COMPARATIVE EARLY LIFE HISTORIES OF WESTERN ATLANTIC SQUIRRELFISHES (HOLOCENTRIDAE): AGE AND SETTLEMENT OF RHYNCHICHTHYS, MEEKI, AND JUVENILE STAGES

James C. Tyler, G. David Johnson, Edward B. Brothers, Diane M. Tyler and C. Lavett Smith

ABSTRACT

Fishes of the family Holocentridae have a morphologically distinctive postlarval "rhynchichthys" stage characterized by extensive head spination, including a prominent serrate rostral spine. In most species the rhynchichthys physiognomy persists until settlement, which occurs within a size range of about 30–50 mm SL. The two species of *Holocentrus* have a uniquely protracted pelagic period during which they transform from the rhynchichthys at about 40 mm SL to a distinctive, unornamented, and relatively streamlined prejuvenile "meeki" stage that may reach 74 mm SL prior to settlement. Analysis of daily growth increments in lapilli of recently settled juvenile and adult holocentrids confirms that the pelagic stages of *H. ascensionis* and *H. rufus* grow more rapidly and settle at significantly greater ages and larger sizes than other holocentrids. A microstructural transition zone in the otoliths of these two species probably corresponds to the rhynchichthys-meeki morphological transformation of these pelagic stages. In other holocentrids examined a similar microstructural transition corresponds to the rhynchichthys-juvenile morphological transformation associated with settlement onto reefs. The average age and size of small juveniles of *H. rufus* collected at their earliest appearance during censuses of shallow reefs was 67 days and 66 mm SL, but the average pretransition increments in their lapilli was only 44. Limited data for *H. ascensionis* are similar, but differ in average age (59 days) and size (56 mm SL) at settlement and number of pretransition increments (48). The size of specimens found in museum collections also substantiates that *H. rufus* is larger at settlement (and has a larger maximum size meeki stage) than *H. ascensionis*. The two meeki stage specimens for which we have otolith data (for *H. rufus*, both slightly less than 50 mm SL) lack the expected transition mark. However, their ages at capture (38 and 43 days) suggest that they are newly transformed from the rhynchichthys stage, and marginal transition marks are difficult to identify. Daily growth increments were validated in one meeki stage *H. rufus* and two rhynchichthys stage *Sargocentron coruscus* that were maintained, respectively, for five and nine days in aquaria after strontium infusion of their otoliths. The rapid morphological transformation of the meeki stage into a benthic juvenile within two days of capture, including overnight change in coloration from blue above and silver below to orangish red with pale stripes, is described.

As part of our ongoing survey of early life history stages and settlement of fishes at the Smithsonian Institution marine laboratory at Carrie Bow Cay, Belize, in the western Caribbean, we collected two small elongate silvery blue fishes (Fig. 1) in a moored plankton net on the shallow reef flat. Our first impression was that these were probably some type of planktivorous percoids such as emmelichthyids or inermiids, but we soon realized that they were a pelagic stage of the common squirrelfish *Holocentrus rufus*. Although we were aware that squirrelfishes have a pelagic postlarval "rhynchichthys" stage, our two specimens were significantly larger (58–59 mm SL) and more streamlined than any rhynchichthys we had seen and, more importantly, they did not have the prominent rostral spine and other head spination (occipital and opercular) typical of that stage.

Our subsequent investigations located numerous specimens of this distinctive pelagic prejuvenile stage representing both species of *Holocentrus* (*rufus* and *ascensionis*) in the collections of several museums in the United States. We also
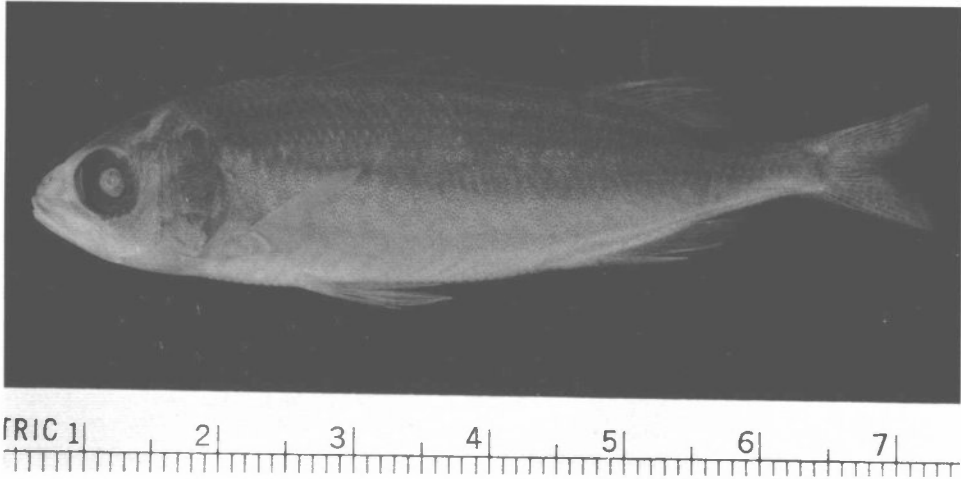
Figure 1. *Holocentrus rufus,* meeki stage, USNM 316408, 58.9 mm, 9 November 1988, Carrie Bow Cay, Belize.

learned that it had been described originally as a new species, *H. meeki* (Bean, 1906a), and that its true identity had been first recognized by Beebe (1936) based on his observations of transformation of captive specimens at Bermuda.

The "meeki" stage apparently is unique among holocentrids to *Holocentrus* and little is known about it. Because it attains significantly larger sizes than the larval rhynchichthys stage, we presumed that *H. rufus* and *H. ascensionis* have an extended pelagic duration. However, the otoliths of the two species of *Holocentrus* had distinct transition zones at about the same daily increment count as those of other species of holocentrids examined, suggesting that all of the species had settled to the reef at approximately the same age. This enigmatic finding led us into a more extensive analysis of presettlement and juvenile age and growth of *Holocentrus* in comparison with that of other western Atlantic holocentrids based on museum specimens as well as those collected for otolith analysis. In the process, we collected several meeki stage *H. rufus* at Carrie Bow Cay, strontium marked the otoliths of one of them and observed its transformation into a juvenile in an aquarium.

The purposes of this paper are to present the results of the comparison of presettlement and juvenile age and growth in seven species of five genera of western Atlantic holocentrids, with an emphasis on the pelagic meeki stage of *H. rufus* and its transformation to the benthic juvenile stage. The data are supportive of two hypotheses relating to the ecological significance of the meeki stage of *Holocentrus*: (1) *Holocentrus* has a longer average pelagic existence than other western Atlantic holocentrids; (2) the meeki stage represents an extended period of competency and individuals have the ability to rapidly transform to benthic juveniles when exposed to the appropriate environmental stimuli.

METHODS

Specimens are from the National Museum of Natural History (USNM), American Museum of Natural History (AMNH), Academy of Natural Sciences of Philadelphia (ANSP), Field Museum of Natural History (FMNH), Museum of Comparative Zoology (MCZ), and Yale Peabody Museum, Bingham Oceanographic Collection (YPM). We also examined larval and juvenile holocentrids from the Royal Ontario Museum (ROM) and Dana Collection, Zoologisk Museum, University of Copenhagen (ZMUC) but found none pertinent to the present study.

All specimens of presettlement stages of holocentrids collected during the course of this study are catalogued at the USNM (most with the otoliths removed), but the more numerous specimens of settled juveniles and adults collected for otolith analysis were not retained.

All measurements are in standard length (SL). Size of specimens collected for otolith analysis is given to the nearest whole mm, whereas data on all museum specimens is given to the nearest tenth of a mm for specimens under 100 mm.

Lateral line scale counts are of tube-bearing scales.

We follow Matsuura and Shimizu (1982) in recognizing *Sargocentron* as the valid generic name for the species previously referred to *Adioryx* (in the western Atlantic, *coruscus* and *vexillarius*).

Throughout the text CBC refers to Carrie Bow Cay (Ellen Cay), Belize (16°48′N, 88°05′W), a small barrier reef island about 18 km east of the nearest point on the mainland (Sittee Point, south of Dangriga).

Our collections of larval fishes at CBC were made with stationary plankton nets of 1 m and 0.5 m diameter and 0.505 mm mesh during periods of 2 weeks duration of nightly sampling at least once and usually twice a year (in different months) in each year between 1986 and 1992, for a total of about 140 evenings of collecting. The nets were set in water less than 1 m deep (about 7 m from shore) in a back–reef sea grass bed over which there usually was at least a moderate onshore flow of water. Most of these collections were made at night between 1900 and 2200, for successive 30-min periods, and on each of the three evenings that we collected meeki stage *Holocentrus* (four specimens in toto) in these stationary nets there was a strong onshore (toward the west) wind driving a swift flow of oceanic water over the reef crest and across the back reef.

Freshly captured presettlement stages of *Holocentrus* and *Sargocentron* were placed in a solution of 5 g strontium chloride per 2,000 ml of sea water for 24 h and then transferred to a tank with running sea water, where they were fed each evening with fresh plankton (from light trap collections). At the end of the holding period, the aquarium specimens were placed in 95% ethanol, immediately measured, and subsequently dissected for otoliths. In referring to the number of days specimens were kept alive in aquaria, only full days are counted; i.e., the day of the evening of capture and the day of the morning of preservation are not included.

Juvenile and adult holocentrids were collected at CBC, St. Croix, and Panama (San Blas) with handnets, quinaldine, and rotenone. In Panama, study reefs were censused on a daily basis by divers attempting to capture all new recruits.

All otolith aging was done on lapilli following the methods detailed in Brothers (1987, 1990), Brothers and McFarland (1981), and Keener et al. (1988). Ground and polished frontal sections of the lapilli were read with video-enhanced light microscopy at an optical magnification of 1,000× (electronically scaled to 2,500×). Increment counts and strontium marks for validation of daily deposition were confirmed with an SEM. Microstructural transitions presumed to be associated with settlement or other eco-behavioral/morphological shifts were identified using criteria established for other reef fishes (Brothers, 1984; Brothers and McFarland, 1981; Brothers et al., 1983; Brothers and Thresher, 1985; and Keener et al., 1988). Back calculations to spawning dates include an estimated correction factor of 2 days for the time from fertilization to the formation of the first increment, whereas specimen ages are post-hatching and do not include the 2-day correction factor.

Previous Studies of *Holocentrus* Early Life History

The planktonic rhynchichthys postlarval stage common to all holocentrids was first described by Valenciennes (1831: 503) and its morphology is relatively well studied in some species (e.g., for *Sargocentron vexillarius* by McKenney, 1959). Its most distinctive features are the prominent serrate spines on the rostrum, occiput, and opercle.

The large pelagic meeki prejuvenile stage unique to *Holocentrus* is poorly known. It was first described as a new species, *Holocentrus meeki,* by Bean (1906a: 31; fuller description and illustration in Bean, 1906b: 42, 43) based on two specimens, 70.3 and 74.1 mm, from Bermuda. Beebe and Tee-Van (1933: 73, 74) briefly redescribed *H. meeki* based on Bean's two specimens and apparently a few others also from Bermuda. Beebe (1936) was the first to recognize that *Holocentrus meeki* is not a valid species but, rather, represents the prejuvenile stage of *H. rufus* and *H. ascensionis.* He reported on hundreds of specimens of *H. meeki* collected at Bermuda during September 1935, including 66 specimens recovered in excellent condition from the stomachs of tunas and six specimens taken in one evening of night-lighting and maintained in aquaria. Of the latter Beebe (1936: 198) wrote: "Before our eyes, little by little, in the course of several weeks they changed from

Holocentrus meeki to the common squirrelfish, *Holocentrus ascensionis*. The soft dorsal and anal fins increased in height, the depth of the body became greater, the greenish metallic tints gave place to rose and scarlet, and the abrupt, unlovely profile of the caudal peduncle slowly took form in our aquariums. There was no doubt about the fact that *meeki* is the immature stage of *ascensionis*."

