DAILY AND SUMMER-WINTER VARIATION IN MASS SPAWNING OF THE STRIPED PARROTFISH, *SCARUS CROICENSIS*

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ABSTRACT

The "striped" phase of the striped parrotfish, *Scarus croicensis*, engaged in mass spawning during afternoon periods on a deep (24 m) coral pinnacle off Discovery Bay, Jamaica. During morning periods the fish occurred in a large foraging group on shallow reefs and moved to the spawning site in early afternoon. The occurrence of spawning rushes per day in June was about six times that during January. *Chromis cyanea* and *Clepticus parrai* fed on freshly released eggs of *S. croicensis*. Mass spawning by *S. croicensis* was similar to that of *Sparisoma rubripinne*.

The striped parrotfish, *Scarus croicensis* Bloch (Figure 1), is the smallest (reaching 25 cm SL, standard length) but the most common member of this genus in the tropical western North Atlantic (Randall 1968; Böhlke and Chaplin 1968). Like other scarids, *S. croicensis* is a benthic herbivore grazing on algal-covered rock and coral surfaces and is seldom found at depths below 30 m. The species possesses dimorphic color phases, termed the "striped" phase (male and female) and the "terminal" phase (male only), believed derived from striped phase females by protogynous sex reversal (Ogden and Buckman 1973).

Aspects of the general biology of this fish have been reported on by several authors. Ogden and Buckman (1973) followed movements of tagged individuals in Panama and found daily migrations between feeding and sleeping areas. Feeding was largely carried out in foraging groups of up to 500 individuals with a characteristic set of associate, but less numerous species. Buckman and Ogden (1973) described territoriality by striped phase females and terminal phase males. Barlow (1975) discussed the sociobiology of *S. croicensis* in comparison with three other species of parrotfishes and described their feeding pattern, group sizes, density, and color variation. He also added some notes on spawning behavior of *S. croicensis*.

Randall (1963) reported both mass spawning by the striped phase of *S. croicensis* and pair spawning by terminal phase males and striped phase females. Randall and Randall (1963) described pair spawning at St. John, V. I., during February,
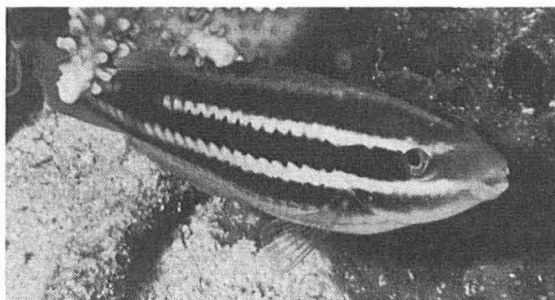

FIGURE 1.—Striped parrotfish, *Scarus croicensis,* with "contrast" color pattern approximately 100 mm standard length at Discovery Bay, Jamaica.

March, April, June, and August, and with their limited observations they felt that pair spawning accounted for most of the reproduction of the species. Buckman and Ogden (1973) commonly observed pair spawning at depths of 9-13 m, but also as shallow as 3 m, in Panama. Munro et al. (1973) found females of the striped parrotfish in ripe condition from March to May near Jamaica.

In August 1971 a large spawning group of striped parrotfish was encountered on a deep coral platform (24 m) offshore from the Discovery Bay Marine Laboratory on the north coast of Jamaica. This species is by far the most common parrotfish along this coast, which is heavily fished using Antillean fish pots. This spawning group consisted of several hundred individuals. Its reproductive activity was sufficiently regular and observable that investigation of diel patterning of spawning seemed feasible. Widely scattered observations from 1971 to 1975 indicated the continued presence of this group. During January and June

1975 systematic observations of spawning behavior were conducted.

MATERIALS AND METHODS

For purposes of determining diel variation of spawning activity, the daylight period (from sunrise to sunset) was divided into 16 equal periods. As occasional checks during the morning indicated that the spawning population was not present at the spawning site and was not spawning elsewhere, only the latter eight periods of the day were included in this study. Since day length varied considerably between January and June observations, the length of each period also varied by the same factor. The change of day length during each of the two series of observations was only a few minutes.

