual level only. We believe that attempts to interpret sequential hermaphroditism in the context of zygote production, or adjustment of numbers of entire populations (Fishelson, 1970; Moe, 1969; Smith, 1967), will run into difficulties, especially where the organism concerned have highly dispersive larvae.

The above assumptions accommodated the situation in which a single large male individual would dominate a group of smaller females, within a site defended against other males. All male recruitment was assumed to be via the sex-inversion of females from within the group. However, as the studies of Reinboth (1962, 1970) have shown, this is simply one aspect of a complex and variable pattern of sexual ontogeny. Therefore, we also attempted to account for the phenomenon of dual patterns of male identity, monandry and diandry (Reinboth, 1967), which is characteristic of many species of labrids.

Similar patterns of sex-inversion and dual male identity occur in the Scaridae, which are closely related to the Labridae, and are highly characteristic of coral reef environments (Reinboth, 1968). We will present evidence that the scarids also conform to the model developed to account for protogynous sex-inversion in labrids. In doing so, we emphasize that the expression of dual male identities is complex and not really amenable to a straightforward classification of sexual behavior and ontogeny.

In teleost fishes a protogynous sequence of sexual succession is the dominant mode of hermaphroditism. However, any attempt to interpret the significance of protogyny in fishes must deal with two sorts of biases; (1) taxomonic biases, as protogynous fishes seem to be restricted to particular groups, and (2) spatial biases, in that there are more species of protogynous fishes (in terms of both relative and absolute estimates) in coral reef waters than anywhere else. The problem as to why such biases exist is beyond the scope of this paper, which is confined to a review of hermaphroditism in the Scaridae of Heron Island, Great Barrier Reef. Our approach has been strictly correlative. To resolve the questions considered, two sorts of experimental studies are required. Those in which monitoring and manipulation of individuals under natural conditions play a major part (Robertson, 1972; Reinboth, 1973; Buckman and Ogden, 1973; Ogden and Buckman, 1973), and those in which the influence of environmental factors on the ontogeny of sexual development may be assessed (Harrington, 1971).

B. Methods

The data presented here were collected mainly at two localities on a patch reef at Heron Island (Lat. 23° 26'S, Long. 152°E), a part of the Capricorn group of reefs at the southern extremity of the Great Barrier Reef. Collections were made in January and February, 1967, and in the same months during 1972 and 1973.

To obtain data on the relative abundance of individuals of different species, counts of individuals were made in 5 x 50 m and 10 x 100 m transects. Measured areas of substrate were also observed for fixed periods of time. Grazing intensity was assessed as the number of bites taken by each individual from the substrate during this time. Individual scarids were followed for a fixed period of time, usually 10 min, and all feeding activities and interactions were recorded. Estimates of the relative abundance of the different grazing substrates were obtained by running 10 metre line transects across the various areas in which scarid observations were carried out. Large scale distribution of substrates was estimated from maps of the outer reef-slope, covering approximately 4000 square metres.

For gonad analysis scarids were collected individually and from poison stations. Attempts were made to cover the entire range of the species observed when collecting. Gonads and gonoducts were either immediately dissected out and fixed in Bouin's fluid, or the entire specimen was fixed in 10% formalin by injection into the body cavity. Size was measured in mm and expressed as standard length.

C. Results

The following species of scarids were recorded from Heron Island: *Bolbometapon bicolor, Calotomus spinidens, Scarus rubroviolasceus*, S. gibbus*, S. venosus*, S. forsteri*, S. bleekeri, S. sordidus*, S. flavipectoralis*, S. lunula*, S. formosus*, S. schultzi*, S. oviceps*, S. sexvittatus*, S. niger*, S. scaber, S. ghobban*, S. chlorodon*, S. lepidus, S. fasciatus*, S. globiceps** and one undescribed species of *Scarus*.

Although it has been assumed that all of the above species are protogynous, it has only been confirmed by histological examination in those

marked with an asterisk. The present investigation concentrated on
nine of the most abundant species in the study area. These are listed
as follows in order of local numerical abundance: *S. sordidus, S. fascia-
tus, S. globiceps, S. niger, S. forsteri, S. venosus, S. formosus, S. lunula* and
S. sexvittatus. It was not possible to distinguish between small indi-
viduals of *S. fasciatus* and *S. globiceps* under water. They are identified
as *S. glob/fasc*.

All these species were diurnally active herbivores grazing on calcar-
eous substrates, and the vast majority were distributed within the
upper 12 m of the reef slope. The populations sampled at Heron Island
were members of species widely distributed in the tropical Pacific and
Indian Oceans and were thus near the southern limits of their range.

I. The Relationship between Color Phase and Size

The majority of scarids from the study area were dichromatic, and un-
like many species of labrid fishes, the dichromatism in the different
phases was sharply discontinuous.

Of the 22 species listed above, there were only 3 which did not fit
the picture of discontinuous dichromatism. *Scarus niger* showed no dif-
ferentiation of color over the adult size range. In the case of *Scarus
schultzi*, larger individuals were more brightly colored but the dichro-
matism did not involve sharply distinct color patterns. *Scarus gibbus*
did not fit the pattern of usual scarid dichromatism. Two color vari-
ants, red and green were observed each occupying the full size range,
and it is thought that these may represent a color polymorphism.

In the remaining 20 species, large individuals were more brightly
colored than small individuals. The former were usually characterized
by a green body coloration with intricate and distinctive patterns of
red, orange or blue markings on the head and opercula. The latter were
either grey, brown or reddish overall and usually lacked any distinc-
tive anterior markings. For the purposes of this study these phases
were called "gaudy" and "drab" respectively.