At the time of Beebe's writing, *H. ascensionis* and *H. rufus* often were considered only varieties or subspecies and usually were referred to under the older name *H. ascensionis* (Osbeck, 1765) rather than *H. rufus* (Walbaum, 1792). The characters of *H. meeki* described by Bean and by Beebe and Tee-Van include a high lateral line scale count (54–55) and a short upper jaw reaching only to the level of the front of the eye. These are the two most important external features distinguishing *H. rufus* from *H. ascensionis,* and our examination of the cotypes of *H. meeki* (FMNH 5079 and 96015) verifies that they are *H. rufus.*

Fowler (1944: 100, 101) described a new genus and species, *Beloholocentrus atractus,* based on seven presettlement holocentrids from Courtown Key or Cayos del Es Sudeste in the western Caribbean (off Nicaragua, 12°25′N, 81°25′W), six in the meeki stage and one in the rhynchichthys stage. The range of lateral line scale counts (48–53) and upper jaw lengths (reaching posteriorly to between anterior edge of pupil and middle of eye) given by Fowler encompass both *H. rufus* and *H. ascensionis.* In his review of the western Atlantic species of *Holocentrus,* Woods (1955: 95) surmised that *Beloholocentrus* was based on the rhynchichthys stage of *H. ascensionis* and the meeki stage of *H. rufus.* We have examined the type specimens of *B. atractus* (ANSP 70079 and 70080) and find that the holotype (56.6 mm) and five larger paratypes (52.5–56.1 mm) are meeki stage *H. rufus,* and the smallest paratype (24.0 mm) is a rhynchichthys stage *H. ascensionis.*

Woods (1955) recognized four subgenera of *Holocentrus,* with *H. rufus* and *H. ascensionis* comprising the subgenus *Holocentrus,* based on the specialized association of the swim bladder with the auditory bulla (Nelson, 1955: 126) that is absent in the other subgenera (*Adioryx, Flammeo,* and *Sargocentron*). He distinguished *H. rufus* from *H. ascensionis* based on its high lateral line scale count and shorter upper jaw (for all but the smallest specimens) and, in specimens of greater than 70 mm, its longer preopercular spine and shallower depth. Woods (1955) had only a single meeki stage *H. ascensionis,* 61 mm from the Virgin Islands (FMNH 46198), and his smallest settled juvenile of *H. ascensionis* was 52 mm. He found the 70 and 74 mm cotypes of *H. meeki* to have all the diagnostic characteristics of *H. rufus,* and synonymized the two. In addition to the cotypes, he had available five other meeki stage *H. rufus,* 67–71 mm, from Bermuda (FMNH 49077). Woods (1955: 109) mentioned that the smallest settled juveniles of *H. rufus* he examined were: 71 and 72 mm from Bermuda; 58–67 mm from Brasil; and 52 mm from Puerto Rico. We have not been able to locate the juvenile specimens from Brasil or Puerto Rico but we accept the data from the Puerto Rican specimen of an exceptionally small settlement size in *H. rufus.* Woods concluded that *H. ascensionis* usually transforms at a smaller size than *H. rufus.* On the basis of our examination of numerous juveniles of both species we support Woods' conclusion.

In the most extensive treatment to date of western Atlantic holocentrids, Woods and Sonoda (1973) accorded generic rank to *Holocentrus, Adioryx* (now *Sargocentron*), and *Flammeo.* They distinguished the two species of *Holocentrus* as follows: lateral line scales 51–54 in *rufus,* 46–50 in *ascensionis*; length of upper jaw 11.4–13.4% SL and reaching posteriorly to level of middle of pupil in *rufus,* 13.6–15.8% SL and reaching to or beyond posterior margin of pupil in *ascensionis*; length of lower jaw 14.7–17.1% SL in *rufus,* 17.2–19.8% SL in *ascensionis*; body depth 28.8–33.0% SL in *rufus,* 32.9–37.2% SL in *ascensionis*; preopercular spine

length 5.6–9.9% SL in *rufus*, 5.4–6.4% SL in *ascensionis*. Woods and Sonoda (1973: 337) noted that the lateral line scale counts in *H. ascensionis* are rarely 51 and in *H. rufus* very rarely 50.

Woods and Sonoda (1973) listed *Beloholocentrus atractus* only in the synonymy of *H. ascensionis*. However, Woods (1955) had previously postulated correctly that it was based on both rhynchichthys stage *H. ascensionis* and meeki stage *H. rufus*, and it should have been listed in the synonymy of both species. Less understandable is the listing by Woods and Sonoda of the *H. meeki* of Beebe and Tee-Van (not of Bean) as a "false reference" under *H. ascensionis*, with the comment that this reference is based on a description of *H. ascensionis* from Bermuda. As noted above, the *H. meeki* of Beebe and Tee-Van is based mostly on the original description of Bean and gives the high lateral line scale count and short upper jaw length typical of *H. rufus*. *Holocentrus meeki* of Bean (1906a) and of Beebe and Tee-Van (1933) are both properly listed in the synonymy of *H. rufus*. There is no text discussion of either the rhynchichthys or meeki stages of *Holocentrus* in Woods and Sonoda (1973), and the meeki stage has not been elaborated upon since Beebe (1936) and Woods (1955).

One of the most distinctive features of both the rhynchichthys stage of all holocentrids and the meeki stage of *Holocentrus* that has been noted by previous authors is the presence of a series of seven to nine, occasionally ten, fleshy lobes or papillae supported by bony crenulations of the infraorbitals along the posterior and posteroventral margin of the orbit (Fig. 2). The lachrymal bears a series of sensory pores that are continued posterodorsally as progressively more prominent pore-bearing lobes, usually two lobes on each of the first through fourth infraorbitals and a smaller dorsalmost pored lobe on the fifth infraorbital (dermosphenotic). The four lobes on the third and fourth infraorbitals usually are the largest. When there is variation in the number of papillae, it usually is in the number on the first and second infraorbitals. The fleshy margin of the dorsal edge of the orbit along the frontal ends just above the dermosphenotic in a flexible flap aligned with the curvature formed by the distal ends of the postorbital papillae.

We presume that these postorbital papillae are hydrodynamically efficacious in the oceanic presettlement stages. Similar postorbital papillae are found in several unrelated small, planktivorous fishes such as the serranid *Schultzea*, the pomacentrid *Lepidozygus*, and the anomalopid *Anomalops*. Johnson and Rosenblatt (1988) speculated that these papillae serve a hydrodynamic function.

RESULTS

Rhynchichthys Stage.—We examined about 85 rhynchichthys stage western Atlantic holocentrids, ranging in length from 12 to 46 mm length. We could only identify these to species after the lateral line scales were sufficiently developed to be counted without special preparation, at about 19 mm. Eleven such specimens proved to be *Holocentrus*, and all of them had the low lateral line counts typical of *H. ascensionis*. We have no explanation for our failure to identify any rhynchichthys stage *H. rufus*.

The 11 rhynchichthys stage *H. ascensionis*, 18.9–42.3 mm ($\bar{x}$ = 28.1), have a shallower body (25.4–29.3% SL, $\bar{x}$ = 27.1) and longer preopercular spine (7.3–12.4% SL, $\bar{x}$ = 9.8) than in meeki and larger stages. The pterygiophores of the soft dorsal fin are not sufficiently ossified to determine their insertion pattern from radiographs.

Meeki Stage.—***Holocentrus rufus.*** We located a total of 50 specimens (37.8–74.1 mm, $\bar{x}$ = 54.5) of meeki stage *H. rufus* in museum collections, including the four we collected at CBC (Fig. 1). Because the morphometrics of this stage have not
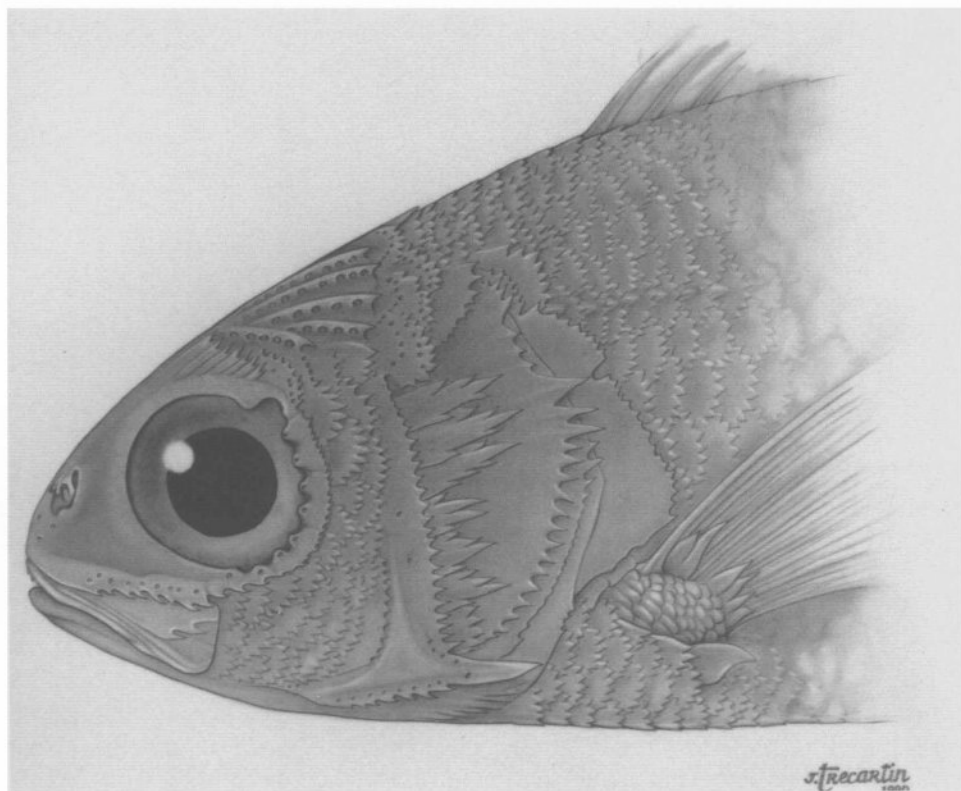
Figure 2.   *Holocentrus rufus,* meeki stage, USNM 316408, 58.9 mm, 9 November 1988, Carrie Bow Cay, Belize, detail of head.

been sufficiently described previously, we record the following diagnostic data for a sample of 20 of the specimens examined: lateral line scales 50–55 ($\bar{x}$ = 53.1); maxillary length 10.1–12.2% SL ($\bar{x}$ = 10.9); body depth 20.9–29.3% SL ($\bar{x}$ = 24.9); preopercular spine length 6.0–7.5% SL ($\bar{x}$ = 6.8).

Based on radiographs of meeki stage specimens, juveniles, and adults, we identified an additional diagnostic difference between most specimens of *H. rufus* and *H. ascensionis.* In both species there are usually 14 pterygiophores supporting the dorsal-fin soft rays and these insert between the neural spines of the 13th and 19th vertebrae. *Holocentrus rufus* usually (68% of 66 specimens) has the first 10 soft dorsal-fin pterygiophores in five pairs between the neural spines of the 13th to 18th vertebrae, followed by four pterygiophores between the 18th and 19th neural spines. *Holocentrus ascensionis* usually (59% of 75 specimens) has the first eight pterygiophores in four pairs between the 13th and 17th neural spines, followed by three pterygiophores between the 17th and 18th and three between the 18th and 19th neural spines.

These two patterns of pterygiophore insertion can be helpful in distinguishing groups of small specimens of *H. rufus* and *H. ascensionis,* but there is variation so that they do not unequivocally characterize each species. For example, the 2-2-2-2-2-4 pattern characteristic of most *H. rufus* also was found in 24% of the specimens of *H. ascensionis* rather than its characteristic 2-2-2-2-3-3 pattern.

