

GONOCHORISM, PROTOGYNOUS SEX-CHANGE AND SPAWNING IN THREE SPARISOMATININE PARROTFISHES FROM THE WESTERN INDIAN OCEAN

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ABSTRACT

The sexual structures of populations of three sparisomatine parrotfishes from Aldabra (Indian Ocean) are examined and the color phases of each species are described. Notes are given on their ecology and spawning. *Leptoscarus vaigiensis* evidently is a gonochorist, the first parrotfish known to be so. *Calotomus spinidens* has both sex-changed males and gonochoristic males, while *C. carolinus* may have only sex-changed males. In contrast, only sex-changed males have been found in other sparisomatines examined previously.

Since Reinboth (1968) demonstrated that several parrotfishes undergo functional protogynous sex-reversal, the list of species known to exhibit this type of sequential hermaphroditism has expanded considerably. The family Scaridae is divided, at present, into two subfamilies, the Scarinae and the Sparisomatinae (Schultz, 1958). Twenty-nine species of scarinines are now known to be protogynous, along with eight species of the sparisomatine genera *Sparisoma*, *Cryptotomus* and *Nicholsina* (Reinboth, 1968; Choat, 1969; Choat and Robertson, 1975; Robertson and Warner, 1978; Yogo et al., 1980; Randall and Bruce, in press).

Two types of males are known to exist in various species of scarids, those which are derived from females (secondary males), and those which show no signs of ever having passed through a female phase and appear to be born as males (primary males). The gonads of each type of male are morphologically quite different at the microscopic level (Reinboth, 1962). Reinboth (1967) introduced the terms monandry and diandry to distinguish the condition in which only primary males are present in a species from that in which both primary and secondary males are present. To date, no parrotfishes have been discovered in which only primary males occur. All but one of the 11 scarinines that have been examined in sufficient detail have been shown to be diandric; *Scarus niger* being the exception (Choat and Robertson, 1975). In contrast, all of the seven species of two genera of sparisomatines that were extensively sampled at one Caribbean site by Robertson and Warner (1978) were found to have only secondary males. Further, those authors also found that in at least three *Sparisoma* species some males were secondary gonochores; such males had testes that were secondary in structure, but they had changed sex without having passed through a functional female stage. In their role in the mating systems of each species, these small secondary-gonochore males were functional analogs of primary males.

The present study was undertaken primarily to determine whether the absence of primary males might be characteristic of the subfamily Sparisomatinae. To do so, we examined the population structures of three species of two genera not previously studied: *Leptoscarus vaigiensis*, *Calotomus spinidens* and *C. carolinus*.

MATERIALS AND METHODS

The Study Species

The status and nomenclature of the Indo-Pacific Sparisomatinae species is confused, especially in the genus *Calotomus*. Smith (1956) considered this group of parrotfishes to belong to a different family

from other reef-dwelling parrotfishes that have bright colors. He listed three sparisomatines from South Africa and Aldabra Atoll (Smith, 1949; 1955); these represent two species considered here (our *Leptoscarus vaigiensis* and *Calotomus spinidens*). Schultz (1958; 1969), in his revision of the parrotfishes of the world, recognized two species of *Calotomus*, *Calotomus spinidens* (Quoy and Gaimard, 1824) and *C. japonicus* (Valenciennes, 1840). One of us (R.W.B.), in collaboration with J. E. Randall of the Bishop Museum, has undertaken a revision of *Calotomus*. We positively identified the 19th century types. This work, which has yet to be published, revealed that Schultz (1958; 1969) was in error; *C. spinidens* as listed and described by Schultz is, in fact, two species; *C. viridescens* (Rüppell, 1835) and *C. carolinus* (Valenciennes, 1840). While *C. viridescens* appears to be confined to the Red Sea, *C. carolinus* is a wide-ranging species and one of the three species of Sparisomatinae found at Aldabra and studied by us. As listed and described by Schultz, *C. japonicus* also represents two valid species, *C. japonicus* (Valenciennes, 1840) which appears to be confined to the coasts of southern Japan and islands in the East China Sea, and the true *C. spinidens* (Quoy and Gaimard, 1824), a small, widely distributed species which is present at Aldabra. The third member of the Sparisomatinae that we studied at Aldabra is *Leptoscarus vaigiensis* (Quoy and Gaimard, 1824), another wide-ranging species, which appears to be free of nomenclatorial chaos. Schultz (1958) recognized one species of *Leptoscarus*, *L. vaigiensis*, and paired the "male" and "female" color phases. Full descriptions of these species and their distributions will be published elsewhere (Bruce and Randall, in preparation).