The distribution of color phase as a function of size in nine of the
most abundant species, is shown in Fig. 1. The lower size limits for
each color phase represent the size at which sexually mature individ-
uals were first detected by histological examination and spawning
observations. All nine species, with the exception of *S. niger*, are
dichromatic with sharply discontinuous color phases. In all instances
where it was possible to collect large numbers of individuals there
was considerable size overlap in the color phases, although gaudy phase
individuals always had a greater mean size than the drab phase ones.
Color transitional specimens were observed in most species, but were
never abundant. The data in Fig. 1 reflect this. In nearly all species,
distinctive juvenile color phases were observed.

There appear to be no predictable trends in the degree of overlap be-
tween color phases. Field observations confirmed that the degree of
overlap in the color phases of *S. formosus, S. lunula* and *S. forsteri* would
increase if larger collections were made. The large range and variance
shown by the different color phases suggest that a considerable degree
of flexibility is involved in the process of transformation from one
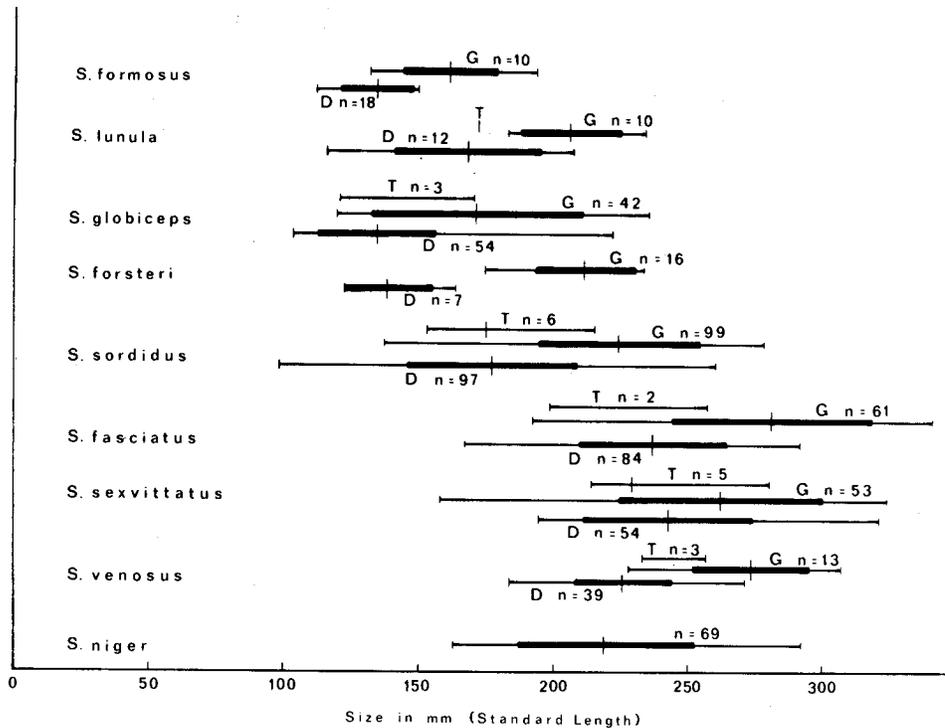color phase to another.

Fig. 1. The size distribution of color phases in nine species of scarids. Lower size limits are estimates of the size at which sexual maturity occurs. The vertical line represents the mean, the black bar one standard deviation each side of the mean. (D) drab phase, (G) gaudy phase, (T) transitional phase, (n) sample sizes in each phase

II. Sex Structure of Scarid Populations

The same specimens used to compile Fig. 1 were also examined to determine their sexual identities. Slight discrepancies in numbers between Fig. 1 and Table 1 indicate that we were unable to examine all individuals histologically. The data in Table 1 show that scarids are very close to the labrids in their patterns of sexual identity. Following Reinboth (1962, 1970), four sexual identities were recognized: females, primary males, secondary males and individuals undergoing sexual transition. Primary males were presumed to be true male gonochorists. Secondary males comprised false male gonochorists, that is secondary males from juvenile females (Harrington, 1971), and males derived from mature females.

Primary males had large testes with centrally located sperm ducts. The gonoducts of primary males were massive, with numerous connective tissue septae. The testes of secondary males clearly indicated their ovarian origin by being lobate, with a central lumen and peripheral sperm ducts. The gonoducts were similar to those described for secondary male labrids (Reinboth, 1962). Arbitrary criteria were used for defining transitional gonads, as functional females may have sperm crypts and functional males, atretic eggs. However, no instances of simultaneous maturity of male and female products in the same gonad were found.

Table 1. Color and sex distribution in nine species of scarids collected at Heron Island. $1°♂♂$ refers to primary males, $2°♂♂$ to secondary males and t to sexually transitional individuals. Sizes are grouped in 20 mm intervals of standard length

(A) *S. formosus*

Color phase	Drab		Gaudy	
Sexual identity	♀♀	$1°♂♂$	$1°♂♂$	$2°♂♂$
61 - 80	1			
81 - 100				
101 - 120	2	1		
121 - 140	8			1
141 - 160	6	1	1	3
161 - 180				5
181 - 200				1
Sexually mature	105 mm	?		

(B) *S. lunula*

Color phase	Drab		Transitional	Gaudy
Sexual identity	♀♀	$1°♂♂$	t	$2°♂♂$
61 - 80				
81 - 100	1			
101 - 120	2			
121 - 140	1			
141 - 160	1			
161 - 180	5	1	1	
181 - 200	1			5
201 - 220	2			2
221 - 240				3
Sexually mature	115 mm	?		

(C) *S. forsteri*

Color phase	Drab			Gaudy	
Sexual identity	♀♀	$1°♂♂$	t	$1°♂♂$	$2°♂♂$
61 - 80	12	4	1		
81 - 100	4	4			
101 - 120	3				
121 - 140	3				
141 - 160	2				
161 - 180	1				1
181 - 200					3
201 - 220				2	2
221 - 240				3	3
Sexual maturity	120 mm	?			