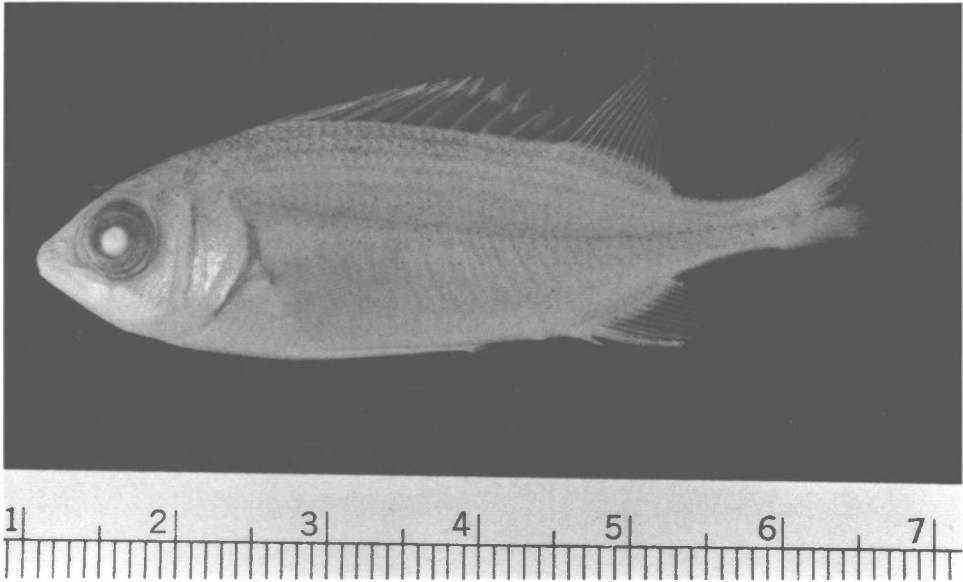The coloration of preserved meeki stage specimens of both species of *Holocen-*

Figure 3. *Holocentrus rufus*, USNM 316462, captured 21 March 1991, Carrie Bow Cay, Belize, as a meeki stage and aquarium reared; transformed overnight on 22–23 March; preserved on 27 March at 51.3 mm.

trus is dark bluish black to brown above, abruptly grading into silver on the lower two-thirds of the body (Fig. 1), in sharp contrast to the horizontally striped (and reddish pink color) pattern that characterizes juveniles and adults (Fig. 3).

Holocentrus ascensionis. We located only nine specimens (47.9–59.8 mm, $\bar{x}$ = 54.5) of meeki stage *H. ascensionis* in museum collections, identified by the following diagnostic features, based on all specimens: 45–50 ($\bar{x}$ = 47.9) lateral line scales; maxillary length 12.1–13.1% SL ($\bar{x}$ = 12.5); body depth 28.8–32.9% SL ($\bar{x}$ = 30.5); preopercular spine length 6.1–8.0% SL ($\bar{x}$ = 7.0, about the same as in meeki stage *H. rufus*).

Transformation of Meeki Stage. —The meeki stage specimen captured on 21 March 1991 at 2300 at CBC in a stationary net close to shore was metallic dark blue with greenish overtones above and silver below. It maintained this bluish silver coloration without any trace of red both when immediately placed in a strontium solution and when taken out the following evening on 22 March at 1900 and placed in an aquarium. It also had the typical short caudal peduncle, low soft dorsal and anal fins, short upper caudal fin lobe, and prominent postorbital papillae of the meeki stage when transferred from the strontium to the grow-out aquarium. By the following morning of 23 March at 0700 the coloration of the specimen had turned to plain orangish red, and by 0800 a faint horizontally striped pattern with pale silvery interspaces was evident. The reddish striping effect became increasingly prominent from ventrally to dorsally during the next hour, with the margin of the spiny dorsal fin becoming whitish by later that day.

During the course of its subsequent days in the aquarium the soft dorsal and anal fins increased in height, the caudal peduncle and the upper caudal fin lobe increased in length, and the prominence of the postorbital papillae decreased.

When preserved on 27 March at 0600 in alcohol for otolith examination, the specimen (Fig. 3) measured 51.3 mm and proved to have all of the diagnostic features of *H. rufus*.

Beebe's (1936) description of the transformation of meeki stage *H. rufus* as taking place gradually over several weeks is somewhat at variance with our observations. We found the color change to be dramatically rapid, during one night and early morning and the major morphological changes in fin height, caudal peduncle form, and postorbital papillae resorption at least mostly accomplished within 5 days.

During its 5 days in the grow-out aquarium with two previously collected and transformed rhynchichthys stage *Sargocentron coruscus* (whose transformations were closely similar to that of the meeki stage), the transformed meeki stage *H. rufus* was relatively secretive, spending most of the time both day and night in shelter cavities in coral rubble, venturing out only infrequently even at night to feed on the provided plankton. In challenging and displacing the two smaller specimens of *S. coruscus* for shelter sites, the *H. rufus* made repeated agonistic displays of rapid beatings of the caudal fin.

Size at Settlement. — In order to provide an approximation of the size at settlement, we examined specimens of *Holocentrus* in museums with extensive holdings of western Atlantic reef fishes (USNM, AMNH, ANSP, ROM). Juveniles of *H. ascensionis* of ca. 50–60 mm (smallest 49.3 mm) are relatively common in these collections, as are those of *H. rufus* of ca. 60–70 mm SL (smallest 55.7 mm). These data suggest that *H. ascensionis* usually settles at about 50 to 55 mm, although obviously sometimes larger because its meeki stage obtains at least 59.8 mm, whereas *H. rufus* settles at no less than about 55 mm and more typically between 60 to 70 mm. The latter supposition is supported by the relatively large size obtained by the meeki stage of *H. rufus* (up to 74 mm). Our collections of specimens for otolith examination of recently settled *H. rufus* of 58–73 mm from St. Croix and of *H. ascensionis* of 48–62 mm from Panama are in close agreement with our data from museum specimens. The meeki stage *H. rufus* from CBC that transformed in an aquarium was only 51.3 mm when preserved 5 days after capture. This is significantly smaller than any of the recently settled juveniles we collected or found in museum collections. We presume that capture, strontium marking, and aquarium rearing induced transformation at an unusually small size. However, settlement must occasionally occur naturally at this size because Woods (1955: 109) reported a 52 mm juvenile *H. rufus,* a specimen we cannot locate.

Seasonality of the Meeki Stage. — The two type specimens of *H. meeki* Bean (1906a) were collected in Bermuda on 6 September 1905, and the numerous specimens reported on by Beebe (1936) were all collected in Bermuda during unspecified days in September 1935. The specimens described by Fowler (1944) as *Beloholocentrus atractus,* all but one of which are meeki stage *H. rufus,* were collected at Courtown Key in the western Caribbean on 30 March 1941.

Woods and Sonoda (1973: 341, 342) did not distinguish meeki stage *H. rufus* in their list of materials examined, all of which are from the Field Museum. We examined all of the Field Museum holdings of *Holocentrus* and found, in addition to the cotypes of *H. meeki,* two other lots of meeki stage *H. rufus,* both collected off Bermuda in September. We also found two lots of meeki stage *H. ascensionis,* collected in March and September.

We collected meeki stage *H. rufus* at CBC in March, September, and November. Most of the other 50 meeki stage *H. rufus* examined in this study were collected

in or around September (the fall months). There appears to be an additional peak of abundance in March and April (Fig. 4) and specimens were taken in every month except December and January. These collections were made over many years by many people and organizations (with some bias geographically for Bermuda because of the biological station there and the Ocean Acre pelagic fish program that extensively sampled in that area) and can be considered to be relatively random for date of collection.

The nine meeki stage *H. ascensionis* we examined were collected in January, March, May, September, November, and December. The newly settled juveniles of *H. ascensionis* we collected in Panama were taken in January, March, May, June, July, and November.

The above data clearly indicate that both species of *Holocentrus* have long breeding seasons.

The largest specimens of meeki stage *H. rufus* have been collected in the fall (September) and the smallest specimens in the late summer to fall (July through October), whereas the specimens collected in the earlier months of the year (March through June) are of moderate size. Our sample size is too small to draw statistically significant conclusions. One possibility is that the presence in the spring of only moderate size specimens of the meeki stage is indicative of a small number of cohorts resulting from early spring breeding, whereas the presence in the fall of small to large specimens represents many more cohorts from a greater number of months of mid-year to fall breeding. However, the otolith analysis necessary to confirm this speculation is impossible on these formalin preserved museum specimens.

Spawning Periodicity. —Our back calculated spawning data for *H. rufus* are based on a single collection of small juveniles made in the middle of October at St. Croix and yield dates from the middle of July to the middle of August (except for two unusual specimens discussed below with dates in September), with most of the specimens spawned in August and settled in October. This single sample was focused on collecting recently settled juveniles of *Haemulon* spp. and cannot provide information on breeding season duration in *Holocentrus*; however, we are not surprised by the availability of numerous recently settled juveniles in October because of the abundance in museum collections of the meeki stage, the largest specimens of which were most commonly collected in and around September.

The two meeki stage *H. rufus* collected at CBC, from which we obtained otoliths, were spawned in August and February; museum collections show this stage to be present in all months except December and January. This suggests a long breeding season.

Our back calculated spawning data for *H. ascensionis* is based on specimens from Panama collected in January, March, May, June, July, and November. It suggests that spawning takes place during a large portion of the year, with peaks of activity in the spring and fall. In these samples none were spawned from June to late September. Our analysis of the few specimens of meeki stage *H. ascensionis* in museum collections suggests that it occurs throughout the year, presumably indicating a long breeding season.

The only previous information on the breeding season for the two species of *Holocentrus* is that of Munro et al. (1973), who examined the gonads of specimens from Jamaica. Sexually active specimens of *H. rufus* were found throughout the year but with a decreasing proportion in the summer months. Although a low
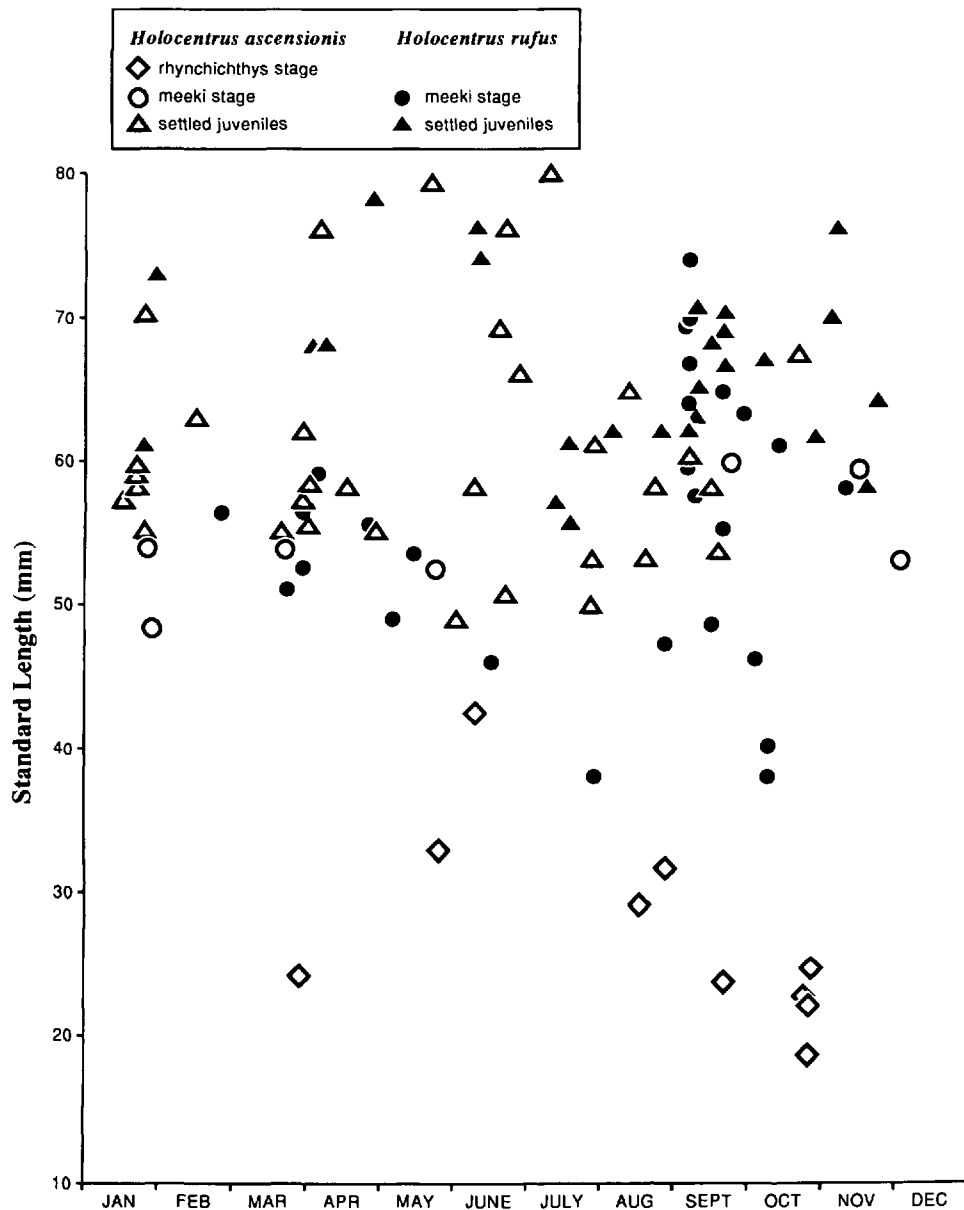
Figure 4. Early life history stages of *H. rufus* and *H. ascensionis* by size and date of capture: symbols represent individual lots, with only the smallest specimen shown; two juvenile *H. ascensionis* and one meeki stage *H. rufus* for which only the month of collection is known are shown as having been collected in the middle of the month; those few lots in which the collecting dates are given as a several-day period are shown as the middle of that period; those few specimens without even a month of collection are not included in the figure; also not included are two lots of uncertain taxonomic status (six meeki stage specimens from Angola and a single small specimen from Cuba) discussed in the text.

percentage of the trap-caught shallow-water samples were ripe from February to June, the fraction was so low that it was hypothesized that there was either an offshore breeding movement or trap avoidance during breeding. Samples of *H. ascensionis* were obtained only from January to May and all contained some ripe specimens, with a greater proportion ripe in February.

