

SPAWNING AND LARVAL DEVELOPMENT OF THE HOGFISH, *LACHNOLAIMUS MAXIMUS* (PISCES: LABRIDAE)

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ABSTRACT

Spawning of the hogfish, *Lachnolaimus maximus*, along a reef-sand interface near the insular shelf edge off southwestern Puerto Rico was observed over a period of 20 months by scuba diving. Eggs were collected and returned to the laboratory for hatching. Male-female ratio was about 1:10. Males patrolled elongate territories, which did not change during the 20 months, during the afternoon. Males initiated spawning by a courtship display using the prolonged dorsal fin spines and other fins. If the female responded, an elaborate process, termed the spawning rush, occurred during which the gametes were released. A male spawned with one female at a time, but often spawned with several females during an afternoon. Peak spawning was from December to April. There was no evidence that spawning was influenced by current speed or direction or by lunar or tidal periodicity. Eggs were planktonic, about 1.2 mm in diameter, lacked visible pigment, and hatched in 23 hours at 25.5°C. They were preyed on extensively by yellowtail snappers, *Ocyurus chrysurus*. Larvae, which survived in the laboratory up to 50 days, lacked a distinct transformation to juveniles but gradually acquired pigment and juvenile form after 13 days. Free-swimming postlarvae formed mucous bubbles at night.

The hogfish, *Lachnolaimus maximus* (Walbaum), is the largest tropical western Atlantic labrid, reaching about 11 kg (Randall and Warmke 1967); adults are conspicuous members of many reef communities. A highly prized food-fish, it is taken incidentally with other fishes, particularly by spear or hook and line.

It is a protogynous hermaphrodite, but there are no primary males. Color patterns are distinctive between sexes. Males, which are more highly pigmented, have a dark reddish brown mask on the head. Also of the same hue are the base and first soft rays of the dorsal fin, the base of the rays in the lunate caudal fin, the pelvic fins, and the leading edge of the anal fin. The color of these darkened areas varies in intensity, depending on the nervous state of the male. The pectoral fins are yellow and there is an elongate spot on each side of the body. Females lack the reddish brown darkening, but possess a black spot about the size of the eye at the posterior base of the dorsal fin. The first three dorsal fin spines are greatly prolonged in males, much more than in females. Males also have filaments on the anal fin, soft dorsal fin, and margins of the caudal fin. The snout is longer in males and has a concave profile.

Although various aspects of its biology, such as food habits (Reid 1954; Randall and Warmke 1967; Davis 1976) and growth (Davis 1976), have been well documented, little has been published on spawning or early life history. While scuba diving on a shelf-edge coral reef off southwestern Puerto Rico to study reef fish spawning, I encountered a large spawning population of hogfish. I was able to observe the courtship display and spawning rush over a 20-mo period from December 1977 to July 1979. I also was able to collect large numbers of fertilized eggs, which were returned to the laboratory and hatched. A large number of larvae were kept alive up to 30 d, while smaller numbers were maintained to 50 d. I was able, therefore, to describe and illustrate in some detail the development of larvae from hatching through the juvenile stage.

METHODS

Observations of Courtship and Spawning

The site was visited 154 d during the 20 mo. From December through March, when spawning was high, visits were daily, if possible, but during the summer, visits were usually weekly.

Males and females were observed both at close range and also from the maximum distances possible. The presence of observers had less effect on

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the behavior of males than females, but no disturbance was noted if the observer moved no closer than about 4-8 m. Only during early phases of the spawning rush would rapid movements by a diver cause the female to abort the spawning rush. Once the spawning rush had reached an advanced point, however, the observer could approach quickly without interrupting. Fish frequently observed seemed to become accustomed to the observers.

Motion pictures (16 mm) were made of different aspects of spawning behavior. These were analyzed frame-by-frame to determine the duration of each act and the orientation of the fish during the rapid spawning rush.