During the winter observations (12-28 January), the day length was 11 h 10 min with 42 min for each period. During summer (19-29 June), the day length was 13 h 10 min with 50 min for each period, an increase of 17% in day length. Water temperature at the study site varied between 26° and 29°C seasonally.

The number of spawning rushes, the upward dash by groups of parrotfish culminating in the release of eggs and sperm, occurring during 15 min within the observation period was counted by an observer (wearing scuba equipment). This time was chosen as the minimum for measurements of spawning rush frequency due to the somewhat irregular occurrence of the rushes on a minute by minute basis. In the latter portion of the study, data were recorded minute by minute for the full

15-min period. The observers were tethered near the spawning site by lines attached to the bottom which caused them to float nearly motionless at 21 m depth, approximately 3 m above the substrate. This allowed observations to be made from a consistent location, minimized movement needed to stay in position, and decreased the depth of the observers slightly to allow more bottom time for observations with no or short decompression at the end of the dive. The presence of the observers did not seem to interrupt or affect the spawning behavior as the population did not move away or cease spawning after the observers' arrival.

Color motion pictures (16 mm) were made of spawning and feeding behavior of *S. croicensis*, including some at two times normal film speed for slow motion analysis of movement. Films were analyzed on a frame by frame basis.

GENERAL BEHAVIOR

A general profile of the area near the spawning site is presented in Figure 2. Sand channels run between fingers of reef directed seaward which gradually slope from a shallow reef crest to a zone dominated by the branched coral *Acropora cervicornis* at 10-13 m depth. At the seaward edge of this *A. cervicornis* zone, the reef slopes steeply to a sandy bottom at 24-25 m depth. Beyond this point the sand bottom either slopes rapidly downward to the near vertical dropoff or has an outer reef rising above it, often resembling a rounded pinnacle and somewhat trapping the sediment behind it. The pinnacle of "Dancing Lady Reef" was the location of the spawning observed in this study. On the
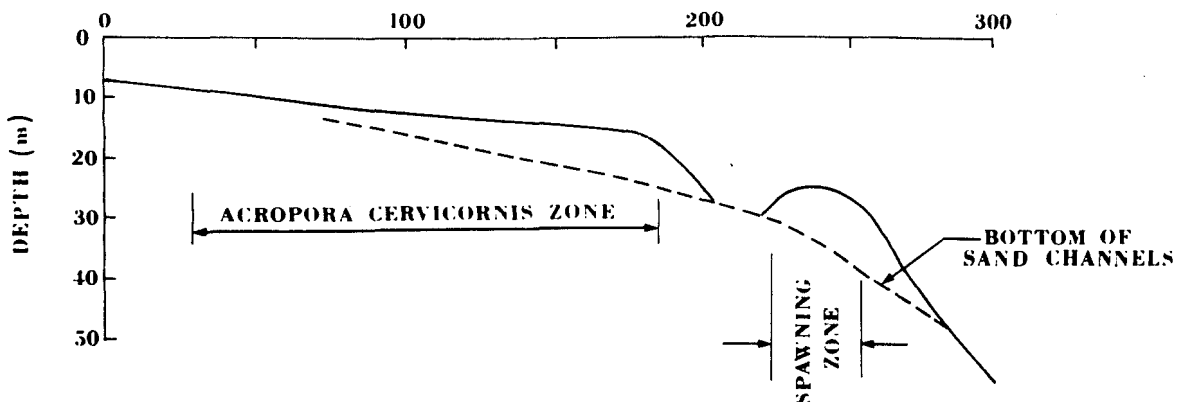

FIGURE 2.—Bottom profile of "Dancing Lady Reef" offshore from the Discovery Bay Marine Laboratory. Vertical exaggeration is 2×.

outer face of this pinnacle, the reef drops away steeply and at a depth of 50-70 m becomes nearly vertical in profile.

In Jamaica *S. croicensis* occurred in foraging groups similar to those described by Ogden and Buckman (1973) in Panama. In the vicinity of the spawning site only one sizeable foraging group occurred. Although no tagging experiments were carried out, this group almost surely constituted the major portion of the spawning population studied. During morning hours this group ranged as much as 300 m inshore from the spawning area onto the shallow reefs to depths of as little as 7 m. They also ranged only about 100 m in either direction parallel to shore along the reef.