Planktonic Duration and Settlement Age.—The microstructure of the lapillus of the holocentrids examined in this study is typical of that of such reef fishes as grunts (Brothers and McFarland, 1981), groupers (Keener et al., 1988), and other relatively large and fast growing reef fishes (Brothers and Mathews, 1987). Five or six fine increments (1–2 μm) surround a spherical primordium and core (Fig. 5); thereafter the increments increase in width to 10–20 μm. In the area of counts 35–50 the increments gradually narrow to less than 10 μm. Beyond this area there is a more abrupt narrowing of increment width that usually is associated with a general decrease in optical density and growth interruptions in some regions (especially in the posteromedial quadrant). A decrease in contrast between light and dark subunits of the increments often is apparent for about three days at this transition. The features just described are typical of "settlement marks," which have been demonstrated to coincide with eco-behavioral/morphological transitions in the early life history of fishes with pelagic larvae (references above plus Brothers, 1984; Brothers et al., 1983).

Transitions are only discernible when they are not at the extreme periphery of the otolith, i.e., a fish collected on the day of settlement or within a few days thereafter may not have an obvious settlement mark. More than one transition mark may be present in fishes with especially complex early postsettlement life histories (e.g., haemulids; Brothers and McFarland, 1981). The transitions in the lapilli of squirrelfishes sometimes are rather subtle and difficult to determine. This is particularly true for the two species of *Holocentrus,* and especially *H. rufus.* In approximately half of the specimens of *H. rufus* examined we find a second, weaker transition in the region of counts 60–70. The significance of this second abrupt narrowing of increment width is unclear. It is so subtle that its consistent identification is questionable. Furthermore, its significance may be related to as yet unrecognized habitat or eco-behavioral phenomena. As explained below, we hypothesize that it most likely is a weakly differentiated settlement mark.

We validated the daily periodicity of increment formation by strontium marking (Brothers, 1990) the otoliths of newly captured meeki stage *H. rufus* and rhynchichthys stage *Sargocentron coruscus* at CBC. Examination of the otoliths of specimens in these stages and of individuals that have transformed into juveniles during a period of laboratory captivity helps to confirm the significance of the microstructural transitions described above.

A 48.5 mm meeki stage *Holocentrus rufus* collected in September 1990 at CBC and preserved at capture had 36 increments in the lapillus and no observable microstructural transitions. A 51.3 mm (at preservation) meeki stage *H. rufus* collected in March 1991 was strontium marked (Fig. 6) and kept alive for five days before preservation; it transformed into a benthic juvenile after the first day in the aquarium. There are 43 increments in its lapillus prior to the strontium enriched increment and four complete increments beyond the strontium mark (the total increment count of 48 equals age in days after hatching). The lapillus of this strontium marked specimen had the increments that were deposited in captivity slightly narrower than the others, creating the appearance of a transition. However, just as with the aquarium transformed specimens of *Sargocentron co-*
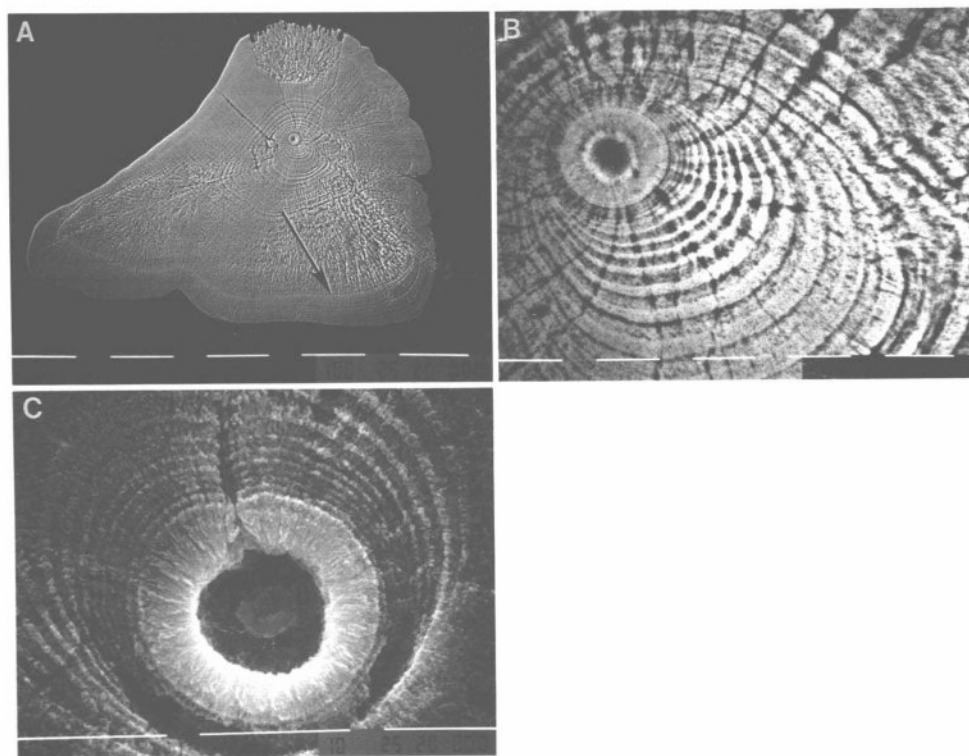
Figure 5.   SEM images of ground, polished, and etched lapilli from two specimens of *Sargocentron coruscus*, eight days after strontium marking. A. Back-scattered electron image of entire frontal section from specimen 33.1 mm; arrow points into faint bright band near otolith margin that corresponds to the increment with strontium enrichment; total number of increments is 45, with eight complete increments beyond the mark; scale line = 100 μm. B. Detail of A, showing primordium, core, and early larval growth region; scale line = 10 μm. C. Secondary electron image of primordium and core surrounded by fine growth increments from specimen 35.6 mm; scale line = 10 μm. Here and in Figs. 6–7 the sets of numbers in the bar of coding at the lower right of the micrographs are, respectively, from left to right: the magnification in microns (μm); the accceleration in KeV; the working distance in mm; and an unused identification code.

ruscus discussed below, we cannot eliminate the possibility that this is a laboratory artifact. The lapillus of the aquarium transformed *H. rufus* simply did not have a clear and unequivocal transition either before or after the strontium mark.

Of three rhynchichthys stage *Sargocentron coruscus* captured in March 1991 at CBC, a 31.6 mm individual was alcohol preserved at capture. It has 32 increments and no microstructural transition or "settlement mark." The other two specimens were strontium marked (Fig. 7) and held for a total of nine days before preservation, having transformed into juveniles after the first day in the aquarium. Each specimen deposited eight complete increments after the strontium enriched increment. The precapture increment counts of these 33.1 and 35.6 mm specimens are, respectively, 34 and 32. The nine (strontium mark plus eight beyond it) increments formed during captivity (coinciding with the transformation to juvenile morphology and behavior) are narrower than those formed during the
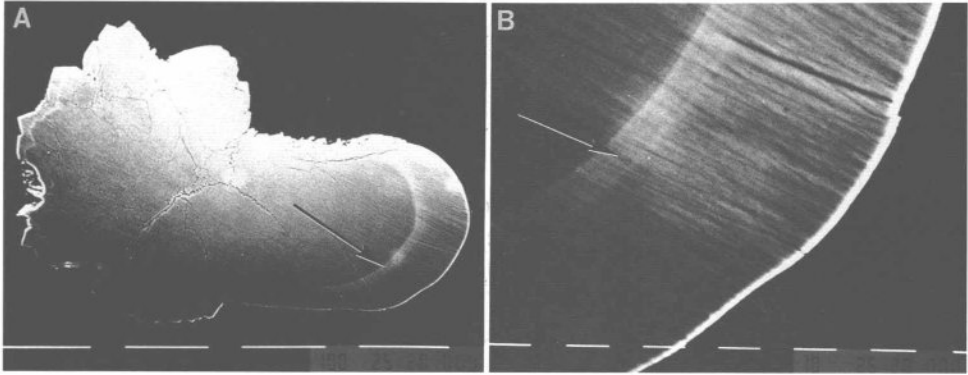
Figure 6.   SEM images showing strontium enriched band on ground and polished lapilli from *Holocentrus rufus*, 51.3 mm, four days after marking; back-scattered electron images; arrows point into the strontium enriched band; increments are not apparent in this unetched specimen. A. Frontal section; scale line = 100 μm. B. Detail of A; scale line = 10 μm.
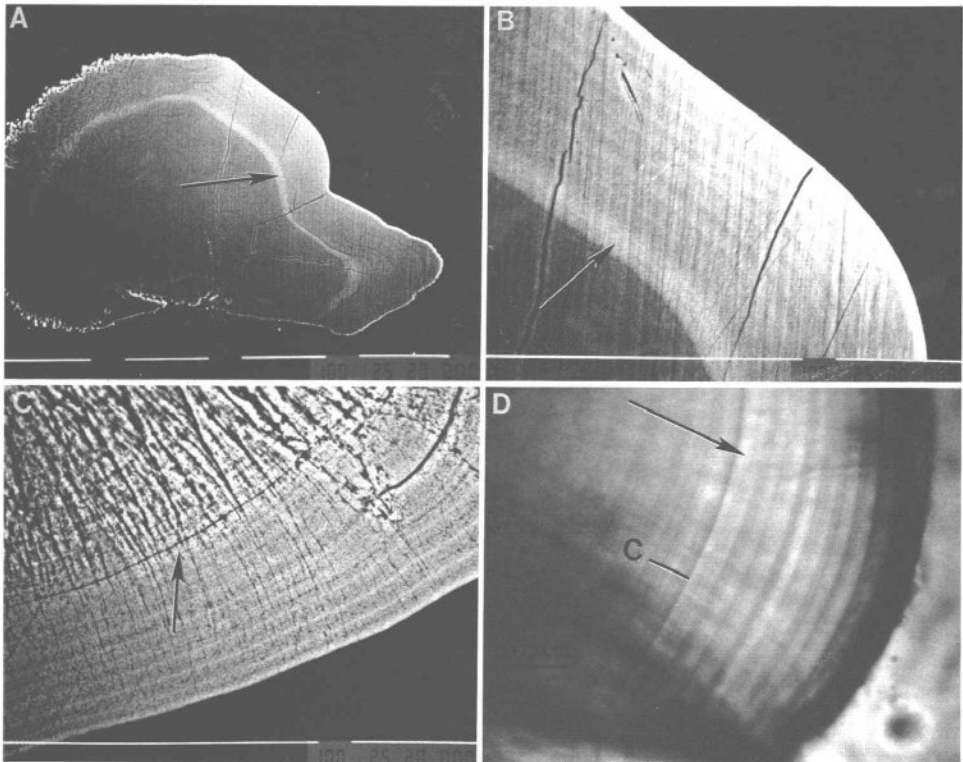

Figure 7.   SEM images (A–C, back scattered) and light micrograph (D) showing strontium marks in lapilli from two specimens of *Sargocentron coruscus*, eight days after marking; arrows point into strontium enriched band. A. Frontal section from 35.6 mm specimen, unetched; scale line = 100 μm. B. Detail from 33.1 mm specimen, unetched; scale line = 100 μm. C. Detail from 33.1 mm specimen, etched; scale line = 100 μm. D. Margin of lapillus from 33.1 mm specimen, unetched; note interruption at end of line from C = capture; scale line = 20 μm.