The Study Area

Data were collected at Aldabra Atoll (9°25'S, 46°22'E) from July through December of 1975 by D.R.R. and R.R., and from October 1975 to August 1976, and November 1977 through January 1978 by R.W.B. Observations were made and specimens collected on shallow areas on the seaward side of Ile Picard, near the research station. The general habitats in that area are described by Robertson et al. (1979) and Robertson (in press). Price (1971) has described the intertidal seagrass beds in which the study species were found. He lists *Thalassia hemprichii*, *Cymodocea rotundata* and *C. ciliata* as "the most characteristic and immediately evident taxa" with *Halodule uninervis*, *H. wrightii* and *Syringodium isoetifolium* as being distinctive in localized areas.

Data Collection

For each species an effort was made to obtain substantial numbers of fish representative of the full range of sizes and color phases present in the study area. Fish were not collected during periods of sexual activity. Specimens were collected by spearing and dissected while fresh. The ovaries of almost all females were discarded after they had been sexed macroscopically. The testes of all males, and the gonads of all fishes whose sex could not be determined by naked eye, were preserved in Bouin's solution and analyzed histologically.

RESULTS

Leptoscarus vaigiensis.—In many wrasses and parrotfishes, two distinctly different color phases are evident among the adult fishes. Females and, if they exist, small males belong to the initial phase (IP), while large males belong to the terminal phase (TP). As a general rule an individual begins life in the IP and, if it is or becomes a male, ends it in the TP (Reinboth, 1975; Warner and Robertson, 1978).

In *L. vaigiensis*, the IP fish in life has a green-brown body, darker above and more whitish below. The head and body are covered with pale blotches, the lower flank, anal and pelvic fins are spotted with brown, and the pectoral fin base is dark. The TP fish in life is a slightly darker green-brown than the IP fish, and is darker above and more yellowish below. The head, body and caudal fin bear small blue spots, and a white medial stripe runs along the body from just posterior to the operculum to just anterior of the caudal peduncle. This species is sexually dimorphic in that 2–7 laterally projecting canines are situated above the upper dental plates of mature males, but not females.

There was considerable overlap in the size ranges of the IP and TP fish in this species (Fig. 1), and females achieved virtually the same maximum standard length (SL) as TP males (182 mm versus 183 mm). The only IP males found were small individuals. They constituted 10.1% of all IP fish that were collected, and

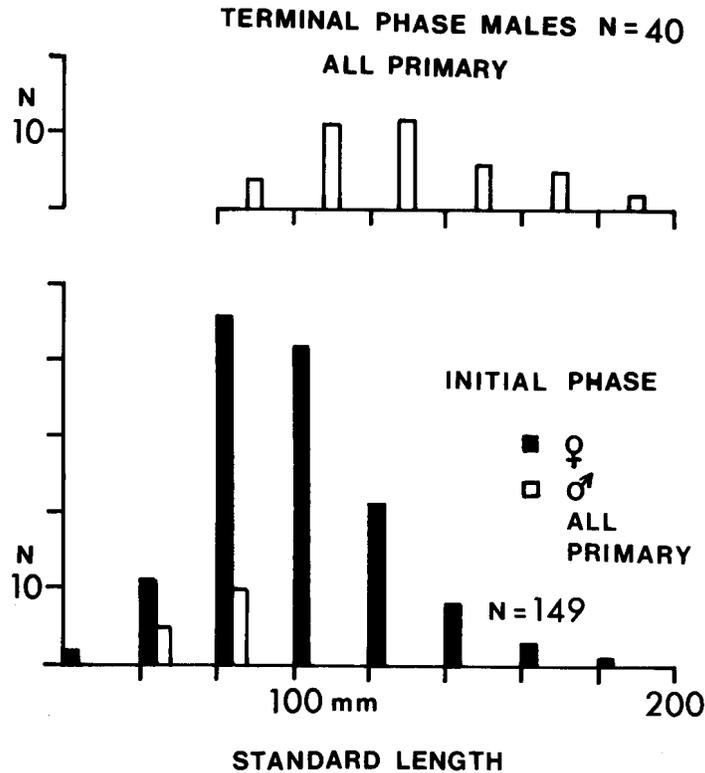


Figure 1. Sexual structure of the population of *Leptoscarus vaigiensis*. Number of individuals of different phenotypes in each 2-cm size class are shown. Although a total of 43 TP males were examined, three were not included here because data on their sizes was misplaced.