These foraging groups consisted of several hundred *S. croicensis* (the exact number being impossible to determine in most cases) plus a few other fishes. In one instance at least 410 individuals of *S. croicensis* were visible in photos taken of the entire group. Only a few terminal phase males were seen in these groups. The group swam about 1 m above the substrate in the *A. cervicornis* zone and descended en masse at intervals to feed. Algae were scraped from rock surfaces of the reef, particularly from the dead lower portions of the branches of *A. cervicornis*.

Mixed foraging groups consisting largely of *S. croicensis* have been reported by Buckman and Ogden (1973) and Itzkowitz (1974). In the former two species of acanthurids (*Acanthurus chirurgus* and *A. coeruleus*); a hamlet, *Hypoplectrus puella*; a goatfish; and a few other parrotfishes were typically found associated with the foraging groups. Similar composition of associated species was observed in the present study. Only *A. coeruleus* among the surgeonfishes occurred with the foraging group. However, *A. chirurgus* is relatively rare in the study area. A different species of hamlet, *H. indigo,* also occurred with the foraging group rather than *H. puella*. Among fishes observed occasionally joining foraging groups and not mentioned by Buckman and Ogden (1973) was *Halichoeres maculipinna*.

The functionality of such schooling behavior has been commented on before. Various Indo-Pacific surgeonfishes form schooling groups which behave much like the foraging groups of *S. croicensis* (Jones 1968; Randall 1970; Barlow 1974). Randall (1970), Barlow (1974), and Vine (1974) believed this foraging herd was a method for the surgeonfishes to swamp the defenses of territorial food competitors, in the former instance an acan-
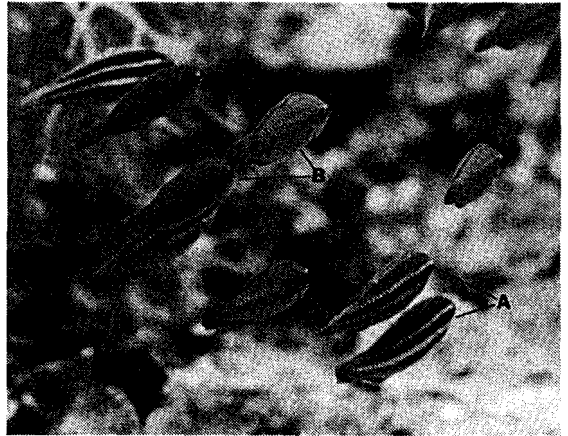

FIGURE 3.—Striped phase individuals of *Scarus croicensis* at Discovery Bay, Jamaica, in the "contrast" color form (A) and "gray" form (B). Standard length is approximately 100 mm.

thurid and in the latter a pomacentrid. This also seems to be the case in the present study. When the foraging group entered the territory of *Eupomacentrus planifrons,* attacks were quickly directed at a few members causing an escape reaction in the few individuals near the center of attack. The group was largely undisturbed by the actions of the damselfish.

Two color forms of striped phase *S. croicensis* were seen in both foraging and spawning groups. The first had two broad dark stripes separated by thinner pale stripes, the dorsal surface dark and the snout yellowish. This form is termed the "contrast" (Figures 1, 3). The second color form, termed the "gray" form does not have the sharp contrast between dark and pale stripes (Figure 3). The stripes are apparent on the head, but posteriorly they become much less distinct. The scales near the caudal peduncle, even in the center of the dark stripe, are pale-edged and resemble a checkerboard pattern. In foraging groups one-fourth to one-half of the indivuals had the gray color pattern and the remainder were of the contrast pattern. No functional role could be assigned to these color forms. The possibility does exist that they represent male and female, but this could not be established.

MASS SPAWNING BEHAVIOR

Spawning occurred on the deep coral pinnacle (Figure 2) of Dancing Lady Reef at 24 m depth. This pinnacle is the feature with the greatest re-

lief for a distance of several hundred meters along the outer face of the reef. Transects were swum along the sloping face for 200-300 m each direction from the study area while spawning was underway at that site and no other spawning aggregations were encountered. In one instance a group of several *S. croicensis* were observed spawning on the seaward face of a shallow reef immediately west of Dancing Lady Reef at 18 m depth.