(D) *S. globiceps*

Color phase	Drab			Transitional		Gaudy	
Sexual identity	♀♀	1°♂♂	t	1°	t	1°♂♂	2°♂♂
61 – 80	27	5					
81 – 100	17	4	1				
101 – 120	18	9			1	1	
121 – 140	15	6		1		2	1
141 – 160	9	5				7	4
161 – 180		1		1		7	1
181 – 200		2				3	4
201 – 220						4	6
221 – 240		1					1
Sexual maturity	115	103 mm					

(E) *S. sordidus*

Color phase	Drab		Transitional		Gaudy	
Sexual identity	♀♀	1°♂♂	1°♂♂	t	1°♂♂	2°♂♂
61 – 80	10					
81 – 100	15	2				
101 – 120	5	1				
121 – 140	12	3				1
141 – 160	20	3	1		1	1
161 – 180	18	1		3	1	3
181 – 200	19	1		1	1	15
201 – 220	10			1		24
221 – 240	7				1	17
241 – 260	3					22
261 – 280					1	11
Sexual maturity	135 mm		98 mm			

(F) *S. fasciatus*

Color phase	Drab			Transitional		Gaudy	
Sexual identity	♀♀	1°♂♂	t	1°♂♂	t	1°♂♂	2°♂♂
81 – 100	9	2					
101 – 120	10	1	1				
121 – 140	6	2					
141 – 160	9	6					
161 – 180	10	4					
181 – 200	12			1		1	2
201 – 220	7	3				1	3
221 – 240	23	8				1	

(F) *S. fasciatus* (cont.)

Color phase	Drab			Transitional		Gaudy	
Sexual identity	♀♀	1°♂♂	t	1°♂♂	t	1°♂♂	2°♂♂
241 - 260	21	2			1	3	6
261 - 280	10	4				4	4
281 - 300	2					2	12
301 - 320						3	7
321 - 340						1	8
341 - 360							1
Sexual maturity	183 mm	167 mm					

(G) *S. sexvittatus*

Color phase	Drab			Transitional	Gaudy	
Sexual identity	♀♀	1°♂♂	t	t	t	2°♂♂
61 - 80	10	1				
81 - 100	8					
101 - 120	7					
121 - 140	7					
141 - 160	4					1
161 - 180	5					
181 - 200	5					
201 - 220	14		2	4		5
221 - 240	7					7
241 - 260	18				3	7
261 - 280	6			1		7
281 - 300						10
301 - 320	6					7
321 - 340						4
Sexual maturity	194 mm	?				

(H) *S. venosus*

Color phase	Drab				Transitional	Gaudy
Sexual identity	♀♀	1°	2°	t	t	2°♂♂
61 - 80	1					
81 - 100	2					
101 - 120	2					
121 - 140	5					
141 - 160	2		1			
161 - 180	1			1		
181 - 200	6					
201 - 220	11	1				1

(H) *S. venosus* (cont.)

Color phase	Drab				Transitional	Gaudy
Sexual identity	♀♀	1°	2°	t	t	2°♂♂
221 - 240	12	1			1	1
241 - 260	8				2	1
261 - 280	2					4
281 - 300						6
301 - 320						1
Sexual maturity	184 mm ?	?				

(I) *S. niger*

Sexual identity	♀♀	t	2°♂♂
61 - 80	3		
81 - 100	1		
101 - 120	4		
121 - 140	3		
141 - 160	5		
161 - 180	9		1
181 - 200	7	1	3
201 - 220	13	1	2
221 - 240	5	1	5
241 - 260		1	11
261 - 280			8
281 - 300			1
Sexual maturity	163 mm		

In the majority of species there was a statistical relationship between size, color phase and sexual identity (Table 1). The probability that a gaudy phase individual would be a male was overwhelming. No female gaudy phase individuals were collected. In the case of *S. sexvittatus*, 3 gaudy phase individuals were transitional. Drab phase individuals were strongly biased toward the female identity. The proportion of drab males ranged from 27.9% in *S. globiceps* to 1.02% for *S. sexvittatus*. The few transitional specimens collected displayed a variety of sexual identities (Table 1).

Sub-division of the primary and secondary male identities revealed very little in the way of a predictable relationship with color phase and sex, with the exception that the majority of functional drab phase males were primary in derivation. A minority were transitional or secondary. The distribution of male identities in the gaudy phase tended to reflect the distribution in the drab phase.

Color transitional specimens were either primary males or sexually transitional. In the case of *S.niger* (dichromatism absent), the sexual identities were size distributed, with secondary males having a greater mean size than females. Patterns of sexual ontogeny inferred from the data appear to conform to the dual male scheme of classification (mon-

andry and diandry) of Reinboth (1967). However, the condition of dian-
dry is highly variable, ranging from the situation in which primary
males make up only 1% of the drab population to that in which they
approach 30%. True monandry seems to be a restricted condition, and
given the flexibility of labroid sexual ontogeny the term should be
used with caution.

Histological examination of gonads, coupled with observation and col-
lection from spawning assemblages, enabled an estimate of the lower
limit of sexual maturity to be made. In the diandric species, *S. sor-
didus*, *S. globiceps* and *S. fasciatus* , drab phase males were substantially
smaller than females, when first mature. In the case of *S. sexvittatus*,
a 157 mm gaudy secondary male with mature sperm in the gonoduct was
smaller than any mature female examined. This suggests that primary
males will come to sexual maturity at an earlier age than females,
and also that females (by undergoing prenuptial transition) may enter
into the reproductive population at an earlier age than if they had
remained females.

Also, in diandric species, both primary and secondary males contribute
to the gaudy male phase. In the case of *S. sordidus*, the proportions of
primary males to females in the drab phase is essentially similar to
that of primary to secondary males in the gaudy phase. Inspection of
the size frequency distribution in the drab phase suggests that primary
males leave this phase via color transition at a smaller mean size than
do females via sexual transition.