Collection and Rearing of Eggs

Eggs were collected with fine mesh dip nets (sold as "brine shrimp nets") 10 by 15 cm with mesh openings of about 100 μ in diameter. After some practice, an observer could follow a pair on their spawning run and quickly locate the diffuse cloud of gametes when they were released. The cloud was either constantly observed or squirted with ink mixed with seawater from a plastic bottle to provide a reference mark. About 45 s to 1 min were needed to assure fertilization. After that time, eggs were collected by passing the net through the water where the eggs occurred. In one smooth motion, the net was then everted into a plastic bag and the bag was filled with water from the area where the gametes occurred, in hope of obtaining more sperm in the water and thereby increasing the chances of fertilization. Eggs collected before 45 s had elapsed generally were not fertile. Since the ability to see the cloud of gametes decreases with each second, the collection of planktonic eggs with a small hand net is a contest between the time required for fertilization and the ability of the collector to discern the location of the eggs. Although the ink helps to locate the eggs, it quickly disperses or tends to rise or sink because of the differences in density. I found it valuable to remain about 0.5-1.0 m away from the cloud, once it had been located, and focus on sediment particles, opaque eggs, or larger zooplankton rather than trying to follow the rapidly dispersing cloud. If the bag is clear plastic, the eggs, once inside, can be seen easily. It helps to face the sun (underwater) and backlight the eggs by blocking out the sun directly to the eyes with a hand behind the bag.

The eggs in the bags were transported to the

laboratory in buckets partially filled with seawater, and were released into aerated closed-circuit 80 l aquaria within about 90 min of being collected. Rearing methods followed Houde and Tanaguchi (1977). The aquarium was constantly illuminated by a twin 20-watt fluorescent lamp. A culture of *Chlorella* was introduced at hatching. Later larvae were fed wild zooplankton collected with 53 μ mesh nets. Temperatures were maintained at 25°-27°C.

Selected eggs and larvae were preserved in 3% Formalin². Larvae were illustrated from preserved specimens by a camera lucida attachment on a dissecting microscope.

The Study Site

The study site was located on the insular shelf edge 16 km ESE of La Parguera, Puerto Rico (approximate position: lat. 17°54'N, long. 66°57'W). It is typical of most reefs off the south coast of Puerto Rico and the Virgin Islands (MacIntyre 1972; Adey et al. 1977). It is an elevated ridge about 100-150 m wide, paralleling the actual shelf break, and has a rocky substrate with abundant coral, particularly on the seaward and inshore flanks. Minimum depth is about 16 m. Near the study area the seaward portion slopes gently to about 18-19 m depth, then plunges downward at an angle of about 60° to oceanic depths. The inshore side slopes downward at about 10° until it meets a nearly level sandy-rubble plain. This slope, termed the "moat slope," is where most spawning activity by *L. maximus* was observed.

Water temperatures varied between 24° and 27°C, visibility between 50 and 10 m. The area is within the trade wind belt of the Atlantic tropics and is consistently exposed to easterly winds of moderate force (Glynn 1973). Waves usually consisted of a small wind produced chop associated with larger swells. Wave heights of 1-2 m were common, but seldom exceeded 2 m. Complete calms would occasionally occur, most often during winter. These calms were associated with lee-shore conditions on the southwestern coast and occurred only a few percent of the time. Currents were generally east to west, paralleling the shelf edge, but occasionally they were completely reversed or ran strongly off or onto the shelf. Clearest water occurred when strong southeast-

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

erly winds drove oceanic water up onto the shelf edge and also produced rough conditions. The most turbid water was either associated with calms, when the normal wind-driven flow from offshore was eliminated, or when large amounts of rain fell on Puerto Rico, particularly during the summer-fall wet season.

OBSERVATIONS

Spawning Groups of *L. maximus*

Males established a territory along the moat-moat slope interface and defended it against the intrusion of other males. The territory was unusual in being very elongate along the moat-moat slope axis, but not ranging far either over the sandy moat or up the moat slope. Males patrolled their territory during the afternoon, passing from one extreme of the sand-reef border to the other without changing direction except as interrupted by spawning rushes with females. Three territories that I closely examined each encompassed about 100 m of the moat-moat slope interface. The turning points at either end remained consistent over the entire 20 mo. During active spawning periods, generally 2-3 min, were required for one "pass" if no spawning occurred.

An estimated 10-15 females occurred with each male during the afternoon. Although I found some evidence that females may remain with the same male during any one day, I could not determine if they changed males at other times.

Time and Conditions of Spawning

Active spawning was observed from December through April, but I could not be sure if spawning also occurred in other months when low water visibility often made observations difficult. Males, however, continued to patrol their territories during the afternoon and were occasionally seen to court females, but no spawning was seen. In any event, it is certain from direct observation that spawning during winter and spring must be at least an order of magnitude above any that may occur during summer and fall. Davis (1976) reported that peak spawning, based on gonad indices, of Florida Keys hogfish is probably in February and March, although some spawning may be occurring in other months. Gonad indices were consistently low from May through August.