The spawning population did not arrive en masse at the spawning site, but rather appeared in small groups over a lengthy period of time. Whether the foraging group breaks up on the shallow reef before the individuals move to the spawning site is not known. The behavior of the striped parrotfish after arrival at the spawning area consists of swimming in small groups around the area within a few meters of the bottom ("milling") and bouts of feeding (from the substrate).

The size of eight individuals speared from the spawning aggregations varied between 80 and 100 mm SL, relatively small for mature specimens. These are deposited in the University of Puerto Rico fish collection (UPR 3452). This sample is biased for small individuals since these were most easily approached and the mean size of specimens in the aggregation was certainly near or over 100 mm SL.

The numbers engaged in milling and the speed and frequency of turns gradually increased. Often groups of 20 or more individuals broke away from the main group and swam as a school farther above the substrate than the milling individuals (Figure 4A, B). The separated group swam increasingly rapidly making abrupt lateral turns ("weaving"). The entire group or a portion of it rushed upward extremely rapidly a distance of several meters (Figure 4C, D) releasing eggs and sperm at the peak of the "rush." They returned to the substrate nearly as rapidly (Figure 4E). Because of the large numbers of individuals present in the spawning aggregation, several separate weaving groups could be present and rush at near the same time. Rushes by some weaving groups began at the level of at least 3 m above the substrate as they were level with the observers' line of sight.

From analysis of motion pictures of spawning behavior the number of fish engaged in a rush varied between 5 and 30 with the mean number about 15 individuals. Generally only about one-half of the group engaged in weaving actually participated in the rush and often a few individuals starting the upward rush were left behind. The entire upward rush and return to the level of the weaving group took <1 s. Of seven rushes which were filmed in their entirety the time for the upward movement varied between 0.21 and 0.40 s and for the return 0.20 and 0.40 s. One rush with return occupied only 0.45 s total. Assuming a distance of 3 m was covered during the upward rush (probably a conservative estimate), the average speed from leaving the weaving group until turning at the point where the gametes are released was around 40 km/h.

The sexual composition of the rushing groups has not been determined. Randall and Randall (1963) believed that the spawning groups of *Sparisoma rubripinne* were predominantly males and that a single female participated in the spawning rush with 3 to 12 males.

A single terminal phase male *Scarus croicensis* was present at the spawning site. This fish vigorously defended a territory near the outer edge of the coral pinnacle and patrolled the area in the "bob-swim" manner with the caudal fin upturned as described by Barlow (1975). No attempts at pair spawning with striped phase females by this fish were observed. The only other parrotfish observed on the deep coral pinnacle was *Sparisoma viride* with only a few present.

SPAWNING FREQUENCY

The frequency of rushes during the daily periods for both January and June is presented in Figure 5. The summer spawning begins earlier in the day, continues later, and has a higher frequency of rushes than during the winter. It is impossible to determine the number of eggs released per rush and whether differences exist between summer and winter. No data are available concerning the number of fish participating in rushes during winter, but observations suggest this was also lower.

Considering an equal number of eggs are expelled on each rush, it appears that the production of eggs by this population of *Scarus croicensis* is about six times greater during a summer day than winter on the basis of the area beneath the curves derived from Figure 5. It is likely that *S. croicensis*, at least in the Caribbean, spawns year round, but the warm months are the most important period of egg production.