However, it is difficult to make inferences concerning the demography
of the different identities on the basis of this sort of information.
If the distribution of primary males in *S. globiceps* and *S. fasciatus*
is examined, an anomaly appears. In each instance, the relative pro-
portion of primary males to secondary males increased with transition
to the gaudy phase. There are a number of mechanisms which might ac-
count for this. There may be a reduced probability of survival of
secondary males. Different schedules of growth and transition may
exist which convert drab primary males at a faster rate than females,
or we may be seeing a reflection of past events in which drab popula-
tions comprised mainly primary males. However, given the present meth-
ods of sampling and our state of knowledge of social organisation and
dispersion in scarids, the argument that the varying proportions of
primary and secondary males reflect a sampling bias cannot be dis-
missed.

If the gonad weights of mature individuals and the different color
and sexual identities are compared, it is obvious that two different
scales of gonad weight to body length relationship are present (Fig.2).
Although gaudy phase individuals have a greater mean length than drab
phase idividuals, their gonads are consistently smaller. This is true
for both male and female drab phase individuals. Sample sizes are too
small and too variable to assess whether there were any consistent
trends within the different male identities in each color phase. How-
ever, on entering the gaudy phase, regardless of whether this is ac-
complished by sex and color succession (female to secondary male) or
by color change alone, the gonad shows a sharp reduction in weight
(Table 2). This reduction can be clearly seen in specimens in transi-
tional coloration and may account for some of the variability seen in
the gonad weights of mature drab phase individuals. A similar conclu-
sion was reached by Roede (1972) concerning Caribbean labrids.
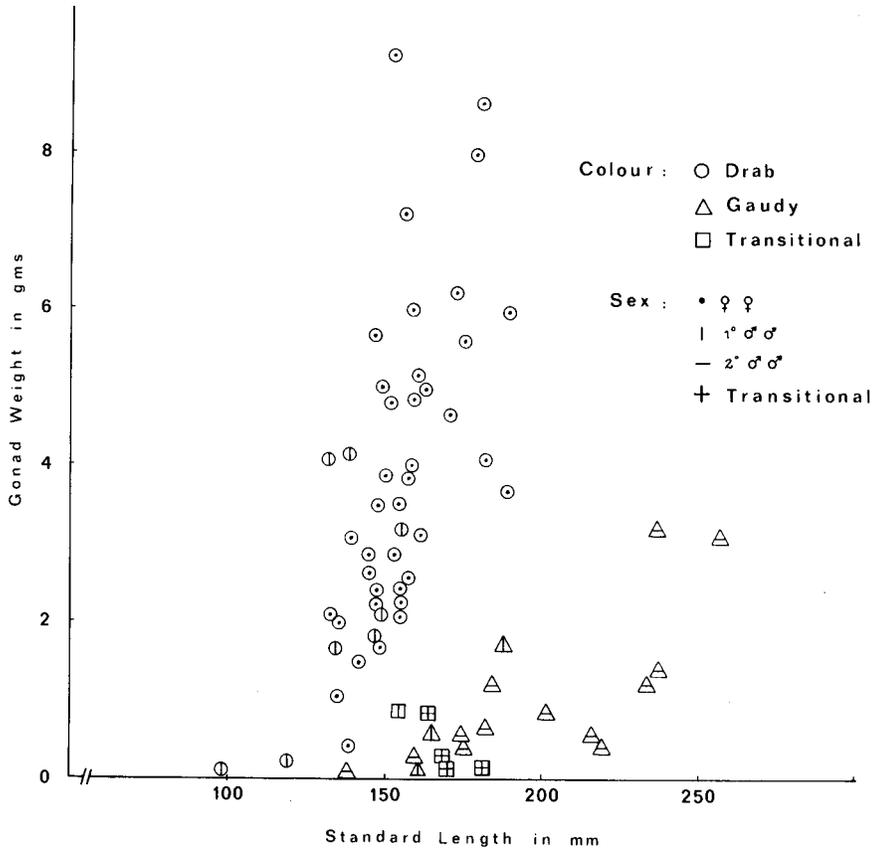
Fig. 2. The relationship of gonad weight to standard length in sexu-ally mature specimens of *S. sordidus* collected during January and February 1972 and 1973

III. Ecology

Scarids gave the impression of being an ecologically uniform group with striking similarities in feeding behavior and distribution. However, a closer examination of the various species revealed a number of subtle differences.

The study sites were two adjacent, but topographically distinct regions of the reef, as shown in Fig. 3. Area A was in a region sheltered from prevailing southerly winds by nearby Wistari Reef. The outer slope of this was covered with luxuriant growth of *Acropora*, the open interstices of which provided a great deal of shelter for reef organisms. The upper and lower boundaries of the reef slope were characterized by a decrease in coral cover and an increase in dead calcareous substrates, when compared to the mid reef slope. The area was subdivided into 4 zones and these corresponded to obvious structural features of the reef (Fig. 3).

Area B was 1.4 kilometres from area A, at the north-west corner of Heron reef. Beyond the reef crest was a shallow shelving area of carbonate rock. The amount of bottom covered in live coral was much less than in area A.

Table 2. Mean gonad weight in grams of drab and gaudy individuals of eight species of scarids. All individuals were mature and collected during January – February 1972 – 1973

Species	Color phase and sex	
	Drab ♀♀	Gaudy ♂♂
S. formosus	n = 15, x̄ = 3.094 ± 1.12	n = 5, x̄ = 0.739 ± 0.647
S. lunula	n = 5, x̄ = 1.572 ± 0.839	n = 6, x̄ = 0.252 ± 0.082
S. forsteri	n = 7, x̄ = 2.056 ± 1.047	n = 4, x̄ = 0.792 ± 0.663
S. venosus	n = 5, x̄ = 3.709 ± 2.81	n = 5, x̄ = 0.499 ± 0.275
S. sexvittatus	n = 5, x̄ = 7.539 ± 4.98	n = 9, x̄ = 0.958 ± 0.914
S. fasciatus	n = 11, x̄ = 8.374 ± 5.370	n = 5, x̄ = 3.264 ± 1.785
	♀♀	♂♂
S. niger	n = 20, x̄ = 3.930 ± 2.185	n = 4, x̄ = 1.452 ± 0.802
	Drab ♀♀	Drab ♂♂
S. globiceps	n = 19, x̄ = 2.41 ± 1.09	n = 12, x̄ = 3.968 ± 6.018
	Gaudy ♂♂	
	n = 17, x̄ = 0.558 ± 0.839	