There is no evidence for lunar periodicity. Dur-

ing peak spawning periods, spawning rushes occurred on all phases of the moon and spawning proceeded day after day with no apparent change over the lunar cycle.

Spawning began in midafternoon, but the exact time of initiation was never observed. Hogfish were spawning by 1.5 h before sunset and continued to spawn until 15-30 min before sunset. Males began to patrol more slowly as sunset approached, and the frequency of spawning rushes decreased quickly. Females seemed to leave the spawning area, or at least were not visible, by about 15 min before sunset. Males continued to patrol slowly until about sunset, then left the immediate area of the sand-reef interface.

During the season of active spawning, current speed or direction, surge on the bottom, and water clarity seemed to have little effect on spawning behavior. Rushes were observed under nearly all conditions encountered. Water temperatures ranged between 24° and 26°C. Day length was short, being near the annual minimum of about 11 h near the start of peak spawning in December and about 12.5 h by April.

Spawning Behavior

A female often indicated her readiness to spawn by moving up in the water column on approach of a male; otherwise, a male would actively court females encountered on his patrol. If a female was seen near the bottom, a male would swim quickly towards her, shifting from pectoral sculling to caudal fin swimming in a burst of speed, and then dive towards her exhibiting a courtship display. This consisted of erecting the three long anterior spines of the dorsal fin and shaking the posterior two of these rapidly back and forth at about 8-10 cycles/s. The posterior portion of the dorsal fin, the upper and lower caudal fin margins, and the pelvic fins were also agitated at a similar rate. Often the male would swoop above the female and dive rapidly towards her while displaying. If no response was elicited, the male would move quickly on to another female or resume patrolling.

The spawning act was part of an elaborate process termed the spawning rush, which could be initiated by the male actively courting the female or by the female simply rising up in the water column as the male approached on his patrol. The rush required 10-25 s total time from the time the fish left the vicinity of the substrate.

On the basis of hundreds of observations and the complete filming of 12 rushes, the spawning rush may be broken down into six distinct periods: 1) Pectoral swim up, 2) tail swim, 3) swim alongside and tilt, 4) release, 5) circle and display, and 6) swim down (Fig. 1).

1) Pectoral swim up—A male approaching from some distance a female which was up above the bottom would swim upward at an angle of 10° - 20° towards the female, using concurrent sculling of the pectoral fins, usually of 2.0-2.5 beats/s. The dorsal and anal fins were folded against the body. As he approached the female, who rose slowly at a steeper angle to match his ascent, the male began to turn laterally and shifted to the second type of swimming.

2) Tail swim—The male folded the pectoral fins against his body and began undulating the caudal fin and posterior portion of his body at about 4 beats/s. Pelvic fins were usually about one-half extended. The female continued to rise slowly as the male approached her from behind. This stage lasted about 2-5 s.

3) Swim alongside and tilt—The male, using the tail only, continued swimming and came forward alongside the female, who was still moving forward. Their bodies were close together, the male slightly behind the female with his snout about even with her eye (Fig. 2). Once alongside, the male angled the dorsal portion of his body outward at about 15° - 20° from the female. This took 0.5-1.5 s. During this phase, the male and female turned laterally 90° - 180° in the direction of the female.

4) Release—At the end of the turn to initiate gamete release, the male started swimming forward more rapidly than the female. As he overtook her, he bent his body laterally towards her, then broke in the opposite direction. At this time the gametes of both sexes appeared to be released. The cloud could usually be seen, but the exact moment of release was difficult to determine. In some cases the male, when he turned toward the female, was sufficiently far forward to actually cross slightly into her path. The sharp break away from the female was accomplished by a sharp flick of the caudal fin. This also served