During the summer the occurrence of spawning rushes might be referred to as epidemic. When the
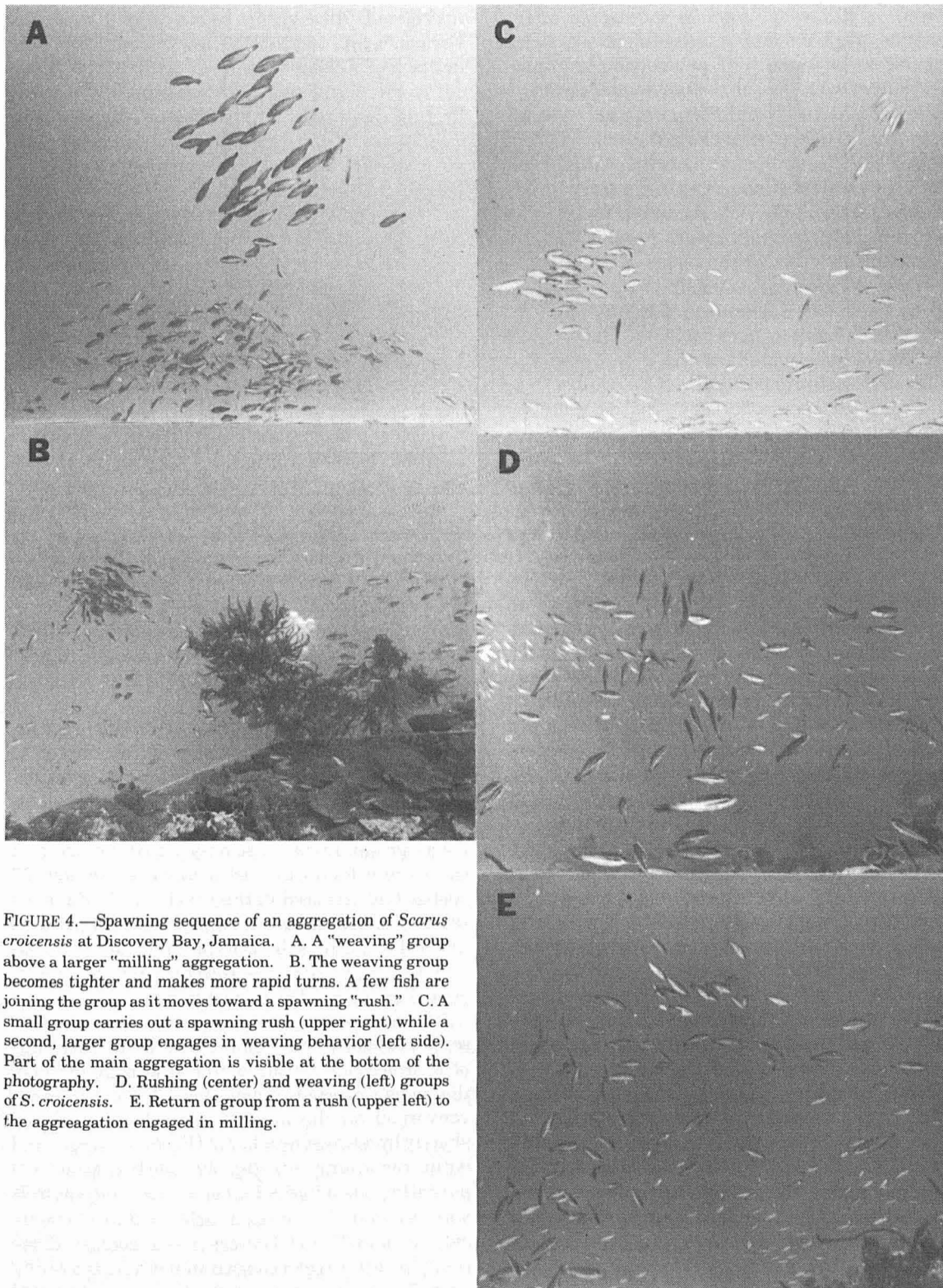
FIGURE 4.—Spawning sequence of an aggregation of *Scarus croicensis* at Discovery Bay, Jamaica.   A. A "weaving" group above a larger "milling" aggregation.   B. The weaving group becomes tighter and makes more rapid turns. A few fish are joining the group as it moves toward a spawning "rush."   C. A small group carries out a spawning rush (upper right) while a second, larger group engages in weaving behavior (left side). Part of the main aggregation is visible at the bottom of the photography.   D. Rushing (center) and weaving (left) groups of *S. croicensis*.   E. Return of group from a rush (upper left) to the aggreagation engaged in milling.
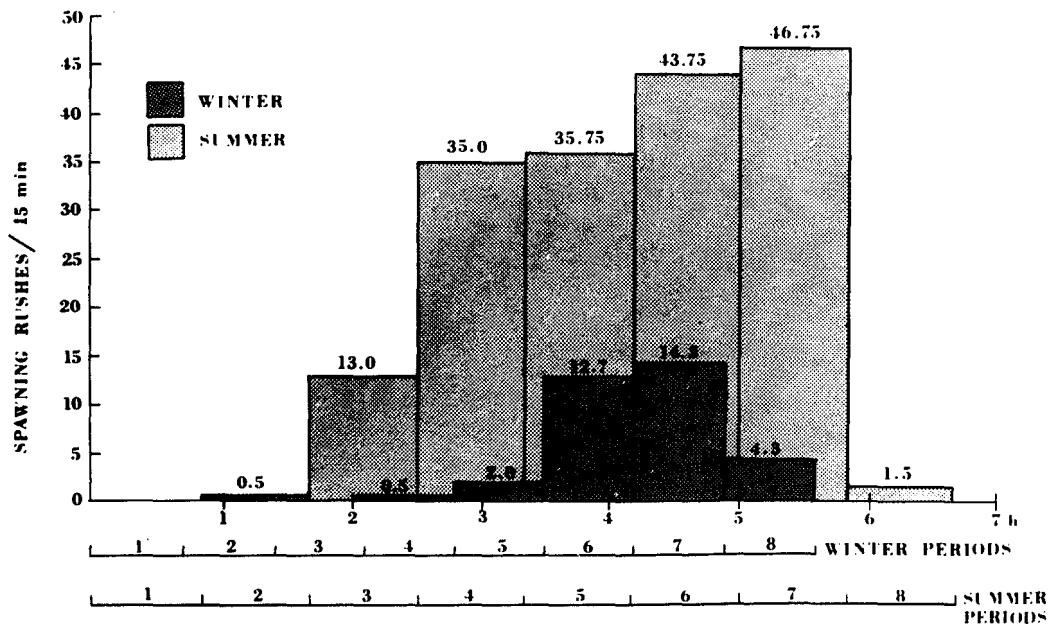
FIGURE 5.—Daily variation of spawning rushes during June (summer) and January (winter) by a population of striped parrotfish at Discovery Bay, Jamaica. The beginning of period 1 represents midpoint of the day and the end of period 8 sunset. Figures represent mean of two observations (periods 1-3) and four observations (periods 4-8).