TABLE 1.—Otolith based pre- and post-transition data bases for seven species of five genera of western Atlantic squirrelfishes. Total counts are included whenever they could be determined, although most specimens larger than about 75 mm SL (and larger than about 55 mm SL in *Plectrypops retrospinis*) of all species could not have the post-transition increments counted accurately (therefore total increments also unknown). Averages are given only for the three species (*Holocentrus rufus*, *H. ascensionis*, and *Sargocentron coruscus*) for which the most data was obtained (the two exceptional specimens of *H. rufus* with 170 and 180 total increments are excluded from the averages; see text for discussion of these two specimens). More numerous specimens of some species, especially *H. rufus*, for which only pretransition increments could be determined are included in Table 2.

Locality	Coll. date	SL	Pretransition	Post-transition	Total	Spawn
			Holocentrus rufus			
St. Croix	15 Mar 80	62	44	126	170	25 Sep 79
St. Croix	15 Mar 80	66	51	129	180	15 Sep 79
St. Croix	15 Oct 80	67	43	49	92	13 Jul 80
St. Croix	15 Oct 80	58	40	32	72	02 Aug 80
St. Croix	15 Oct 80	68	46	22	68	06 Aug 80
St. Croix	15 Oct 80	64	42	17	59	15 Aug 80
St. Croix	15 Oct 80	68	42	22	64	10 Aug 80
St. Croix	15 Oct 80	70	45	22	67	07 Aug 80
St. Croix	15 Oct 80	60	40	19	59	15 Aug 80
St. Croix	15 Oct 80	67	40	20	60	14 Aug 80
St. Croix	15 Oct 80	73	44	24	68	06 Aug 80
St. Croix	15 Oct 80	66	43	18	61	13 Aug 80
St. Croix	15 Oct 80	61	45	40	85	20 Jul 80
St. Croix	15 Oct 80	66	41	19	60	14 Aug 80
St. Croix	15 Oct 80	67	49	16	65	09 Aug 80
St. Croix	15 Oct 80	67	45	17	62	12 Aug 80
St. Croix	15 Oct 80	66	47	21	68	06 Aug 80
St. Croix	15 Oct 80	68	47	22	69	05 Aug 80
Average		66	44	24	67	
			Holocentrus ascensionis			
Panama	30 Jul 84	57	47	16	63	26 May 84
Panama	30 Jul 84	58	50	15	65	24 May 84
Panama	17 Jan 85	56	47	15	62	14 Nov 84
Panama	20 Jan 85	57	46	13	59	20 Nov 84
Panama	24 Jan 85	61	46	19	65	18 Nov 84
Panama	25 Jan 85	59	47	13	60	24 Nov 84
Panama	27 Jan 85	59	49	11	60	26 Nov 84
Panama	15 Mar 85	59	-	-	57	15 Jan 85
Panama	31 Mar 85	61	56	9	65	23 Jan 85
Panama	14 May 85	49	-	-	53	20 Mar 85
Panama	19 May 85	57	48	7	55	23 Mar 85
Panama	19 May 85	57	-	-	57	21 Mar 85
Panama	22 May 85	56	46	15	61	20 Mar 85
Panama	22 May 85	58	55	8	63	18 Mar 85
Panama	02 Jun 85	54	44	14	58	03 Apr 85
Panama	03 Jun 85	54	-	-	50	12 Apr 85
Panama	08 Jun 85	48	43	10	53	14 Apr 85
Panama	08 Jun 85	52	-	-	50	17 Apr 85
Panama	08 Jun 85	54	47	7	54	13 Apr 85
Panama	19 Jun 85	56	48	10	58	20 Apr 85
Panama	06 Jul 85	62	47	33	80	15 Apr 85
Panama	21 Nov 85	59	44	11	55	25 Sep 85
Panama	23 Nov 88	48	43	8	51	01 Oct 88
Panama	23 Nov 88	52	-	-	52	30 Sep 89
Average		56	48	13	59	

TABLE 1.—Continued.

Locality	Coll. date	SL	Pretransition	Post-transition	Total	Spawn
Sargocentron coruscus						
Belize	21 Jul 91	37	35	37	72	08 May 91
Belize	21 Jul 91	38	35	38	73	07 May 91
Belize	21 Jul 91	43	38	61	99	11 Apr 91
Belize	21 Jul 91	45	38	59	97	13 Apr 91
Belize	21 Jul 91	42	38	62	100	10 Apr 91
Belize	21 Jul 91	44	43	55	98	12 Apr 91
Belize	21 Jul 91	38	34	32	66	14 May 91
Belize	21 Jul 91	40	35	35	70	10 May 91
Belize	21 Jul 91	40	34	38	72	08 May 91
Belize	21 Jul 91	41	35	34	69	11 May 91
Belize	21 Jul 91	40	35	37	72	08 May 91
Belize	21 Jul 91	35	35	37	72	08 May 91
Belize	21 Jul 91	37	33	64	97	13 Apr 91
Belize	21 Jul 91	38	34	38	72	08 May 91
Belize	21 Jul 91	42	35	64	99	11 Apr 91
Belize	21 Jul 91	36	33	37	70	10 May 91
Belize	21 Jul 91	35	34	34	68	12 May 91
Belize	21 Jul 91	37	35	38	73	07 May 91
Belize	21 Jul 91	42	32	38	70	10 May 91
Belize	21 Jul 91	38	36	34	70	10 May 91
Belize	21 Jul 91	47	37	66	103	07 Apr 91
Belize	21 Jul 91	37	35	37	72	08 May 91
Panama	21 Mar 86	29	36	4	40	07 Feb 86
Panama	23 Apr 86	30	34	41	75	05 Feb 86
Panama	08 Feb 87	37	38	31	69	29 Nov 86
Panama	08 Feb 87	26	37	0	37	31 Dec 86
Panama	01 May 87	26	35	0	35	25 Mar 87
Average		38	36	39	74	
Sargocentron vexillarius						
Belize	19 Mar 89	95	38	–	–	–
Belize	19 Mar 89	113	34	–	–	–
Belize	19 Mar 89	108	36	–	–	–
Belize	22 Mar 89	42	37	21	58	21 Jan 89
Belize	15 Jul 90	118	36	–	–	–
Belize	15 Jul 90	129	35	–	–	–
Belize	15 Jul 90	109	35	–	–	–
Belize	15 Jul 90	96	35	–	–	–
Belize	15 Jul 90	107	37	–	–	–
Belize	15 Jul 90	100	36	–	–	–
Belize	15 Jul 90	82	37	–	–	–
Belize	15 Jul 90	87	35	–	–	–
Belize	15 Jul 90	96	35	–	–	–
Belize	15 Jul 90	85	36	–	–	–
St. Croix	20 Mar 89	49	37	–	100+	–
Myripristis jacobus						
St. Croix	18 Jan 78	44	50	20	70	7 Nov 77
St. Croix	19 Jan 78	42	45	15	60	18 Nov 77
St. Croix	20 Mar 78	47	58	–	100+	–
St. Croix	20 Mar 78	49	55	–	100+	–
Panama	14 Apr 89	44	40	21	61	10 Feb 89
Panama	14 Apr 89	46	50	15	65	06 Feb 89
Panama	14 Apr 89	41	49	10	59	12 Feb 89

TABLE 1.—Continued.

Locality	Coll. date	SL	Pretransition	Post-transition	Total	Spawn
Plectrypops retrospinis						
Belize	22 Mar 89	35	45	13	58	21 Jan 89
Belize	22 Mar 89	53	39	–	–	–
Belize	22 Mar 89	59	44	–	–	–
Belize	25 Mar 89	78	43	–	–	–
Belize	25 Mar 89	87	47	–	–	–
Flammeo marianus						
Belize	20 Mar 89	120	45	–	–	–
Belize	22 Mar 89	117	37	–	–	–
Belize	25 Mar 89	101	46	–	100+	–
Belize	15 Jul 89	107	36	–	–	–
Belize	15 Jul 89	111	37	–	–	–
Belize	15 Jul 89	111	37	–	–	–
Belize	15 Jul 89	114	37	–	–	–

preceding rhynchichthys stage. Thus, the microstructural transition associated with transformation in the aquarium specimens of *S. coruscus* is similar to the marks seen in the otoliths of other juveniles of similar size and age of this species. We cannot eliminate the possibility that this pattern of otolith growth is a laboratory artifact, and it is not conclusive validation of a settlement mark; however, we have validated the daily periodicity of increment formation in the transforming individuals of both *S. coruscus* and *H. rufus* and can refer unequivocally to the increments as "daily rings."

Two additional series of five and seven rhynchichthys stage *Sargocentron coruscus* were captured, respectively, on 5 and 7 March 1992 at CBC. These were preserved either upon capture in the evening or the following morning after about ten hours in aquaria. The 12 specimens have a size range of 30.3–32.5 mm ($\bar{x}$ = 31.2) and otolith increment count range of 28–34 ($\bar{x}$ = 32.6).

A series of 22 moderate size juveniles of *S. coruscus* ranging from 35 to 47 mm collected in a tide pool at CBC had pretransition (i.e., rhynchichthys) ages of 32 to 43 days and had spent 32 to 66 days as settled juveniles before being collected. Of five juveniles ranging from 26 to 37 mm collected as apparently recently settled juveniles off Panama, the two smallest (both 26 mm, collected in different months) had settled so recently that there was no apparent transition mark at the periphery of the 35 and 37 increments equivalent to their total age. Another specimen, 29 mm, had settled only four days previously (36 pretransition, 4 post-transition) and the remaining two specimens (30 and 37 mm, collected in different months), had, like those from a Belize tide pool, a month or more of existence after settlement before being collected. *Sargocentron coruscus* obviously settles at a smaller size than does *Holocentrus* (the limited data for *S. vexillarius* suggests that it is similar to *S. coruscus* in presettlement increments and settlement size; see Table 1).

Table 1 details and Table 2 and Figure 8 summarize the results of our otolith analyses of the ages of the species of western Atlantic holocentrids examined in this study. We assumed that pretransition counts are equivalent to the pelagic larval (rhynchichthys) duration and that the transition mark corresponds to the settlement to benthic juveniles in all of the species with the exception of *Holo-*

TABLE 2.—Summary of otolith based pretransition data for seven species of five genera of western Atlantic squirrelfishes. All specimens for which pretransition increments could be determined are included, whether or not post-transition and, therefore, total increments were countable. PT = pretransition; SD = standard deviation; Min = least number of pretransition increments; Max = greatest number of pretransition increments; N = number of specimens in which pretransition increments could be determined.

Species	Mean PT days	SD days	Min days	Max days	N
Holocentrus rufus	44.1	3.0	38	51	68
Holocentrus ascensionis	47.8	3.1	43	56	29
Flammeo marianus	39.3	4.0	36	46	7
Sargocentron coruscus	35.5	2.1	32	43	30
Sargocentron vexillarius	35.9	1.1	34	38	15
Myripristis jacobus	49.6	5.5	40	58	7
Plectrypops retrospinis	43.6	2.7	39	47	5
Total					161

centrus. In *Holocentrus*, in which the meeki stage intervenes between the rhynchichthys and the settled juvenile, the transition probably corresponds to the shift from the rhynchichthys to the meeki stage, as discussed below.

Mean pretransition or larval durations (i.e., of the rhynchichthys stage, excluding the prejuvenile meeki stage in *Holocentrus*) are greater in the two species of *Holocentrus* (44 and 48 days for *H. rufus* and *H. ascensionis,* respectively), *Myripristis jacobus* (50), and *Plectrypops retrospinis* (44) than in *Flammeo marianus* (39) and the two species of *Sargocentron* (36 for both), and individual variation in larval duration was not excessive (maximum of 18 but usually 13 or less).