Table 3. Relative proportions of different substrates estimated by 10 meter line transects in Area A and Area B. Area A has been subdivided as shown in Fig. 3. All substrates on which scarids were observed to graze are identified as G.S. The remainder are live coral (L.C.) macroscopic algae (Alg.), sand, sponge and soft coral (S.C.). Values are mean percentages

		G.S.	L.C.	Alg.	Sand	Sponge	S.C.
Area A							
Reef Crest	n = 8	73.8	21.9	3.7	0.2	0.2	0.2
Reef Slope (1)	n = 4	26.7	40.3	1.9	31.1		
Reef Slope (2)	n = 4	8.4	86.9	1.2	3.3		0.07
Patch zone	n = 5	60.7	6.5	2.9	26.5		3.4
Area B							
Reef Slope	n = 5	87.3	2.2	0.1	10.1		0.27

In Area A, counts of scarids in 50 x 5 meter transects running parallel to the reef crest, revealed that the different species were not distributed evenly within and between the different zones (Table 4). *S. sordidus* was a possible exception. The richest scarid fauna, in terms of both individuals and species, occurred on the reef crest where the greatest amount of grazing substrate was also found (Table 3). However, the amount of grazing substrate does not alone determine the abundance of scarids. Counts made on the outer slope of area B revealed a relatively impoverished scarid fauna, although the amount of grazing substrate was greater (Table 3). When patterns of scarid abundance on a local scale were examined, high variances were observed in some species counts (Table 4). *S. fasciatus* on the crest and patch zone is a case in point. This species displayed a considerable range of movement,

with transient groups of spawning individuals being observed in the
patch zone and large mobile feeding schools on the reef crest at high
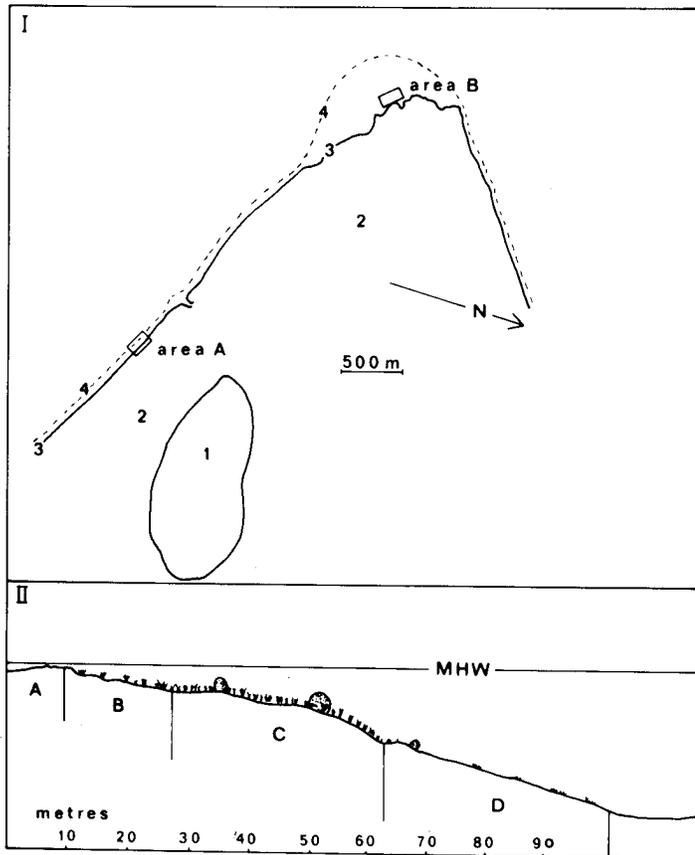water.

Fig. 3. (I) Western tip of Heron Island reef showing the positions of
study areas (A) and (B). (1) Sand Cay. (2) Reef Flat, emergent at high
water. (3) Reef Crest. (4) Approximate position of the 12 meter depth
contour. (II) Profile of the reef at area (A) showing the subdivisions
of the reef used in Table 4. (A) Reef Crest. (B) Outer Slope (1).
(C) Outer Slope (2). (D) Patch Zone

Numerous observations made on feeding scarids showed that all of them
were feeding on plant material, although a certain amount of animal
material may have been included. Most grazing occurred on calcareous
substrates derived from coral skeletons in various stages of decay.
These supported a short turf of small algae, fragments of which were
found to be the major food item in parrot fish stomachs. In Table 5,
the major categories of substrates grazed by scarids are listed. From
the data shown, it can be seen equal areas of the different grazing
substrates were not browsed upon uniformly. In terms of the numbers
of species involved, and also the amount of grazing carried out, sca-
rids showed preferences for certain substrates. Two substrates were

grazed more intensively than any others by a great number of scarids. These were dead patches on *Porites* growths and dead *Acropora hyacinthus* plates.