data are analyzed on a minute by minute basis, over 90% of the spawning rushes observed occurred during only 33% of the 1-min periods. Since the group engaged in a spawning rush is considerably smaller than the total population at the spawning area, it is possible for several groups to carry out a spawning rush separately, but nearly simultaneously. The occurrence of the first rush by a group seems to trigger other groups to spawn. A flurry of rushes lasted a period of 1-4 min and in one case reached a frequency of 35 rushes in a 1-min period. This number may be underestimated due to the difficulty in observing and counting such rapid events. The period between groups of rushes was spent in milling about close to the substrate and feeding on exposed rock surface of the reef.

The time between episodes of epidemic rushing varied during the day in summer periods. During early periods when some spawning occurred (period 3 and to a lesser extent period 4) often 5-7 min would elapse without any rushes occurring. In one case there was 9 min between rushes. Later in the day, at times of peak spawning (periods 5-7), these nonspawning periods were reduced to 1, 2, and occasionally 3 min.

PREDATION

Mackerel (either cero, Scomberomorus regalis, or king mackerel, S. cavalla) twice attempted to prey on Scarus croicensis at the top of the spawning rush, once apparently successfully. These attacks interrupted the spawning behavior of the entire group. In one case only 1 rush occurred in the 10 min following the attack even though 67 rushes had occurred in the previous 15 min. On a third occasion, a lizardfish, Synodus sp., rushed upward from the substrate in an unsuccessful attempt to prey on Scarus croicensis and thus interrupted spawning for a short period.

Chromis cynaeus and Clepticus parrai were observed to feed actively on the freshly released eggs of S. croicensis. Within 5-10 s after completion of the spawning rush, numerous Chromis cyaneus converged on the area of egg release, followed shortly by a lesser number of Clepticus parrai, and while remaining in a tightly bunched group apparently picked individual eggs from the water. It was estimated that as many as 200 Chromis cyaneus and 20-30 Clepticus parrai composed one group picking eggs released in a single spawning rush. The group remained tightly bunched and fed

for about 1 min, moved slowly with the current (and presumably with the eggs), and dispersed quickly returning as individuals to a position closer to the substrate. Whether dispersion of the released eggs, depletion of the eggs by feeding, or some other factor caused cessation of the feeding by *Chromis cyaneus* and *Clepticus parrai* is not known. A few hundred predators, each ingesting at least one egg every few seconds for periods of nearly 1 min, could eliminate a significant portion of the eggs released in any given spawning rush.