None of the otoliths of these species of holocentrids showed the kind of pretransition microstructural patterns that characterize many fishes with extended larval life and competency such as some gobies, eels, labrids, and acanthurids. In all of these other families of fishes the pretransition patterns are characterized by an extended series of gradually (over weeks to months) narrowing increments followed by an abrupt widening of the increments at settlement (e.g., for labrids; Cowen, 1991). Furthermore, for many species of gobies and labrids long larval life is not correlated with larger size at settlement. We conclude, therefore, that the relatively large size at settlement in holocentrids is primarily a function of accelerated growth acting over an extended pelagic duration.

Although the significance of the "settlement mark" or microstructural transition in *Holocentrus* remains somewhat ambiguous (although most likely corresponding to the rhynchichthys-meeki transition), we were able to determine growth rates, time of spawning, and maximum duration of presettlement life through otolith aging of newly or recently settled individuals of both species of *Holocentrus.* Total ages of small juveniles of *H. rufus* usually are 60–69 days and of *H. ascensionis* usually 50–65 days. Most newly settled juveniles have a transition mark at 40–50 days in the case of *H. rufus* and 45–55 days in *H. ascensionis.* The difference between the pretransitional count and the total age in the specimens examined suggests two possible scenarios: (1) the otolith transition may be a true settlement mark, and settlement occurred on average about two (in *H. ascensionis*) to three and a half (in *H. rufus*) weeks prior to capture; or (2) the transition corresponds to the rhynchichthys-meeki transformation, which occurred about two to three and a half weeks prior to settlement (respectively for *H. ascensionis* and *H. rufus*). As explained below, the evidence favors the latter scenario, which requires either
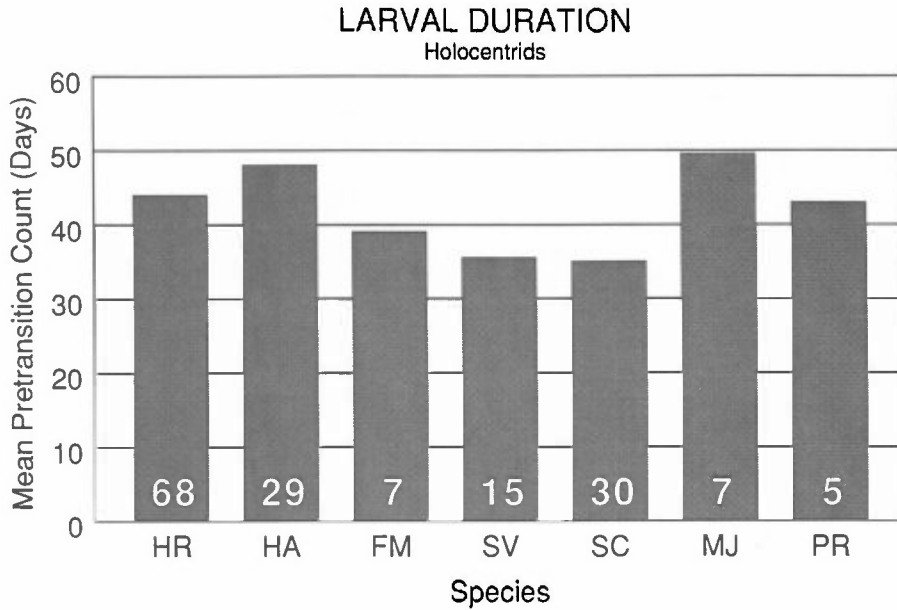
LARVAL DURATION
Holocentrids

Figure 8.   Mean larval (rhynchichthys) duration (posthatching) as determined by number of pretransition increments in lapilli for: *Holocentrus rufus* (HR), *H. ascensionis* (HA), *Flammeo marianus* (FM), *Sargocentron vexillarius* (SV), *S. coruscus* (SC), *Myripristis jacobus* (MP), and *Plectrypops retrospinis* (PR). Number (N) at bottom of column is number of specimens for which pretransition increments could be determined.

that the examined juveniles were captured within a day or two of settling or that these species do not generate a transition mark that corresponds to settlement.

Interpretation of Microstructural Transition in *Holocentrus*

Our data demonstrate clearly that the young of *Holocentrus rufus* and *H. ascensionis* pass through an uniquely specialized prejuvenile stage and settle to a benthic habitat at significantly larger sizes than those of other holocentrids we have examined (Tables 1, 2). This suggests two possibilities relative to growth and pelagic duration of these two species. They settle at approximately the same age as other holocentrids and thus grow faster and/or they spend a significantly longer time in the pelagic mode and thus are significantly older than other holocentrids at settlement. We believe that both of these factors are operating. A plot of length versus age (Fig. 9) indicates that the presettlement growth rate of the two species of *Holocentrus* is more rapid than that of the other two species of holocentrids (*Sargocentron coruscus* and *Myripristis jacobus*) for which we have comparable data. However, we presume that a major advantage of a pelagic postlarval stage is that it provides considerable temporal flexibility in the settlement process, thus increasing the probability of settlement into a favorable habitat. This advantage would be realized only if pelagic duration is greater for the two *Holocentrus* species than for other holocentrids.

We would predict, then, that the age at settlement for *Holocentrus* is significantly greater than that for other holocentrids. A relatively straightforward test of this prediction should be available by comparing presettlement daily growth records in the otoliths of juvenile and/or adult *H. rufus* and *H. ascensionis* with those of
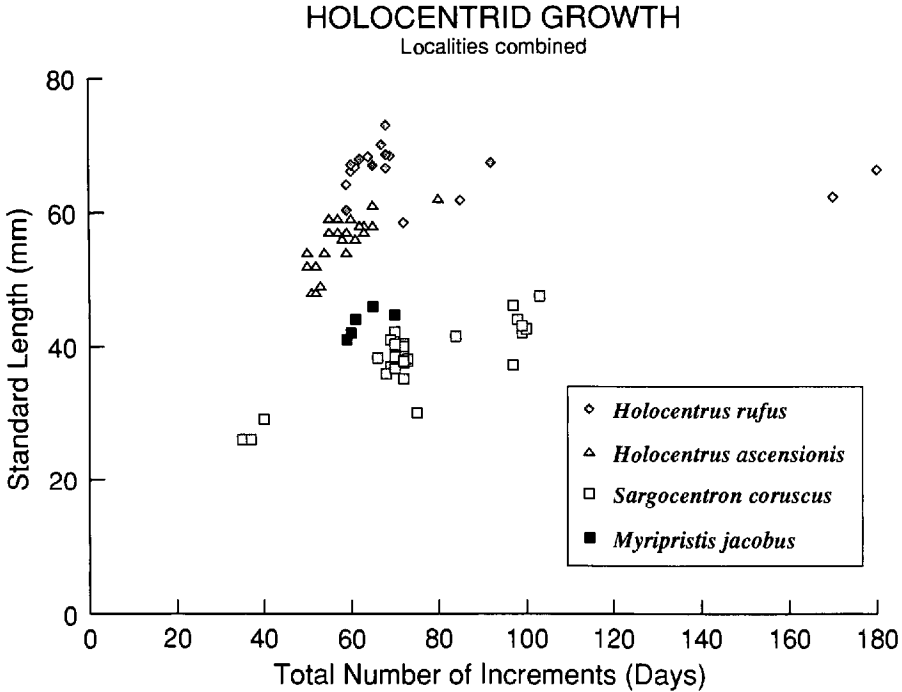
HOLOCENTRID GROWTH
Localities combined

Figure 9. Estimated growth rates for settled juveniles of four species of western Atlantic holocentrids based on total number of increments in lapilli. The specimens of the two species of *Holocentrus* are all recently settled (with the possible exception of the two specimens of 170–180 days age, see text discussion), as are the three smallest specimens of *Sargocentron coruscus*; the other specimens of *S. coruscus* are 31–66 days postsettlement and those of *Myripristis jacobus* are 10–21 days postsettlement (Table 1).

other holocentrids. We assumed initially that the transition mark in all holocentrids corresponds temporally to settlement onto the reef and the morphological transformation associated with it, as is presumed to be the case for most marine species. We were surprised, then, to find that the average number of days prior to this mark in *H. rufus* and *H. ascensionis* is roughly equal to or only slightly greater than that in other holocentrids. Furthermore, we expected, but did not find, much greater variability in age at transition in *Holocentrus,* as compared to other holocentrids, reflecting the temporal flexibility provided by the meeki stage.

There are three ways to explain these observations: (1) our prediction that *H. rufus* and *H. ascensionis* have a substantially protracted pelagic duration is incorrect. Instead, their accelerated growth rate alone accounts for the larger size and they settle at about the same age as other holocentrids; (2) the transition mark in the two species of *Holocentrus* does not correspond temporally with settlement, but with some event that takes place during the pelagic phase, the most logical being the morphological transformation from the postlarval rhynchichthys stage to the prejuvenile meeki stage; (3) a combination of 1 and 2 (accelerated growth over a protracted pelagic duration).

We have been unable to reject unequivocally either of the conflicting primary (1 and 2) hypotheses based on the available data, although the preponderance of evidence supports correspondence of the transition mark with the rhynchichthys-meeki transition rather than with settlement. Below, we discuss various aspects

of the data, concentrating initially on *H. rufus,* for which we have otolith data from both meeki stage and postsettlement individuals.

Small juveniles of *H. rufus* collected at their earliest appearance during censuses of shallow reefs were an average of 66 mm and 67 days old (excluding the two exceptional specimens discussed below). Thus, small juveniles of this size have a standard length equivalent to their age. These presumably are individuals that had just settled from the water column. This surmise is borne out by data from the smallest juvenile specimens of *H. rufus* in museum collections, indicating that size at settlement is about 60–70 mm. We are unable to age these museum specimens but presume that, as with the census specimens, their age is roughly equivalent to their standard length.

If the transition mark in the otoliths of *H. rufus* corresponds to settlement, then the newly settled specimens should either have no such mark or one just formed at the margin, and the otoliths of larger juveniles and adults should have this mark at approximately 60–70 days. In fact, the transition mark occurs at an average of 44 days, with a range of 38–51. If we are correct that settlement occurs at about 65 days, it is clear that the transition mark was generated prior to settling and probably corresponds to the morphological rhynchichthys-meeki transformation. The latter hypothesis is weakly corroborated by the presence, in about half of the specimens, of a second, faint transition mark at 60–70 days that temporally corresponds to the estimated age at settlement indicated by the preceding data.

An unequivocal corroboration of this hypothesis would be provided by the presence of a transition mark in the otolith of one or more specimens still in the meeki stage. Unfortunately, evidence from the only two meeki stage specimens for which we have otolith data is equivocal. There is no evidence of a transition mark in the otoliths of either of these specimens, despite the fact that they had obviously undergone the rhynchichthys-meeki transformation. A probable explanation for the absence of the transition mark is that they had just completed this transformation and the mark was being initiated at the margin of the otolith, where it is difficult to identify. This is borne out by the relatively young age of both specimens. One, 48.5 mm, had only 36 total increments, two fewer than the minimum number of pretransition increments found in any other specimen (Table 2). The other, which was 51.3 mm 5 days after capture, had 43 increments at capture, only five more than the minimum. Moreover, both specimens are relatively small (<50 mm at capture), although they are not the smallest among the 50 meeki stage specimens we have examined (37.8–74.1 mm, $\bar{x} = 58.2$).

The alternative hypothesis, i.e., that the transition mark in *H. rufus* corresponds to settlement, would require that the reef census and museum specimens referred to above were not newly settled when collected, because the otoliths of the former had an average of 24 post-transition increments and the latter were of equivalent size (and thus, presumably, age). Although we cannot entirely discount this possibility, we believe it is unlikely that *H. rufus* could consistently go uncollected for an average of more than three weeks after settling.

The early life history data for *H. ascensionis* is similar to that for *H. rufus,* although there are small differences in duration of stages. In small juveniles standard length is equivalent to age in days (Table 1). The average time to the putative rhynchichthys-meeki transition is 48 days (vs. 44 in *H. rufus*), and the average duration of the meeki stage (based on post-transition increments in newly settled reef census specimens) is 13 days (vs. 24). These limited data suggest that *H. ascensionis* has a slightly longer rhynchichthys stage and a somewhat shorter meeki stage than *H. rufus.*

In summary, the preponderance of evidence, although somewhat equivocal, strongly suggests that both species of *Holocentrus* settle at a larger size and greater age than other holocentrids because of rapid growth during the prolonged pelagic period afforded by the unique meeki stage and that the transition mark on the otolith is that of the rhynchichthys-meeki transformation rather than, as in other holocentrids, to the rhynchichthys-juvenile settlement.