Table 4. Relative abundance of scarids at area A (4 localities) and in area B

Species	Area A				Area B
	Crest	Slope (1)	Slope (2)	Patch	Area B
	n = 6	n = 7	n = 3	n = 6	n = 5
S. sordidus	29.2 ± 22.6	10.7 ± 7.4	4.0 ± 3.6	6.5 ± 6.9	2.8 ± 3.3
S. glob/fasc	60.5 ± 68.3	7.4 ± 9.4	1.0 ± 1.0	4.1 ± 8.4	2.6 ± 2.4
S. globiceps	0.8 ± 0.9	1.8 ± 1.6	–	0.5 ± 0.8	–
S. fasciatus	2.2 ± 4.3	2.8 ± 2.6	1.7 ± 1.1	4.0 ± 6.4	–
S. niger	2.8 ± 2.4	1.4 ± 1.2	3.7 ± 2.1	0.2 ± 0.4	–
S. formosus	4.1 ± 3.9	1.6 ± 1.5	0.3 ± 0.6	–	–
S. forsteri	1.0 ± 2.3	–	–	2.8 ± 2.3	5.2 ± 3.7
S. venosus	0.7 ± 1.2	–	1.0 ± 1.0	0.7 ± 0.8	4.6 ± 3.8
S. lunula	2.8 ± 6.4	0.1 ± 0.4	1.7 ± 2.1	2.3 ± 1.7	–
S. gibbus	1.0 ± 1.5	0.4 ± 0.8	0.7 ± 0.6	–	1.3 ± 1.4
S. chlorodon	0.4 ± 0.5	–	–	–	49.4 ± 50.2
S. sexvittatus	1.8 ± 1.7	0.1 ± 0.4	0.7 ± 0.6	0.2 ± 0.4	–
S. oviceps	0.83 ± 1.2	0.3 ± 0.5	–	–	–
S. schultzi	–	–	0.3 ± 0.6	–	0.6 ± 0.9
S. ghobban	–	–	–	0.3 ± 0.5	0.2 ± 0.4
S. rubroviolaceus	–	–	–	–	0.2 ± 0.4
S. scaber	0.2 ± 0.4	0.3 ± 0.5	–	–	–
S. flavipectoralis	–	–	–	3.3 ± 4.2	–
Scarus sp.	–	–	–	0.3 ± 0.8	–

If the grazing substrates are considered in terms of unbroken surface area and permanence, the massive *Porites* structures must be ranked first. The grazed areas, which were devoid of polyps, offered an extensive and flat surface which was covered with a turf of filamentous algae. This was raised above the reef sediments and sand pockets. Large *Porites* growths on the outer slope were also the most permanent reef structures present. Twelve *Porites* growths observed in 1967 were present in 1973, despite the passage of two cyclones, which extensively damaged other corals in the intervening years (Connell, 1973). Dead *Acropora hyacinthus* plates were more readily disturbed by being broken up and buried in sediment, but they still offered large uninterrupted grazing surfaces. The fragments of *Acropora* rubble and the thickets of dead stalks and holdfasts were prone to disturbance by wave action and abrasion, and were covered by shifting reef sediments.

From this outline of feeding behavior and distribution, we conclude that the smaller, less mobile, scarids are usually associated with cover in the form of *Acropora* growths. Open environments, with a high proportion of grazing substrate, harbour larger species which form

Table 5. Major grazing substrates on reef slope, area A. Approximately 5 square meters of substrate were observed for 10 minute periods

Substrate	Dead *Porites* surface	Dead *Acropora hyacinthus* plate	*Acropora* rubble in sand	Impacted carbonate rock	Dissected carbonate rock	Dead *Acropora* thickets	Bases of live *Acropora*
Observations	n = 14	n = 13	n = 22	n = 5	n = 5	n = 3	n = 9
Numbers							
Total scarids	46	62	63	20	9	15	8
$\bar{x}$ number	3.3	4.7	2.8	4.0	1.8	5.0	0.9
Most abundant species %	*S. niger* (30.4)	*S. glob/fasc* (50.0)	*S. sordidus* (30.1)	*S. sordidus* (35.0)	*S. flavi-pectoralis* (33.3)	*S. sordidus* (53.3)	*S. flavi-pectoralis* (25.0)
Grazing intensity							
Total bites	3514	5475	1360	351	162	433	135
$\bar{x}$ bites	251.2	421.0	61.8	70.2	32.4	144.3	15.0
Most intensive grazer % bites	*S. niger* (27.7)	*S. glob/fasc* (65.0)	*S. venosus* (31.2)	*S. forsteri* (38.7)	*S. flavi-pectoralis* (54.9)	*S. sordidus* (60.3)	*S. flavi-pectoralis* (37.0)

schools. Both types of species tend to graze selectively on large and permanent calcareous substrates.

These tendencies are shown clearly by the two species, *S. niger* and *S. faciatus*. *S. niger* is of interest, in that it is the only species present in the study area which lacks dichromatism in the adult stages, it is the only species which could be classified as monandric, and it is the only one which was found concentrated about the large permanent grazing substrates. It was never seen in schooling associations, and showed little change in numbers or distribution with the tidal cycle. *S. niger* achieved its greatest abundance on the outer reef slope in areas covered with branching *Acropora*. Here *S. niger* was associated with massive *Porites* growths. Its dependence on shelter is suggested by its absence in counts made at the N.W. corner, where numerous *Porites* growths occurred. Maps covering 1040 and 3025 square meters respectively, showed that large *Porites* growths in area A were minority components of the substrate. They were estimated at 0.7% and 1.1% of bottomcover respectively, and were isolated islands of clean grazing substrate used mainly by *S. niger*, surrounded by abundant cover in the form of *Acropora* growths.

S. fasciatus showed considerable variability in its pattern of distribution on the reef. This could be correlated with the tidal cycle. At low water, large schools congregated on the reef slope. Table 6 shows the variation in numbers of *S. fasciatus* on the reef slope in relation to tidal level. Far less variability was seen in *S. niger*. Observations on the reef flats at high water revealed that *S. fasciatus* moved onto the flats, grazing across extensive areas and returned to the outer slope with the falling tide. Few other scarids exploited these grazing resources.