These groups of egg predators form after only a small percentage of spawning rushes. During the "epidemic" rushes of summer periods, there are too many eggs released at several locations for these predators to significantly deplete the number released. During winter periods when rushes were few, there did not seem to be sufficient gamete release for the egg predators to wait for rushes to occur and consequently no predation on eggs was observed during these periods. The predation on newly released eggs of *S. croicensis* is obviously an intentional activity of the predators, not a chance occurrence, but probably serves only as a "bonus" for these fishes which normally spend lengthy portions of the day feeding on particulate zooplankton in the water column (Davis and Birdsong 1973).

DISCUSSION

The mass spawning behavior of *S. croicensis* is similar to that described for *Sparisoma rubripinne* by Randall and Randall (1963). The movement of the population to the deep-reef area in the early afternoon, its behavior before and during rushes, the epidemic rushes, and other behavior is nearly identical. This similarity in mass spawning between genera lines in parrotfishes is interesting.

It would be most informative to know the numbers needed before both foraging aggregations and striped phase spawning aggregations occur. Small groups of 15-20 *Scarus croicensis* have been seen moving together between bouts of feeding, but seem easily deterred by damselfishes defending territories.

At least on the north coast of Jamaica, mass spawning probably contributes most of the eggs produced by *S. croicensis*. Pair spawning was never observed in the vicinity of Discovery Bay although terminal phase males were present but never abundant. The summer season is certainly the most active reproductive period.

The occurrence of mass spawning by parrotfishes at specific locations on the reef is a relatively long-term phenomena. In the present case nearly 4 yr have elapsed since the initial encounter with the spawning group and the location of spawning has not varied. More interestingly, the spawning location of *Sparisoma rubripinne* at Reef Bay, St. John, investigated by Randall and Randall (1963), was visited in March 1977. Following the directions provided by those authors, a group of approximately 200 *S. rubripinne* were found engaged in spawning during the late afternoon. The presence of a spawning aggregation in what is believed the identical location on the reef after 17 yr in similar numbers to that previously reported indicates a stability and importance of spawning locations not previously documented. The occurrence of spawning by *S. rubripinne* on 3-4 March extends the period reported by Randall and Randall (1963) and supports their belief in year round spawning. Also the water temperature of 25.8°C was slightly lower than that previously reported.

The reasons for the abundance of *Scarus croicensis* compared with some other scarids (such as *Sparisoma rubripinne*) are difficult to determine. Randall (1967) reported three species of fishes (*Mycteroperca interstitialis, M. venenosa,* and *Caranx ruber*) which definitely preyed on *Scarus croicensis*; however, individals of *Scarus* (not identifiable to species) were found in guts of several other predatory fishes. Ogden and Buckman (1973) added *Epinephelus striatus* and *Scomberomorus regalis* as predators of *Scarus croicensis*. Due to overfishing, few large predatory fishes are found on the outer reef at Discovery Bay. Indeed, few of the larger species of *Scarus* and *Sparisoma* occur there for the same reason. This may be an important factor allowing relatively high numbers of *Scarus croicensis* to occur there and schooling behavior to be effective in overwhelming the defenses of territorial herbivores.

Alevizon and Brooks (1975), in examining two coral-reef fish assemblages (Islas Las Aves, Venez. and Key Largo, Fla.), found *S. croicensis* to be only a minor component of one (Florida) and of no consequence at the other (Venezuela). Possibly they sampled areas where *S. croicensis* was not abundant. In other areas *S. croicensis* may be absent, even though the environment seems typical of that in which it normally occurs. At Isla Desecheo, a small (1 km²) island 20 km west of Puerto Rico in the Mona Channel, extensive diving operations failed to reveal the presence of *S. croicensis* even

though we have specifically searched for it. Other scarids occur there, and there seems no simple reason for the nonoccurrence of *S. croicensis* at this island.

ACKNOWLEDGMENTS

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