Museum Material Examined

Specimens are listed by stage, alphabetically by institution, and numerically by catalog number.

Holocentrus ascensionis. — Rhynchichthys stage: 11 specimens, 18.9–42.3 mm ($\bar{x}$ = 27.4). ANSP 70080, 1, 24.0 mm, western Caribbean off Courtown Key, 30 March 1941 (paratype of *Beloholocentrus atractus* Fowler; see under the meeki stage of *H. rufus* for the holotype and 5 other paratypes of this nominal form); MCZ 49112, 1, 33.0 mm, western Gulf of Mexico off Mexico, 24 May 1954; MCZ 85242, 1, 24.6 mm, eastern Caribbean west of Dominica, 28 Oct 1967; USNM 194239, 1, 23.4 mm, west central Atlantic off New York, 21 Sep 1959; USNM 194240, 1, 29.2 mm, west central Atlantic off Virginia, 18 Aug 1958; USNM 194241, 1, 42.3 mm, west central Atlantic off New Jersey, 8 Jul 1957; USNM 194244, 1, 31.7 mm, west central Atlantic off New York, 27 Aug 1959 (a late rhynchichthys); USNM 194446, 1, 18.9 mm, western Caribbean north of Colombia, 26 Oct 1956; USNM 194447, 2, 22.0–30.0 mm, western Caribbean off Nicaragua, 24 Oct 1956 (the larger of the two a late rhynchichthys); USNM 194448, 1, 22.6 mm, western Caribbean off Nicaragua, 22 Oct 1956.

Meeki stage: 9 specimens, 47.9–59.8 mm ($\bar{x}$ = 54.5). AMNH 28246, 1, 47.9 mm, Bahamas, 2 Dec 1966; AMNH 34159, 2, 54.3–54.9 mm, Bahamas, 26 Jan 1968; ANSP 72757, 1, 48.7 mm, Misteriosa Bank in western Caribbean, 27 Jan 1937; FMNH 46198, 1, 59.8 mm, U.S. Virgin Islands, before 26 Sep 1911; FMNH 66994, 2, 54.1–58.5 mm, eastern Caribbean off Montserrat, 21 Mar 1966; MCZ 34740, 1, 59.5 mm, Cuba, 16 Nov 1937; USNM 317254, 1, 52.5 mm, Serrana Bank in western Caribbean, 20 May 1962 (see under juveniles of *H. ascensionis* for 2 slightly larger specimens collected with this).

Juveniles and adults: 118 specimens, 49.3 mm and larger. AMNH 8746, 1, 51.8 mm, Panama, 8 May 1924; AMNH 31980, 1, 54.2 mm, Bahamas, 18 Jan 1968; AMNH 33235, 1, 57.3 mm, Bahamas, 23 Jan 1968; AMNH 33502, 2, 55.4–59.2 mm, Grand Cayman, 5–12 Mar 1973; AMNH 34251, 2, 55.6–61.3 mm, Bahamas, 28 Jan 1968; AMNH 34252, 1, 55.0 mm, Bahamas, 28 Jan 1968; AMNH 74100, 6, 54.5–90.6 mm, Jamaica, 7 Apr 1969; AMNH 74770, 1, 54.8 mm, Bahamas, 5 Mar 1985; ANSP 84442, 2, 52.9–74.9 mm, Bahamas, 19 Aug 1955; ANSP 88453, 1, 55.5 mm, western Caribbean off Courtown Key, 30–31 Mar 1941; ANSP 97567, 1, 61.8 mm, Bahamas, 31 Mar 1959; ANSP 97811, 1, 49.3 mm, Bahamas, 1 Jun 1962; ANSP 115134, 1, 57.9 mm, Bahamas, 21 Jan 1968; ANSP 116299, 1, 63.4 mm, Bahamas, Feb 1965 (no day); ANSP 116460, 1, 64.7 mm, Bahamas, 12 Aug 1969; ANSP 118644, 1, 59.2 mm, Puerto Rico, 20 Jan 1970; ANSP 119808, 1, 59.6 mm, Bahamas, 21 Jan 1968; ANSP 133603, 1, 61.1 mm, Bermuda, 27 Jul 1975; ANSP 137935, 1, 58.0 mm, Bahamas, 25 Aug 1972; ANSP 138239, 1, 76.7 mm, Grenada, 21 Jun 1965; ANSP 142701, 1, 75.9 mm, Grenadines, 6 Apr 1952; ANSP 147462, 1, 56.7 mm, Bahamas, 16 Jan 1968; ANSP 147870, 3, 56.3–62.5 mm, Bahamas, 25 Jan 1968; ANSP 149685, 1, 52.7 mm, Bermuda, 27 Jul 1981; ANSP 149686, 1, 49.8 mm, Bermuda, 27 Jul 1981; FMNH 3250, 1, 70.6 mm, Puerto Rico, 26 Jan 1899; FMNH 5072, 1, 60.2 mm, Bermuda, 6 Sep 1905; FMNH 7205, 1, 58.1 mm, Brasil, 8 Jun 1899; FMNH 48161, 2, 81.2–96.1 mm, Bermuda, 23 Jun 1948; FMNH 60151, 4, 50.7–108.1 mm, Puerto Rico, 20 Jun 1952; FMNH 60154, 1, 66.4 mm, Jamaica, 27 Jun 1953; USNM 126102, 1, 60.4 mm, Puerto Rico, 1899 (no other date); USNM 132530, 1, 129.5 mm, Haiti, Jan 1945 (no day); USNM 132531, 1, 154.4 mm, Haiti, 22 Aug 1945; USNM 164835, 1, 53.7 mm, Bermuda, 19 Sep 1935; USNM 164896, 1, 67.7 mm, Bermuda, 20 Oct 1929; USNM 169956, 2, 58.1–61.4 mm, Bermuda, Sep 1935 (no day); USNM 170175, 2, 55.5–71.1 mm, Grenadines, 17 Mar 1956; USNM 178647, 1, 58.3 mm, Bermuda, 1 Apr 1931; USNM 183487, 1, 56.9 mm, British Virgin Islands, 30 Mar 1958; USNM 190514, 2, 55.3–84.3 mm, British Virgin Islands, 27 Apr 1959; USNM 263108, 7, 79.7–91.1 mm, Ascension Island, 11 Jul 1970; USNM 317254, 2, 79.1–84.4 mm, Serrana Bank in western Caribbean off Nicaragua, 20 May 1962 (see under the meeki stage of *H. ascensionis* for a smaller specimen collected with these); USNM 317257, 3, 107.4–181.0 mm, French Guiana, 6 May 1975; USNM 317258, 48, 69.3–104.2 mm, Ascension Island, 18 Jun 1970.

Juvenile?: MCZ 10972, 1, 50.6 mm, Cuba, no data other than F. Poey specimen, poorly preserved but probably a newly settled juvenile with retention of weak postorbital papillae and not yet fully developed striped color pattern.

Holocentrus rufus. — Meeki stage: 50 specimens, 37.8–74.1 mm ($\bar{x}$ = 58.2). AMNH 9028, 2, 57.6–60.2 mm, Bermuda, close to 8 Sep 1902; AMNH 9029, 4, 64.6–70.1 mm, Bermuda, 8 Sep 1902; ANSP

70079, 1, 56.6 mm, western Caribbean off Courtown Key, 30 Mar 1941 (holotype of *Beloholocentrus atractus* Fowler); ANSP 70080, 5, 52.4–56.1 mm, western Caribbean off Courtown Key, 30 Mar 1941 (paratypes of *Beloholocentrus atractus* Fowler); ANSP 97742, 1, 37.9 mm, Bahamas, 28 Jul 1961; CAS(SU) 45645, 2, 69.5–70.3 mm, Bermuda, 5 Sep 1935 (cleared and stained); FMNH 5079, 1, 70.3 mm, Bermuda, 6 Sep 1905 (lectotype of *Holocentrus meeki* Bean); FMNH 48583, 1, 63.7 mm, Bermuda, 26 Sep 1939; FMNH 49077, 5, 66.6–70.7 mm, Bermuda, 6 Sep 1932; FMNH 96015, 1, 74.1 mm, Bermuda, 6 Sep 1905 (paralectotype of *Holocentrus meeki* Bean); MCZ 41709, 1, 46.6 mm, Bahamas, Jun 1945 (no day); MCZ 43256, 1, 49.0 mm, Massachusetts, 3 May 1960; MCZ 49111, 1, 53.5 mm, Caribbean off Cayman Islands, 12 May 1962; USNM 65291, 1, 61.2 mm, Bermuda, 14 Oct 1906; USNM 164804, 1, 64.6 mm, Bermuda, 19 Sep 1931; USNM 164853, 4, 60.1–62.7 mm, Bermuda, 5 Sep 1935; USNM 178749, 6, 47.3–59.5 mm, Bermuda, 27 Aug 1937; USNM 194243, 1, 40.1 mm, west central Atlantic off North Carolina, 11 Oct 1957; USNM 194570, 1, 37.8 mm, west central Atlantic off North Carolina, 10 Oct 1957; USNM 194571, 1, 46.1 mm, west central Atlantic off North Carolina, 3 Oct 1957; USNM 199100, 2, 55.4–59.1 mm, New York, 22 Sep 1957; USNM 268403, 1, 55.2 mm, British Virgin Islands, 27 Apr 1959; USNM 316407, 1, 48.5 mm, Belize, 15 Sep 1990; USNM 316408, 2, 58.0–58.9 mm, Belize, 9 Nov 1988; USNM 316409, 1, 59.4 mm, east central Atlantic in Gulf of Guinea off Ivory Coast, 4 Apr 1968; USNM 316462, 1, 51.3 mm upon preservation after transformation in aquarium, Belize, captured 21 and preserved 27 Mar 1991; YPM 3469, 1, 56.4 mm, Bahamas, 25 Feb 1927.

Juveniles and adults: 72 specimens, 55.7 mm and larger. AMNH 21339, 1, 64.8 mm, Bahamas, 24 Jun 1964; AMNH 22864, 1, 66.3 mm, Bahamas, 11 Aug 1964; AMNH 28158, 3, 63.2–88.4 mm, Bahamas, 30 Nov 1966; AMNH 33014, 1, 62.7 mm, Bahamas, 19 Jan 1968; AMNH 34102, 1, 61.1 mm, Bahamas, 26 Jan 1968; AMNH 52464, 1, 69.2 mm, Bermuda, 1929–1932 (no other date); ANSP 14148, 1, 74.1 mm, Bahamas, no date; ANSP 84456, 3, 55.7–57.1 mm, Bahamas, 17 Jul 1957; ANSP 84463, 4, 61.8–67.3 mm, Bahamas, 3 Aug 1955; ANSP 84465, 1, 56.7 mm, Bahamas, 12 Jul 1957; ANSP 97536, 1, 61.0 mm, Bahamas, 16 Jul 1959; ANSP 116325, 1, 58.6 mm, Bahamas, 18 Nov 1970; ANSP 121841, 3, 61.4–67.2 mm, Grand Cayman, 28 Oct 1964; ANSP 137936, 1, 61.9 mm, Bahamas, 25 Aug 1972; ANSP 142704, 1, 74.0 mm, Bermuda, 10 Jun 1952; ANSP 145000, 3, 76.5–77.8 mm, Bermuda, 12 Jun 1952; CAS(SU) 45643, 1, 70.5 mm, Bermuda, 12 Sep 1934 (cleared and stained); FMNH 5070, 1, 65.1 mm, Bermuda, 8 Sep 1905; FMNH 5074, 1, 66.1 mm, Bermuda, 22 Sep 1905; FMNH 5076, 6, 68.5–77.9 mm, Bermuda, 18 Sep 1905; FMNH 5077, 1, 68.9 mm, Bermuda, 20 Sep 1905; FMNH 5078, 1, 76.5 mm, Bermuda, 7 Nov 1905; FMNH 5080, 1, 63.3 mm, Bermuda, 9 Sep 1905; FMNH 46209, 2, 62.1–74.5 mm, Bermuda, 6 Sep·1905; FMNH 48519, 1, 68.6 mm, Bermuda, 1908 (no other date); FMNH 48655, 1, 72.7 mm, Bermuda, 31 Jan 1933; FMNH 48723, 3, 70.4–72.8 mm, Bermuda, 21–24 Sep 1937; USNM 57427, 1, 63.8 mm, Florida Keys, 24 Nov 1906; USNM 178617, 1, 119.2 mm, Antigua, 18 Jul 1932; USNM 178654, 1, 68.4 mm, Bermuda, 1 Apr 1931; USNM 178690, 2, 67.5–71.4 mm, Bermuda, 1–14 Oct 1931; USNM 183436, 2, 67.7–85.8 mm, British Virgin Islands, 7 Apr 1958; USNM 190517, 3, 78.3–162.7 mm, British Virgin Islands, 27 Apr 1959; USNM 317256, 2, 120.7–128.5 mm, Barbados, 24 Apr 1969; USNM 317284, 14, 69.9–111.7 mm, Dominica, 5 Nov 1964.