20.3% of the fish in the IP size classes in which they occurred. The smallest female collected with vitellogenic ovaries was 69 mm SL and the smallest mature IP male was 72 mm SL. Some males evidently changed from the IP to the TP shortly after they matured, because TP males as small as 85 mm SL were collected. A total of 43 TP males and 15 IP males were examined histologically; all of them were primary males (Fig. 2).

Spawning was observed during September through November. Ovaries in vitellogenesis were found in females collected in January, May, and July through December, and ripe females were collected in September–November. Sampling was not carried out in the remaining months.

Eight pair spawnings (two participants only) and two group spawnings (more than two participants) were observed. These occurred on five days, 2–3 h after high tide, as early as 0730 and as late as 1700. All sexual activity that was observed took place in grassbeds where the water was 1–2 m deep. Pair spawnings involved TP males, which became aggressive towards each other around spawning time. They also intensified the color of the blue spots on the body and fins and expanded and intensified the white medial stripe when courting females. Each pair spawning was preceded by the male actively following the female and, while rapidly shaking his head from side to side, attempting to place his belly on her back. Eventually the female rose up off the bottom and darted rapidly upwards at 60–90° as the male rushed to join her. The two moved upwards for up to about 1 m, then turned

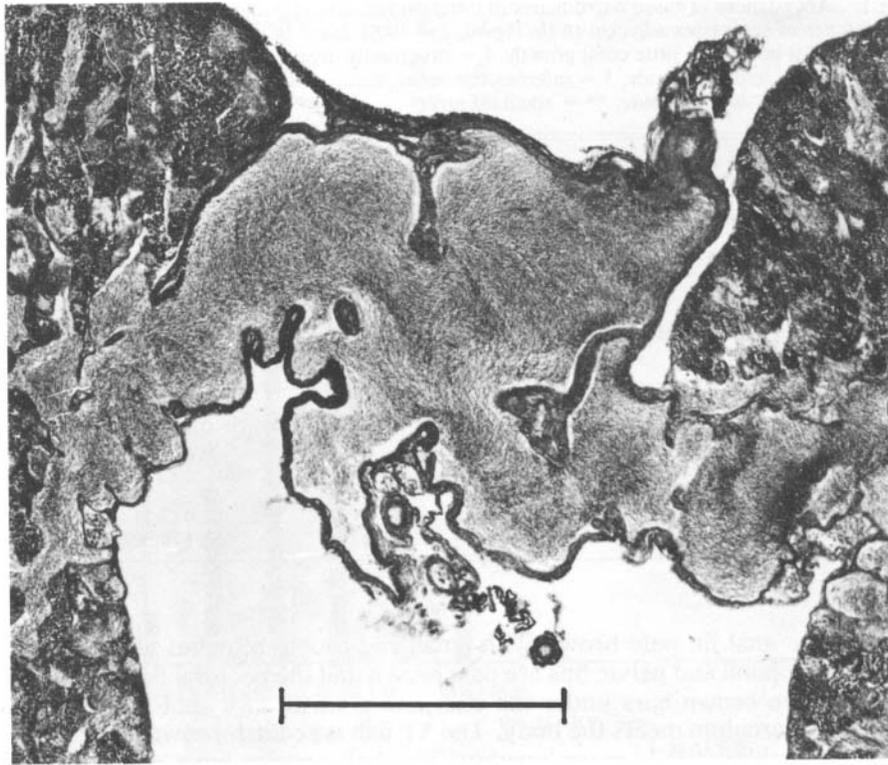


Figure 2. Transverse section of testes of a primary male of *Leptoscarus vaigiensis*. The two halves of the solid gonad are united posteriorly by the tubelike vas deferens. Bar = 500 μm .

and rushed back to the substrate. Events that immediately preceded the group spawnings were not observed and a rapid up-down rush was the only behavior seen. However, groups of up to eight TP males and (presumably) IP males were observed courting what evidently were females. Those groups of males pursued and clustered about the presumed female (a single fat-bellied IP fish), rubbing against her, shaking their heads and placing their bellies on her back in the same manner as TP males did prior to pair spawning. The two group spawnings each involved 5–6 IP fish. Milt was released at the apex of the rush in both pair and group spawnings.