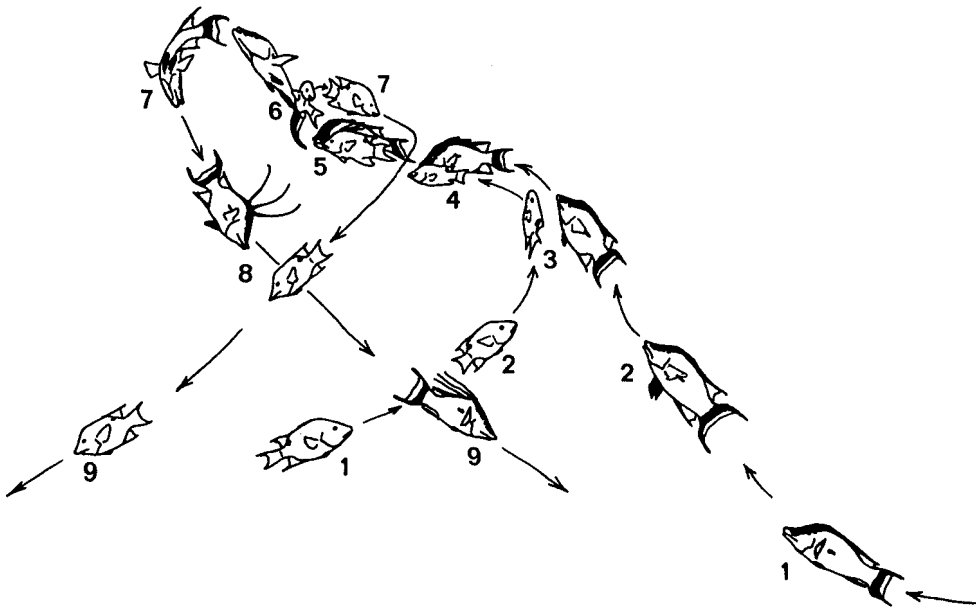


FIGURE 1.—Idealized spawning sequence of *Lachnolaimus maximus* under conditions where the female meets the male in mid-water. The male (right) approaches and initiates the "pectoral swim up" action (1) followed by "tail swim" (2-3) when approaching the female. The lateral turn in "swim alongside and tilt" towards the female (4-5) is followed by the "release" of the gametes (6). "Circle and display" (7-8) precedes "swim down" (9). In this case the male is illustrated as returning in the direction opposite that when spawning was initiated, but this is not always the case. Often the male will continue patrolling in the same direction.