Holocentrus sp.—Meeki stage: USNM 42303, 6, 69.5–78.1 mm ($\bar{x}$ = 72.8), Angola, off São Paulo de Loanda, 12 Dec 1889 (the *Holocentrus hastatus* of Fowler, 1919 and 1936 = *Sargocentron hastatus*).

Sargocentron coruscus.—Rhynchichthys stage: 15 specimens, 30.3–35.6 mm ($\bar{x}$ = 31.7). USNM 316464, 1, 32.3 mm, Belize, 16 Mar 1991; USNM 322231, 7, 30.3–32.5 mm, Belize, 7 Mar 1992; USNM 316463, 2, 33.1–35.6 mm upon preservation after transformation in aquarium, Belize, captured 17 and preserved 27 Mar 1991; USNM 322232, 5, 30.7–31.4 mm upon preservation after transformation in aquarium, Belize, captured 5 and preserved 6 Mar 1992.

Exceptional Specimens of *Holocentrus*

Otoliths.—Two exceptional specimens of *H. rufus* collected at St. Croix in March 1980 are shown with ages of 170 and 180 days in Table 1. These relatively small specimens of 62 and 66 mm have microstructural transitions of 44 and 51 days and back calculated spawning dates in September. Two possible explanations are as follows: (1) the fish settled in the fall and had virtually no growth over the winter; or (2) the fish had an extended pelagic existence with slow growth in the meeki stage and settled just before capture. A corollary of the latter hypothesis is that the microstructural transition at 44 to 51 days in these individuals is not a settlement mark but, rather, delineates the transition between the rhynchichthys

and meeki larval stages, as we postulate is probably the case in *Holocentrus* based on other evidence.

Museum Materials. — Among the hundreds of lots of specimens of *Holocentrus* in museum collections examined in this study, only two do not fully conform with the preceding morphological characterizations of the species.

One of these comprises six meeki stage specimens (USNM 42303), 69.5–78.1 mm ($\bar{x}$ = 72.8 mm), collected 12 December 1889 by the U.S. Eclipse Expedition to West Africa off São Paulo de Loanda (or Loando), Angola. There is no indication in the USNM catalogue and accession records of how the specimens were collected (e.g., plankton net, night light, or bottom trawl). The color pattern (although faded and with a tanish overtone) is dark above and silvery below, the body is streamlined, the head lacks the rostral and other spines found in the rhynchichthys stage, the upper lobe of the caudal fin and the anterior dorsal-fin rays are not elongate, and well-developed postorbital papillae are present, all of these being typical features of meeki stage *Holocentrus*. The largest of the Loanda specimens (78.1 mm) is slightly larger than the largest meeki stage specimen examined from the western Atlantic (74.1 mm).

The Loanda specimens have been described twice in the literature (Fowler, 1919, 1936), incorrectly under the name *Holocentrus hastatus* Valenciennes (1829). The latter is a species of *Sargocentron* commonly recorded from west Africa (Greenfield, 1981), which has a distinctly different physiognomy than that of *Holocentrus*, especially of meeki stage *Holocentrus* as represented by the Loanda material.

The Loanda specimens have all of the external features that distinguish *Holocentrus* from all other holocentrids (Woods, 1955; Woods and Sonoda, 1973; Bohlke and Chaplin, 1968; Greenfield, 1981). However, they cannot unequivocally be assigned to either of the two species presently recognized in that genus. They have the relatively high lateral line scale counts typical of *H. rufus*; the counts of these scales made on both sides of all six specimens are 49–54 ($\bar{x}$ = 51.3). The length of the upper jaw in the Loanda specimens is relatively short, 11.3–11.8% SL ($\bar{x}$ = 11.5), typical of the length in meeki stage *H. rufus*. The relatively great length obtained by the Loanda meeki stage specimens is similar to that found in *H. rufus*, with the Loanda specimens being far larger than any of the meeki stage *H. ascensionis* examined in this study.

In two characters, however, the Loanda specimens are similar to meeki stage *H. ascensionis*; they are relatively deep bodied (greatest depth 27.5–30.1% SL, $\bar{x}$ = 29.1) and have a relatively long preopercular spine (7.1–7.4% SL, $\bar{x}$ = 7.3).

The pterygiophores of the soft dorsal fin in the Loanda specimens are uninformative because they encompass the patterns typical of both *H. rufus* and *H. ascensionis* and an intermediate pattern.

Of the two species of *Holocentrus*, only *H. ascensionis* is known from the eastern Atlantic (Woods and Sonoda, 1973; Greenfield, 1981). The unusual meeki stage specimens from Loanda present several possibilities. If they are *H. ascensionis*, the eastern Atlantic population of that species has significantly more lateral line scales, a slightly shorter upper jaw, and a meeki presettlement stage that reaches a significantly larger size than in the western Atlantic. Conversely, if the Loanda specimens are *H. rufus*, the eastern Atlantic population of that species has a deeper body and a longer preopercular spine.

Because the meeki stage specimens from Loanda differ morphologically from the meeki stage of both *H. rufus* and *H. ascensionis* we suggest that they may represent a distinct taxon at either the subspecific or specific level endemic to the

southeastern Atlantic. The exploration of that possibility is beyond the scope of this work.

The other questionable lot is a single specimen (MCZ 10972, 50.6 mm) of *Holocentrus* from Cuba, with no other data than that it was from the collections of F. Poey. It is poorly preserved and missing numerous lateral line scales, especially on the right side. It has a much faded color pattern that appears to have been dark above and silvery below as in a meeki stage; however, postorbital papillae are only weakly developed. It may represent a specimen that had just settled immediately prior to capture. Because so many scales are missing and other morphometrics are equivocal, we cannot identify the specimen to species. However, we believe it is more likely to be a recently settled specimen of *H. ascensionis* than of *H. rufus,* partially because its size is within the known range of settlement size for young juveniles of *H. ascensionis,* and it is 5 mm smaller than the smallest settled juvenile we have found of *H. rufus* in our surveys of numerous collections of Caribbean fishes (although only slightly smaller than the smallest juvenile reported by Woods, 1955).

LITERATURE CITED

Bean, T. H. 1906a. Descriptions of new Bermudian fishes. Proc. Biol. Soc. Washington 19: 29–34.
———. 1906b. A catalogue of the fishes of Bermuda, with notes on a collection made in 1905 for the Field Museum. Field Columbian Mus. Publ. 108, Zool. Ser. 7(2): 28–89.
Beebe, W. 1936. Food of the Bermuda and West Indian tunas of the genera *Parathunnus* and *Neothunnus.* Zoologica 21: 195–205.
——— and J. Tee-Van. 1933. Field book of the shore fishes of Bermuda and the West Indies. Dover Publ., New York. 337 pp.
Bohlke, J. E. and C. C. G. Chaplin. 1968. Fishes of the Bahamas and adjacent tropical waters. Livingston Publ. Co., Wynnewood, Pennsylvania. 771 pp.
Brothers, E. 1984. Otolith studies on early life stages of fishes: applications to systematics. Pages 50–57 *in* H. G. Moser, ed. Ontogeny and systematics of fishes. Amer. Soc. Ich. Herp., Spec. Pub. 1.
———. 1987. Methodological approaches to the examination of otoliths in aging studies. Pages 319–330 *in* R. C. Summerfelt and G. E. Hall, eds. Age and growth of fish. Iowa State Univ., Ames, Iowa.

———. 1990. Otolith marking. Amer. Fish. Soc. Symp. 7: 183–202.

——— and C. P. Mathews. 1987. Application of otolith microstructural studies of age determination of some commercially valuable fish of the Arabian Gulf. Kuwait Bull. Mar. Sci. 1987(9): 127–157.

——— and W. N. McFarland. 1981. Correlations between otolith microstructure, growth, and life history transitions in newly recruited french grunts [*Haemulon flavolineatum* (Desmarest), Haemulidae]. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 178: 369–374.

——— and R. E. Thresher. 1985. Larval duration, dispersal and biogeography of Indo-Pacific coral reef fishes. Pages 53–69 *in* M. Reaka, ed. The ecology of coral reefs, Vol. 3. No. 2. NOAA Sympos. Ser. Undersea Res., Washington, D.C.

———, D. M. Williams and P. F. Sale. 1983. Length of larval life in 12 families of fishes at One Tree Island, Great Barrier Reef, Australia. Mar. Biol. 76: 319–324.

Cowen, R. K. 1991. Variation in the planktonic larval duration of the temperate wrasse *Semicossyphus pulchher*. Mar. Ecol. Prog. Ser. 69: 9–15.

Fowler, H. W. 1919. The fishes of the United States Eclipse Expedition to West Africa. Proc. U.S. Nat. Mus. 56: 195–292.

———. 1936. The marine fishes of west Africa. Bull. Amer. Mus. Nat. Hist. 70(part 1): 1–605.

———. 1944. Results of the fifth George Vanderbilt Expedition (1941). Acad. Nat. Sci. Philadelphia Monog. 6: 1–583.

Greenfield, D. W. 1981. Holocentridae. 8 un-numbered pages *in* W. Fischer, G. Bianchi, and W. B. Scott, eds. FAO species identification sheets for fishery purposes. Eastern Central Atlantic, Vol. 2.

Johnson, G. D. and R. H. Rosenblatt. 1988. Mechanisms of light organ occlusion in flashlight fishes, family Anomalopidae (Teleostei: Beryciformes), and the evolution of the group. Zool. Jour. Linnean Soc. 94: 65–96.

Keener, P., G. D. Johnson, B. W. Stender, E. B. Brothers and H. Beatty. 1988. Ingress of postlarval gag, *Mycteroperca microlepis*, (Pisces: Serranidae) and other postlarval groupers through a South Carolina barrier inlet. Bull. Mar. Sci. 42: 376–396.

Matsura, K. and T. Shimizu. 1982. The squirrelfish genus *Adioryx*, a junior synonym of *Sargocentron*. Jap. J. Ichthy. 29: 93–94.

McKenney, T. W. 1959. A contribution to the life history of the squirrel fish *Holocentrus vexillarius* Poey. Bull. Mar. Sci. Gulf Carib. 9: 174–221.

Munro, J. L., V. C. Gaut, R. Thompson and P. H. Reeson. 1973. The spawning seasons of Caribbean reef fishes. J. Fish Biol. 5: 69–84.

Nelson, E. M. 1955. The morphology of the swim bladder and auditory bulla in the Holocentridae. Fieldiana, Zool. 37: 121–130.

Osbeck, P. 1765. Reise nach Ostindien und China. Rostock. 552 pp.

Valenciennes, A. 1829. Vol. 3. Pages 1–500 *in* G. Cuvier and A. Valenciennes, eds. Histoire naturelle des poissons. Paris.

———. 1831. Vol. 7. Pages 441–531 *in* G. Cuvier and A. Valenciennes, eds. Histoire naturelle des poissons. Paris.

Walbaum, J. J. 1792. Petri Artedi genera piscum. Pars iii. Pages 1–723 *in* Petri Artedi renovati. Grypeswaldiae.

Woods, L. P. 1955. Western Atlantic species of the genus *Holocentrus*. Fieldiana, Zool. 37: 91–119.

——— and P. Sonoda. 1973. Holocentridae. Pages 331–386 *in* D. M. Cohen, ed. Fishes of the western north Atlantic. Sears Found. Mar. Res., Yale Univ., Memoire 1.