Table 6. Counts of scarids in 100 x 10 meter transects on the reef front (reef slope (1)) area A at high and low water

Species	High water n = 5	Low water n = 5
	x̄ Number	x̄ Number
S. faciatus	3.6	177.5
S. sexvittatus	8.6	6.6
S. sordidus	48.4	23.0
S. niger	4.8	7.8
S. venosus	3.6	1.0
S. globiceps	7.4	5.0
S. glob/fasc	12.4	17.2
S. formosus	0.4	2.0
S. lunula	0.2	–
S. forsteri	0.8	3.0
S. gibbus	1.2	–
S. ghobban	4.4	34.8
S. oviceps	0.2	0.4

IV. Reproductive Behavior and Social Organisation

Both pair and group spawning, as described by Randall and Randall
(1963), were observed in Heron Island scarids. Group spawning was ob-
served most frequently in *S. globiceps*. It always occurred on the outer
slope of the reef, in areas of high current activity. Spawning took
place at, and immediately after, high water. Gaudy males present at
the site of group spawning reacted in three ways. They ignored the
spawning sequence entirely, attacked the drab males participating or,
in a minority of cases, actually joined the spawning run.

Group spawning also occurred in *S. fasciatus* but much less frequently.
In these instances only drab phase individuals participated. Pair
spawning by *S. fasciatus* occurred on the reef front in water deeper than
that of their normal feeding range.

No other instances of group spawning were observed in scarids. Pair
spawnings were frequently observed in most other species and invariably
occurred at the reef crest or reef slope at peak or falling tide. In
all dichromatic species in which pair spawning was observed, the number
of sexually active gaudy males was always a minority of the total num-
ber of gaudy males present at any one time.

As *S. niger* was not dichromatic, males were identified on the basis of
their size and behavioral displays. Active males tended to swim with
the tail and caudal peduncle in a characteristic raised position.
Intra-specific aggression was observed in *S. niger* becoming more fre-
quent with increase in size. This was not confined to periods of sexual
activity. A number of instances of inter-specific aggression, directed
almost exclusively against other grazing scarids, were also observed.
Intra-specific aggression took two forms. Disputes involving a smaller
and a larger individual were transient and resolved by the retreat of
the smaller. Disputes involving individuals of similar size were more
prolonged and carried out at specific sites. These appeared to be
boundary disputes. Inter-specific aggression was directed toward other
species of scarids grazing in close proximity. The greatest focus of
inter-specific aggression occurred around massive areas of *Porites* and
probably explains the abundance of *S. niger* grazing on these substrates.
Only *S. fasciatus* and *S. globiceps* grazed to any significant degree on
these substrates and in nearly all instances did so in schools. Anal-
ysis of observations reveal that *S. niger* engaged in one intra-specific
interaction for every 13 min of observation and one inter-specific
interaction every 19 min from a total of 163 min.

In comparison, *S. fasciatus* showed only one intra-specific interaction
per 29 min of observation, and no inter-specific interaction in 117 min
of observation. The intra-specific interactions occurred only when
gaudy males actually touched in feeding schools. This species browsed
in dense schools over wide areas on a variety of substrates. A number
of these schools showed a mixed species composition and were charac-
terized by intensive grazing on different substrates. Aggressive inter-
actions within and between species were at a minimum during these feed-
ing episodes.

D. Discussion

In summarizing the relationship between dichromatism, sexual succession
and habitat selection in the Scaridae, the following assumptions have
been made:

1. Distinct color phases in scarids represent a compromise between the necessity of concealment and rapid sexual and species-specific recognition.

2. The sexual composition and dynamics of a particular population is a result of selection pressures operating on individuals to produce characteristic mating systems.

3. Coral reef environments are subject to local and unpredictable disturbances even though they do not experience pronounced seasonal regimes.

The numbers of predators present on reefs are enormous, and their numbers must increase almost exponentially with decreasing size of prey organisms. In the scarids examined here, the drab phases of the smaller species (which showed a limited range of movement) were usually brown or reddish, overlaid by light bars or blotches (*S. sordidus*, *S. venosus*, *S. formosus*). We contend this is a disruptive coloration, being effective in species frequenting coral interstices and overhangs. Species which formed feeding schools on the reef crest and flats (*S. fasciatus*, *S. globiceps*, *S. forsteri*) were a uniform pale grey in the drab phase. This is presumably a good compromise pattern, enhancing concealment against a variety of backgrounds in which pale hues predominate. It is difficult to distinguish between small individuals of these species in life which attests to strong uniform selection for such a pattern.

Gaudy coloration is associated with pair spawning and larger size. Rapid recognition by the female with respect to species and sex, is obviously to the male's advantage. Scarids are remarkably similar in morphological and also in meristic characters (Smith, 1956, 1959; Schultz, 1958), and most species overlap in their local distribution. Under these circumstances the convergent color patterns of the drab phase are a liability to a male, which must be quickly and positively identified by the females. Thus, gaudy, sexual and species-specific coloration appears, with the adoption of pair spawning. Group spawning involves different behavioral premises (Randall and Randall, 1963; Reinboth, 1973; Robertson and Choat, 1973). Here the male's close resemblance to the female, inhibits attacks by larger gaudy males and enhances the probability of a successful spawning. In most instances there would be a strong selective advantage in resembling females as closely as possible. Resemblances between drab males and females, and the relative proportions of these to gaudy phase individuals, could be interpreted in the context of automimicry (Brower et al., 1967).

Selection is subjecting the two male color identities to very different demands, as in the Labridae (Robertson and Choat, 1973; Reinboth, 1962, 1973). Within group spawnings, competition for female gametes must be intense. The consequence of this competition, is the development of testes that will deliver a maximum amount of sperm, as rapidly as possible, through a massive gonoduct strengthened with connective tissue septae. Gaudy males have small, sometimes minute testes (Randall and Randall, 1963). Selection should be for greater body size and distinct releaser components in the gaudy pattern. Roede (1972) has argued that a reduction in testes weight in Caribbean labrids, should be interpreted in the context of senescence and a decline in the functional significance of the gaudy (terminal) male phase. The testes of all gaudy phase scarids collected here displayed active spermatogenesis. The only exceptions were occasional sexually transitional individuals. With development of the gaudy phase a reduction in gonad weight occurred, in both primary and secondary males (Fig. 2). Development of the gaudy color phase is therefore associated with access to female

gametes under conditions of reduced inter-male competition during each
spawning event. Reduction in testes size reflects this.