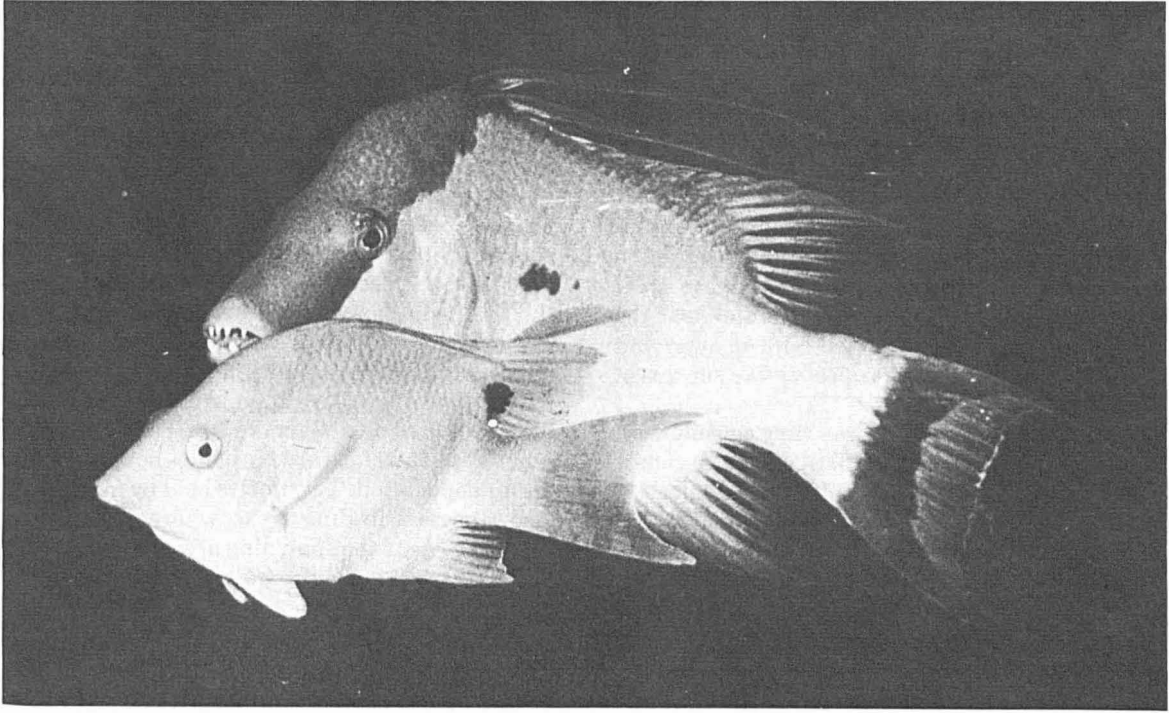


FIGURE 2.—Photograph of spawning pair of *Lachnolaimus maximus* with the smaller female in front of the male. The fish are turning laterally in the "swim alongside and tilt" action just prior to release of the gametes. Photo by C. Arneson at the study site.

to create a turbulent eddy where the gametes had been released to aid in their mixing.

5) Circle and display—When the male broke sharply away from the female, she also turned away, but not as sharply. Both started downward, the male doing a 180° lateral turn while descending. When laterally exposed to the female he initiated a display similar to that used in courtship. The three dorsal spines were erected, the last two shaken. The soft portion of the dorsal and anal fins, the upper and lower margins of the caudal fin, and the pelvic fins were agitated at a rate of 8-10 times/s. This display continued for 1-3 s as the male approached the female and they continued down.

6) Swim down—The male separated from the female and swam downward at a steep angle. She did likewise. He may quickly approach another female and engage in courtship behavior or he may simply rise into the water column if another female is ready to spawn. Occasionally he will court the female he has just spawned with after they have returned to near the substrate, but I have never seen a female spawn two times in rapid succession.

In many instances it was possible to observe the gamete cloud after it had been released. The movements of the fish, particularly the male, produce an area of turbulence where the gametes are thoroughly mixed. On occasion the actual sperm cloud was also faintly visible. Within 15-20 s after release, the gametes will occupy a volume near 1 m³. There are usually several hundred or more eggs released per rush. In some instances no egg cloud could be found, even though the usual procedures for locating it were followed and the observer arrived within a few seconds to the region in which the eggs should have been. It is possible, but not yet proven, that eggs are simply not released on some rushes.

Yellowtail snappers, *Ocyurus chrysurus*, were active predators on the eggs immediately after release. One to as many as ten yellowtail snappers would converge on the egg cloud 1-2 s after eggs had been released and would pick individual items, presumably eggs, from the water. This occurred in about 20-40% of rushes. Generally if yellowtail snappers observed a pair of *L. maximus* rising to spawn, they would attempt to locate and eat the eggs. On occasion individuals

would follow pairs of *L. maximus* so closely that the spawning rush would be interrupted, causing both the male and female to return to the substrate.

Yellowtail snappers were much more abundant at the actual insular shelf edge than at the hogfish spawning area. At the shelf edge they formed loose aggregations of from several hundred to several thousand individuals feeding on zooplankton high above and beyond the shelf edge. Only a relatively few were found near the moat-moat slope interface, some 100 m away, but these few influenced the reproductive success of *L. maximus*.

Gonad indices of both sexes vary considerably during the year (Davis 1976) in a pattern consistent with my observations. Gonad indices of males for each month ranged from about 0.14 to 0.20 (gonad weight as a percentage of body weight) for December to April and from 0.0 to slightly less than 0.10 for June to August. The indices were relatively low compared with those for other Caribbean labrids (Warner and Robertson 1978) but on a level with those of terminal males (both primary and secondary) of some other species. *Lachnolaimus maximus* is monandric (no primary males) (Davis 1976) and harem, and the low gonad indices of males are consistent with the data for larger Caribbean labrids of Warner and Robertson (1978). Males are close to an order of magnitude heavier than other "large" Caribbean labrid males (*Halichoeres radiatus* and *Bodianus rufus*) and two orders of magnitude above those of smaller species. Although the gonad indices are low compared with those of other species, the actual gonad is large. The relative size between large and small labrids may not be very important. Males observed in the present study spawned repeatedly each afternoon during the active season. While data for an entire afternoon were not available, I estimated that at least some males engaged in 50-100 spawning rushes/afternoon and that they were capable of fertilizing each group of eggs released.