Leptoscarus vaigiensis was only seen around seagrass beds, and there it was common (Table 1). Elsewhere on Aldabra, in the granitic Seychelles, and on the coast of Kenya, this species was seen only in the vicinity of marine-grass beds. Individuals were difficult to observe because they frequently dropped out of sight into the seagrasses. No aggressive behavior between sexually inactive individuals of this species was seen. Mixed groups of 20 to 30 individuals of both color phases and different sizes were often seen, as well as mixed groups of *L. vaigiensis* and *C. spinidens*. Individuals fed by taking bites at the marine angiosperms, breaking off blades by an upward pull of the head. Guts of this species contained finely shredded seagrasses with little sediment.

Calotomus spinidens.—Two adult color phases exist. In life, the general body color of the IP fish is light green-brown, being lighter below. The belly is dull

Table 1. Abundances of three parrotfishes in different habitats at Aldabra (1 = sand, coral heads, small patches of seagrasses adjacent to Ile Picard; 2 = 100% cover of seagrasses, seaward side of Ile Picard; 3 = flat limestone, little coral growth; 4 = structurally diverse, irregular limestone with small amounts of hard and soft corals; 5 = intermediate relief, many soft and hard corals; * = each swim was made within 1 h of high tide; ** = standard error)

Habitat	Mean number of Individuals Seen per 10-min Swim			Sample Size
	<i>L. vaigiensis</i>	<i>C. spinidens</i>	<i>C. carolinus</i>	No. of 10-min Swims*
Intertidal (1–3 m depth)				
1. Lagoon edge	5 (9.66)**	6.5 (12.54)	0.2 (0.41)	6
2. Seagrass beds	58.5 (33.28)	20.7 (7.72)	0.5 (1.64)	10
3. Outer reef crest and flat	0	0	1.0 (3.30)	10
Subtidal (outer reef edge)				
4. High relief rock				
a. 3–5 m depth	0	0	0.9 (2.31)	10
b. 6–8 m depth	0	0	0.6 (1.98)	10
5. Soft coral zone				
a. 10–12 m depth	0	0	1.0 (3.1)	10
b. 18–20 m depth	0	0	0.1 (0.32)	10

rose and the anal fin pale brown with small red-brown blotches along its base. The dorsal, caudal and pelvic fins are pale brown and the pectoral fins are hyaline. There are two brown bars under the chin and a small dark spot where the top end of the operculum meets the body. The TP fish is reddish-brown overall (paler on the underside) with a green overlay. The belly scales have a pink anterior margin. The anal fin is dark grey with reddish blotches basally. The pectoral fin base is dark, the fin yellow on its inner half and hyaline on its outer half. The caudal and dorsal fins are brown with a dark grey cast and a series of wavy brown lines on them, and there is a black blotch around the second and third spines of the dorsal fin. There also is a black spot where the top edge of the operculum joins the body. The face has a slight yellow cast behind the eye, the cheeks have a scattering of red-brown spots, and two red-brown lines extend down from the eye behind the mouth to the chin. Under the chin there are two blue-grey bands. The 1–2 pairs of flared canines that are present on the upper jaw of TP fish are better developed in large individuals. Unlike *C. carolinus*, the posterior margin of the caudal fin of *C. spinidens* is rounded at all sizes.

There was much less overlap in the size ranges of the two color phases of this species than in *L. vaigiensis* (Fig. 3). Males were found in most size classes of IP fish and all but one of the 12 IP males were primary males (Figs. 3, 4). Four intersexual individuals were found among the IP fish (Fig. 4). Functional males constituted 10.2% of all IP fish and 11.0% of the IP size classes in which they occurred. The TP contained both primary and secondary males (Fig. 4), but secondary males predominated (Fig. 3). The smallest TP male collected was 81 mm SL; all of the others were over 90 mm SL. Both the smallest female with vitellogenic ovaries and the smallest male with sperm in its testes were 67 mm SL. Because the smallest intersexual fish (at 68 mm SL) was virtually the same size as the smallest mature female, it seems quite possible that some males change sex before they function as females.