Monandry and diandry, with their associated pair and group spawning,
are at opposite ends of an ecological spectrum. The contrasting behav-
ior of *S. niger* and *S. fasciatus* represent different solutions to the
problems confronting grazing herbivores on a coral reef. These "prob-
lems" are the selective forces with which each species must contend.
Scarids and, indeed all herbivores, must gain continued access to
grazing substrates in an environment which may be subject to consider-
able disturbance. Predation is a selective force which can also strongly
influence the dispersion and distribution of different species (Randall,
1963; Talbot, 1965). Finally, selection will favor those individuals
which maximize their contribution to subsequent generations, and this
will be reflected in their particular mating system.

S. niger shows some degree of site attachment and is apparently defend-
ing two categories of resources. The first of these is a permanent
grazing substrate adjacent to cover, from which it will drive away
other herbivores (mainly scarids). Other herbivores reef fishes, for
example, *Pomacentrus flavicauda*, also act in this fashion (Low, 1971).
Secondly, the sexual structure of *S. niger* populations, and the nature
of the interactions within and between groups of individuals, suggest
that this species has a similar pattern of social organization to that
of *Labroides dimidiatus*. Here, most mating occurs within the confines of
a size-ordered group of females, dominated by a single secondary male
which has been recruited from within the group. The male has priority
of access to the entire female gamete crop. Under those circumstances
there will be prolonged bonds between males and females, and bright,
sexually-specific coloration will not be selected for.

S. fasciatus does not defend any particular site, with the exception of
a transient pair spawning territory. In no observed case were groups
of females dominated by a single male. The diandry of this species is
seen as a consequence of a loose social organization, and lack of site
attachment. Selection for diandry is postulated for circumstances sim-
ilar to those in *Thalassoma lunare* (Robertson and Choat, 1973).

Interpretation of the mechanisms determining the numerical proportions
of the sexual identities in a given population, is a more difficult
and compelling problem. Our statement regarding the relative propor-
tions of females, drab males and gaudy males in diandric populations,
implies that adjustment is obtained via some form of balancing selec-
tion. Similar arguments have been advanced by Gadgil (1972) to explain
the occurrence of male dimorphism in ungulates and insects. In scarids
with a loose social organization, the ability of males to fertilize
females becomes more uniformly distributed with size, and in these
circumstances smaller, behaviorally differentiated males may partici-
pate.

Such arguments imply that the frequency of occurrence of different
sexual identities in various mating systems is genetically determined.
However, there are no data as yet, which enables us to predict the
types of progeny that would be produced by the mating of a primary
male and a protogynous female. In addition, there is unequivocal evi-
dence that at least four sexual phenotypes may be expressed in genet-
ically identical populations of the cyprinodontid fish, *Rivulus marmo-
ratus* (Harrington, 1967, 1971). This demonstrates that different sex
phenotypes need not have a genetic basis. Moreover, laboratory experi-
ments have clearly demonstrated that relatively short term environ-
mental influences early in life determine an individual's sexual ontog-
eny and subsequent reproductive activities. In these species, sexual

succession is a gradual process in which seasonal events play an important part. As Harrington (1971) points out, this remains the only model available with which to interpret the genetics of hermaphroditism in fishes.

However, if we adopt such a model for patterns of sexuality in coral reef fishes, some difficulties emerge. Coral reefs harbour diverse assemblages of protogynous fishes exhibiting a variety of mating systems. It is difficult to envisage environmental factors, such as temperature and day length, being the main determinants of sexual identity in these species. Rather, monandric species, such as *L. dimidiatus*, should be subject to strong selective pressures to produce only protogynous females. In the context of the social system described for this species, the production of primary males would lead to a rapid loss of fitness in individuals that did so.

Reports describing rapid sexual succession in two species of reef fishes, *Anthias squamipinnis* (Fishelson, 1970) and *Labroides dimidiatus* (Robertson, 1972), are contrary to the age-distributed, environmentally-sensitive schedule of succession characteristic of *R. marmoratus* (Harrington, 1971). Admittedly, as these are marine fishes with planktonic larvae, detailed environmental histories have not been compiled. However, a general argument for the rapidity of sexual succession in a monandric, site-attached species is compelling. The attainment of male function provides priority of access to numerous female gametes. A rapid development of the male identity and pair-spawning mode enhances this priority. Further experimental work clarifying the influence of age structure, and also environmental factors, on the schedule of sexual succession in such species is awaited.

Finally, we note that unpredictable disturbances result in a great deal of local temporal and spatial heterogeneity on reefs (Glynn, 1968; Connell, 1973; Grassle, 1973). The argument that reef fishes display flexibility of habitat selection in response to a localized heterogeneity has been anticipated by Sale (1972), in an experimental analysis of habitat selection in reef dwelling pomacentrids. Scarids, expecially the widely distributed and abundant *S. sordidus*, appear to possess considerable flexibility within the context of their diandric population structure. Primary males are precociously mature when compared with females. They may leave the drab primary male mode at a small size, via color transition. Females undergo succession at a variety of sizes. Field observations on the spawning activities in both labrids and scarids, strongly suggest that pair and group spawning are opposite ends of a spectrum and not mutually exclusive. A further report of flexibility of social organization and behavior in scarids is provided by Ogden and Buckman (1973), in their study of *S. croicensis*.

With respect to the possible mechanisms which might mediate this flexibility, the suggestions of Harrington (1971) and Reinboth (1973) must be noted. Their suggestions that the density of primary males may have a suppressive influence on the testicular activity of hermaphroditic *R. marmoratus*, and that the density of the gaudy male *Thalassoma bifasciatum* influences the schedule of color transition in this species, point the way to the types of experimental approaches required to answer these questions.

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