The female-male ratio among adults also seems higher than in most other Caribbean labrids. Davis (1976) reported a ratio of 13:1 in the 724 individuals he sampled, which is close to the estimated 10:1 ratio that I observed. Warner and Robertson (1978), however, reported a ratio of only 3:1 or less for most species.

The spawning location, about 100 m from the insular shelf edge rather than at the edge itself, appears contrary to some of the concepts put for-

ward by Johannes (1978). It is true that many reef fishes producing planktonic eggs often move considerable distances to be able to release eggs at insular shelf edges where they may be transported offshore. Hogfish, however, rarely move long distances to spawn. Adults can easily range to the shelf edge for spawning and some individuals probably remain along the shelf edge at night after spawning ceases. The potentially heavier egg predation by yellowtail snapper at the shelf edge may help restrict hogfish spawning to more inshore areas. In addition, hogfish are typically found on the sandy margins of reefs where they feed largely on sand-dwelling molluscs (Randall and Warmke 1967) and the moat-moat slope interface area provides both reef shelter and open sand. Territories held by males may also represent feeding areas, whereas the actual shelf edge near the spawning area has little sand, and consists mostly of rock and coral.

EGG AND LARVAL DEVELOPMENT

Eggs are 1.2 mm in diameter and have a single oil globule 0.17 mm in diameter. They float and lack any visible pigment. They hatched 23 h after fertilization at 25.5°C.

Larvae were reared at about 26°C but the temperature could not be closely controlled. When hatched, the larvae had little pigment. Scattered melanophores occurred in the head region and in a line on the dorsal margin of the body (Fig. 3a). They did not orient until about 24 h after hatch, but the eyes were still unpigmented at that stage (Fig. 3b). A line of melanophores along the ventral surface of the body began to develop at this time. Sometime between 24 and 36 h posthatch the eyes became pigmented. First food was added 31 h after hatch. Larvae seemed to be making feeding strikes by about 42 h posthatch (Fig. 3c). At this stage the amount of pigment along the ventral surface of the body increased and was plainly visible to the unaided eye. The black pigment increased daily until 7-8 d posthatch and then remained stable. At 7 d posthatch feeding with *Artemia salina* was initiated. At this time pigment cells were visible on the tip of the lower jaw and on the lower margin of the gill cover. By 10 d posthatch the fin rays had begun to develop, the pelvic fin buds were apparent, and notochord flexion had occurred.

Gas bladder inflation occurred 10 d posthatch (Fig. 3e) in 10-20% of the larvae. Larvae without the bladder inflated would swim with the tail