At Aldabra, *C. spinidens* was only found in the seagrass beds, where it was

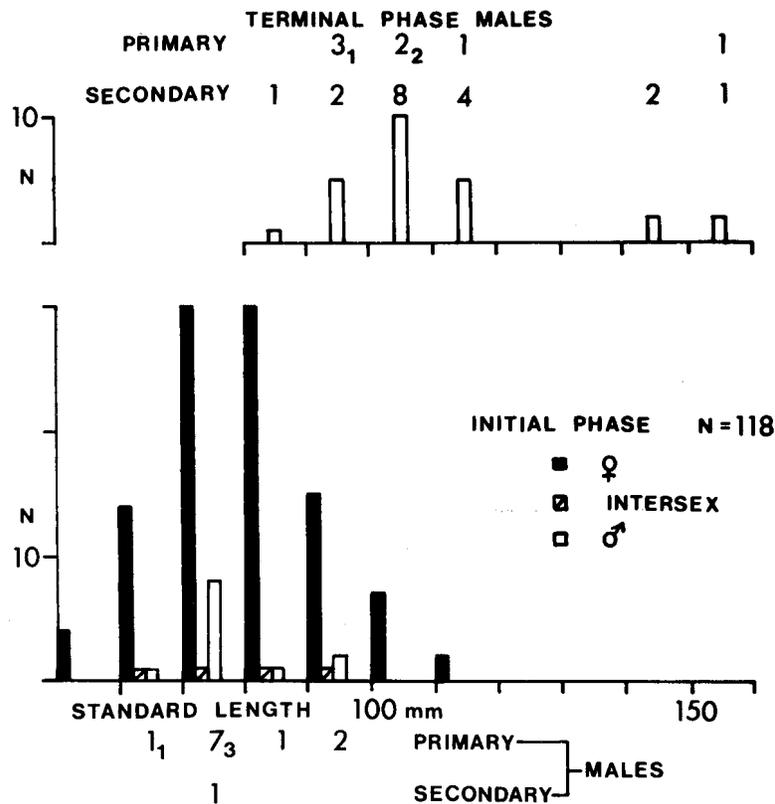


Figure 3. Sexual structure of the population of *Calotomus spinidens*. Number of individuals of different phenotypes in each 1-cm size class are shown. Intersex = individual whose gonads contained large amounts of both spermatogenic and oogenic elements. Numbers in subscript after numbers of primary males refer to individuals that probably were primary males; histological preparations of their gonads were too poor to be absolutely sure of their status.

relatively abundant (Table 1). It was also seen in marine-grass beds on the coast of Kenya.

Spawning was seen during January, August, September and October. Females with vitellogenic ovaries were collected in January, August and October through December and ripe females in August, October and December. More regular sampling was not undertaken.

Spawning was observed several times between 0800 and 1000. It occurred 2–3 h after high tide, when water was pouring out of the lagoon through the channels and over the grass beds on the seaward side of Ile Picard. The water depth was about 1 m at that time. TP fish were very active at this time, rushing about just above the seagrass, fighting with and chasing other TP males. As in *L. vaigiensis*, spawning in *C. spinidens* was preceded by the male shaking his head from side to side while attempting to sit on the female's back. During sexual activity the yellow pectorals and yellowish head of the TP male was very prominent and the body turned pinkish with a sooty overlay. The spawning act was very rapid; a TP and an IP would leave the surface of the grass, rush towards the surface of

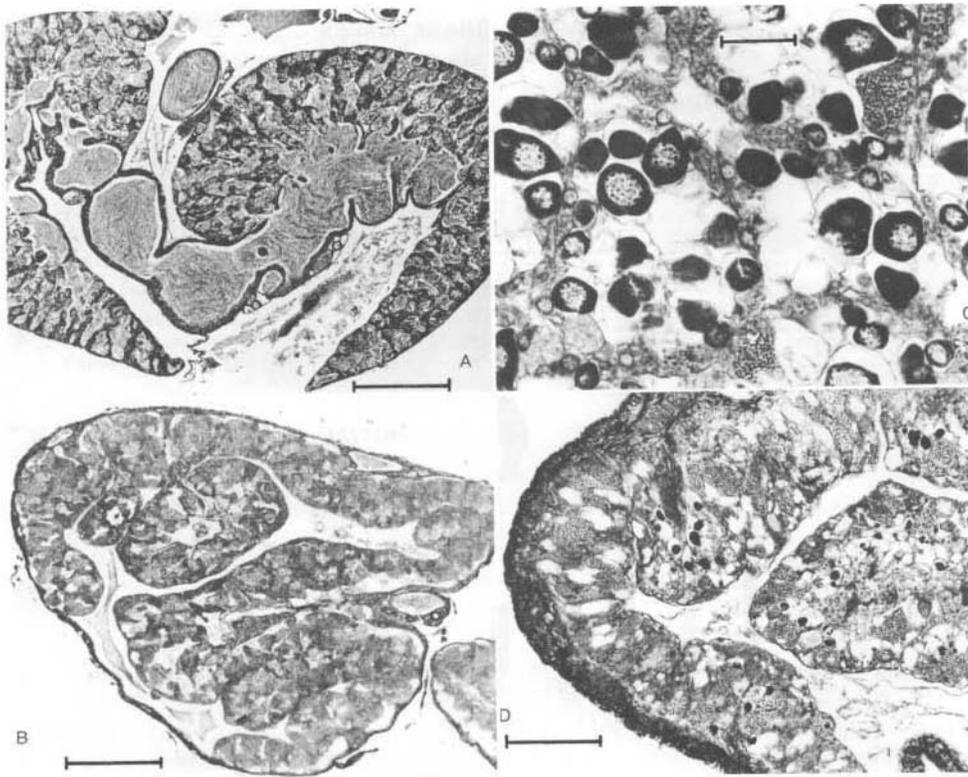


Figure 4. Transverse sections of the gonads of *Calotomus spinidens*: A, Testes of primary males, bar = 500 μm ; B, Testes of secondary male, the former ovarian cavity is clearly visible and the testicular tissue is arranged in the former ovarian lamellae, bar = 500 μm ; C, An early stage of sex change, spermatogenesis is beginning among the small oocytes, bar = 200 μm ; D, Later stage of sex change than C, active spermatogenesis and broken down residual oocytes of the former ovarian stroma are evident, bar = 500 μm .

the water and drop rapidly back down to the grass beds. The two fish, which were side by side, rotated in a spiral during these upward rushes. On several occasions additional TP males participated as satellites in pair spawnings. They darted from hiding places in the seagrass after the pair had taken off in the spawning rush, and joined the pair as it reached the peak of the rush. IP males probably also interfered in TP males' pair spawnings in this same manner, because IP fish were observed to behave in the same manner as the satellite TP males. At the apex of the rush, gonadal products could be seen briefly.

Guts of *C. spinidens* contained fine-shredded seagrasses and there was little sediment present. This species was observed feeding on seagrasses, using much the same method as *L. vaigiensis*.

Calotomus carolinus.—Two adult color phases exist. In life, the IP has a dull olive body with a few pink marks on the lower jaw and anterior to the orbit. The anal and dorsal fins are blotched with pale pink and there is a thin white posterior margin to the caudal fin. The TP is dark bluey-green with reddish-pink stripes radiating around the eye and pink spots on the cheeks. The body scales have pinkish vertical bars, which are sometimes indistinct. The tail is blue-green with

several irregular red-brown bars and a narrow white posterior margin. The pectoral fin is blackish on its anterior half, hyaline on its posterior half and has two rows of pink spots along its base. The anal and dorsal fins have irregular blotchy bands of green and pink. There is a black spot on the front 2–3 spines of the dorsal fin. The pelvic fins are blue-grey with brown mottling. In both color phases the teeth are white. The caudal fin is truncate in small IP fish, emarginate in larger IP fish and deeply concave in large TP fish. A series of 1–3 canines that are found on each upper jaw are larger in TP fish. The TP of this species is the least cryptic of the three species dealt with here.

We collected 22 IP fish that were between 62 mm and 253 mm SL; all were females. They reached maturity in the 160–180-mm size class. We obtained only six TP males, which ranged between 240 mm and 270 mm SL. All were secondary males.

Spawning was observed in January and July, and females with vitellogenic ovaries were found in March, June, July and December. Sampling was not carried out in other months.

Spawning was observed twice, just after high tide. In one case, a TP male that was under observation left the shallow outer margins of the seagrass beds near Ile Picard and swam down the outer reef slope, a distance of about 100 m, to where the water depth was about 12–15 m. In the other case, the male was already on the reef slope when observations were begun. In both instances, the TP male had undergone a color change; his head, which had taken on a yellowish-olive hue, was lighter than the body, the red markings around the eye were visible but not prominent, and the chin was pale. There was a large, light patch on the flank above and behind the opercule, extending forward onto the nape. The remainder of the body was dull green. In addition, his caudal fin was white centrally, due to an expansion of the white posterior margin of the fin and a lightening of the central part of the fin. During the observations, reversals of the color pattern of the TP males were noted, with a fish becoming marbled when he returned to a normal posture and resumed feeding for short periods.