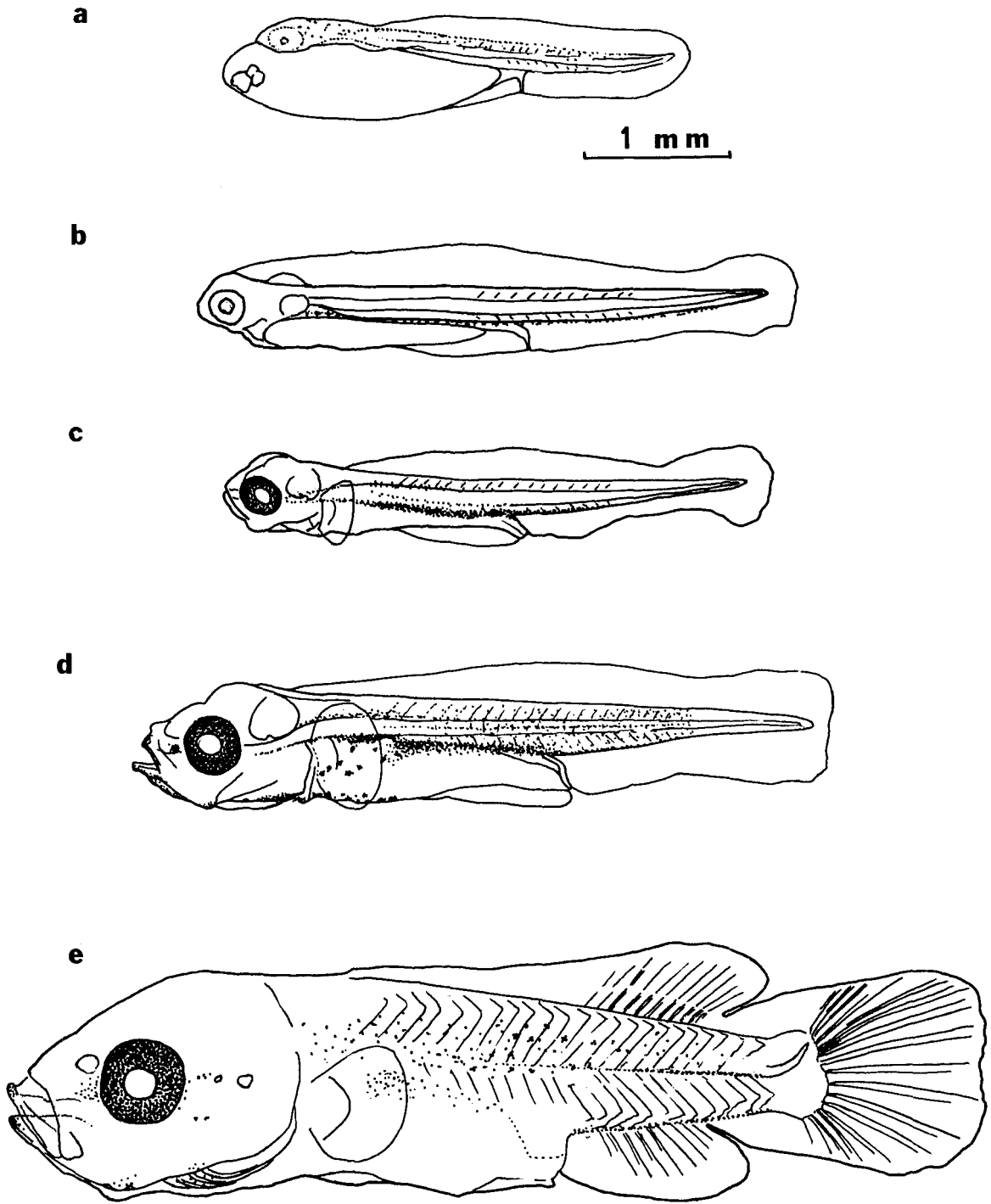


FIGURE 3.—Larval stages of *Lachnolaimus maximus*. a, At hatch; b, 24 h posthatch; c, 42 h posthatch; d, 7 d posthatch; e, 10 d posthatch.

down at an angle of 20° - 30° while those with the bladder inflated would swim with the tail slightly up. By 12-13 d the bladders of nearly all larvae had been inflated.

At 13 d posthatch the first traces of the juvenile color pattern began to appear (Fig. 4a) with the development of three pigmented lobes on the base of the anal fin. Widely scattered brown chromatophores appeared on the body, but showed no discernible pattern. At this point the full complement of dorsal, anal, and caudal fin rays had been developed, but the pectoral rays did not seem fully developed. The pelvic fins con-

sisted of only a slight bulge and the first three spines of the dorsal fin were elongated compared with those more posterior. At this stage the fish were considered to be postlarvae.

At 17 d the body had a distinct brown and white color pattern (Fig. 4b) with the first three dorsal spines elongated. At this stage there was little difficulty identifying the postlarvae as *L. maximus*. The postlarvae did not orient to the bottom of the rearing tank, but remained free-swimming. The lights of the rearing tank were extinguished for the first time overnight at 17 d posthatch. Over one-half of the larvae formed