Prior to spawning, the fish sculled about with his pectoral fins, dipping and rising in the water column as he moved around over a large area in circles and figures of eight. His tail was closed and rigidly bent upwards during this circling. During this time, the fish was not more than 3 m off the bottom and the total area covered was about 30 m in diameter. Spawning commenced when the TP male started rapidly circling an IP fish which was already on the reef slope. In one spawning, the two fish came together and the TP stayed on and against the back of the IP during a short upward rush. In the other case, the two were side by side with their cheeks in contact during the upward rush, which took the form of a partial spiral. Spawning occurred at the apex of the rush, when gonadal products were seen briefly in the water. The pair parted immediately after the spawning. The IP fish dropped to the bottom and started moving up the reef slope, while the TP male remained on the reef slope and continued to scull and circle in the water column. No color change was observed in the IP fish prior to or during spawning.

Calotomus carolinus was widely distributed at Aldabra and was present in all habitats sampled, although always at a low density (Table 1). In the granitic Seychelles and the coast of Kenya, this species was also seen in a variety of habitats. Individuals were usually solitary and aggression between sexually inactive TP males was observed.

Feeding was not localized and individuals would range over tens of meters, grazing on limestone substrates (presumably for the associated algal coating) and

marine angiosperms. Stalks of seagrasses were pulled up by these fishes and the stem and leaves consumed. On the falling tide, many pieces of seagrass drift off the reef flat, out over the reef slope, and *C. carolinus* would pick them out of the water column. It was the only scarid that was seen to feed in this manner at Aldabra.

Guts of this species contained shredded seagrasses, algae and considerable carbonate sediment, the contents being rough to touch. Although not quantified, the gut contents were markedly coarser than those of *C. spinidens* and *L. vaigiensis*.

DISCUSSION

Although the three species are sexually dichromatic, both color phases of each are cryptic and TP males of each change their colors to brighter patterns when sexually active. In addition, the two species that are permanent residents of seagrass beds, *L. vaigiensis* and *C. spinidens*, are quite small. These two species share these characteristics with other labroid fishes that inhabit seagrass beds (Warner and Robertson, 1978; Robertson and Warner, 1978). Prey fishes that live in grassbeds are unable to retreat to shelter in which they would be inaccessible to predators. Palatable, poorly armoured prey fishes rely on either small size and cryptic coloration to avoid detection by predators (Robertson and Hoffman, 1977; Ogden and Zieman, 1977) or very large size to be immune to predators (Ogden and Zieman, 1977). Small size also permits those two fishes to remain in intertidal areas during low tide at Aldabra, when only a thin film of water covers the grassbeds. Neither species showed any tendency to leave seagrass areas and migrate elsewhere when spawning.

Both *L. vaigiensis* and *C. spinidens* have primary males in their populations. Thus the absence of primary males is not characteristic of all species that at present are placed in the subfamily Sparisomatinae. However, the phylogenetic relations of the members of this subfamily are not clear and more research is needed to show whether patterns of population sex-structure do reflect the phylogenetic relations of the different species and genera.

A fairly large sample of *L. vaigiensis* was examined. All 58 males were primary males. Thus *L. vaigiensis* appears to be the first known gonochoristic parrotfish. If it is not gonochoristic then it is diandric and secondary males are very rare. This type of diandry would be unusual; in all the wrasses and parrotfishes that are known to be diandric, secondary males are well represented among the TP males (Choat, 1969; Robertson and Choat, 1974; Choat and Robertson, 1975; Reinboth, 1975; Meyer, 1977; Robertson and Warner, 1978; Warner and Robertson, 1978; Dipper and Pullin, 1979; Nakazono, 1979; Warner and Hoffman, 1980; Yogo et al., 1980; data herein on *C. spinidens*).

Calotomus spinidens is diandric, the only sparisomatine known to be so, and both primary and secondary males are common in its population. The existence of intersexual individuals of the same size as that at which females appear to reach maturity indicates that some secondary males of this species may be secondary gonochores.

It seems that *C. carolinus* may be monandric and that males are either rare or absent in the IP. A larger population sample is required to establish firmly that such is the case, because IP males and primary males are rare, but present, in other species of parrotfishes (Robertson and Warner, 1978).

The population structures of two of the three study species represent significant new types among the sparisomatines, and the total range of variation in pop-

ulation sex-structure among the members of that subfamily has now been shown to be comparable to the range of variation found among the scarinines (Choat and Robertson, 1975; Robertson and Warner, 1978). However, there are similarities between the population structures of *L. vaigiensis* and *C. spinidens* and those of other sparismatinines (Robertson and Warner, 1978). First, in *Sparisoma radians*, *S. chrysopterum* and *L. vaigiensis* females achieve the same maximum size as TP males, the only IP males are small individuals, and very small TP males are often found. Second, in *Cryptotomus roseus*, *Sparisoma viride* and *C. spinidens*, TP males achieve larger sizes than IP fish, and males are found in most IP size classes. In addition, small TP males are uncommon in both *C. roseus* and *C. spinidens*.

While sex-changing fish that function in both sexes are almost universally present among the species of wrasses and parrotfishes that have been examined so far, other sexual phenotypes are not infrequently found—primary males, secondary-gonochore males and gonochoristic females (=primary females; Warner and Robertson, 1978). These phenotypes may represent different genotypes and, for the purposes of this discussion, we will assume they do. There is considerable variation between different species of wrasses and parrotfishes in terms of which sexual phenotypes are present and what proportion of the population they represent. The coexistence of any two such sexual genotypes in a population depends on the ability of individuals of one to maintain a lifetime production of offspring that is equivalent to that of individuals of the other (Warner et al., 1975). Protogynous individuals potentially have a selective advantage over primary males and primary females when large males gain disproportionately large amounts of the matings at the expense of small males (Ghiselin, 1969; Warner, 1975). Sometimes primary males do attain significant levels of spawning activity when they are small; in other cases, they do not appear to do so and may compensate by growing rapidly to the more productive large-male phase (Warner and Downs, 1977). Primary females may be able to coexist with protogynous individuals if they live longer than those sex-changers; although the average daily frequencies of spawning of sex-changers that are in the male phase may be greater than those of females of the same age, the total life-time production of zygotes by long-lived primary females might equal that of shorter-lived sex-changers (Robertson and Warner, 1978).

If the ideas outlined above on the coexistence of different sexual genotypes are correct, then, in a population composed entirely of gonochorists, males should either be highly successful spawners when small or combine some spawning activity with rapid growth, and females should be longer-lived than males if males spawn at higher rates than females do. *Leptoscarus vaigiensis* does appear to be gonochoristic and, from the small amount of information available, its mating system and population structure seem supportive of the above prediction. First, females achieve at least the same size as males; they may live longer than males if they put more energy into gamete production than do males and have less available for growth. Second, small functional TP males are common; a delay in the size at which males changed from the IP to the TP would be expected if small TP males had little or no success in spawning. Third, IP males do spawn, i.e., small males do achieve some reproductive activity, *L. vaigiensis* shares various characteristics with other labroids in which spawning by small males is common: a moderate abundance of individuals, the tendency to be nonterritorial and form schools, and the habit of spawning in grassbeds. In such species, large aggressive males may have difficulty preventing other males, both small and large, from approaching while the large aggressive males are spawning. Males that are likely

to interfere in large males' spawnings are numerous and, by concealing themselves in seagrass, can easily approach close enough to be able to make a short dash to join a large male's spawning (Warner et al., 1975; Robertson and Warner, 1978; Warner and Robertson, 1978). *Leptoscarus vaigiensis* shares these behavioral characteristics with *Sparisoma radians*, in which primary females evidently are present, and probably secondary-gonochore males also (Robertson and Warner, 1978).

In *C. spinidens*, primary males coexist with both protogynous fish and secondary-gonochore males. It seems that primary males do succeed in spawning when small (i.e., in the IP). Males of both color phases evidently interfere in the pair spawnings of large aggressive males and such interference probably is facilitated by the same combination of factors—moderate population densities, schooling tendencies and spawning in grass beds—as in *L. vaigiensis*. *C. spinidens* is less abundant than *L. vaigiensis*, which may reduce the frequency with which small male *C. spinidens* interfere in the spawnings of large males (Warner et al., 1975; Warner and Robertson, 1978; Warner and Hoffman, 1980), and thus make conditions more favorable for the evolutionary persistence of protogynous sex-changers in that species.

The pattern shown by the few data obtained for *C. carolinus* is consistent with correlations previously found between population density, sociality, spawning success of small males and population sex-structure in other labroids. Warner and Robertson (1978) and Robertson and Warner (1978) found that in non-schooling species with low densities, both small males and primary males are relatively rare, which they attributed to small males having a low potential for interference spawning. *C. carolinus* did not school, was less dense, and had fewer small males and primary males than did *L. vaigiensis* and *C. spinidens*.

While the existing data on the mating systems of *L. vaigiensis*, *C. spinidens*, and *C. carolinus* do correlate with what is known of their population structures, many more quantitative data are needed on the longevity and age-specific spawning rates of the different sexual phenotypes in each to thoroughly establish whether these correlations hold and to demonstrate why the three species have such different population structures.

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