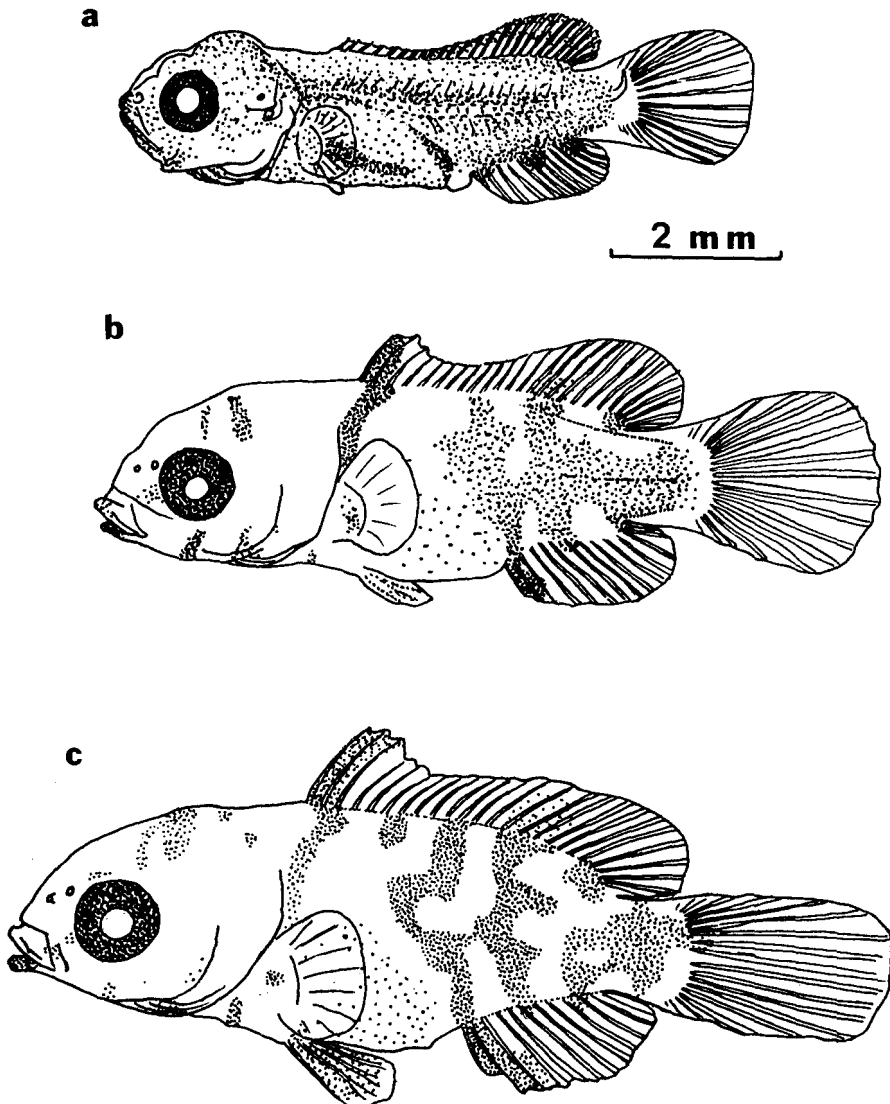


FIGURE 4.—Larval stages of *Lachnolaimus maximus*. a, 13 d posthatch; b, 17 d posthatch; c, 25 d posthatch.

mucous bubbles around themselves that night while floating free in the water near the surface. None rested on the bottom. Such behavior is known in other labrids but had been previously unknown for *L. maximus* or among free-floating individuals. Adults have been observed many times at night with no mucous bubble formation. Bubble formation has not been previously noted for "nonbenthic" labrids. The concept of bubble formation as an antipredator device is supported by its occurrence in postlarvae. Most larvae broke free of the bubbles within seconds after lights were turned on.

At 17 d posthatch, postlarvae tended to stay under material floating on the surface of the water (mostly discarded clumps of mucous bubbles and *Artemia* cysts). Several would stay under a single clump at the surface. No aggressive interactions were noted. Larvae were white and brown, the colors and pattern closely resembling that of *Sargassum*, which may serve as shelter for postlarvae carried into offshore waters.

Ten 18-d posthatch postlarvae were put into an 80 l aquarium with a white sand substrate. Some individuals rested on the bottom the first night, while others remained in the water column, all in mucous bubbles. By 34 d posthatch the fish oriented strongly to the bottom.

Little is known of the early life history of juveniles. Roessler (1964), who reported them from *Thalassia* beds, found some correlation in abundance with density of the bed. The larvae reared in the present study were maintained until about 50 d posthatch, but after about 30 d began dying without obvious cause. They were maintained either in bare aquaria or with a white sand bottom and were never exposed to a *Thalassia* community. They were fed a combination of *Artemia* and wild zooplankton. In their natural environment there may be a diet shift to microinvertebrates at an age when they began dying.

Larvae did not undergo a quick metamorphosis but gradually began to acquire brown and white pigment of juveniles about 13 d posthatch. While still free-swimming the larvae and postlarvae became highly pigmented, which would seem to be a distinct disadvantage in open water. These pigmented young seemed to shelter beneath any floating objects in the rearing aquarium, particularly the shards of their discarded mucous bubbles, which were brown in color. While there are no reports in the literature, their coloration would serve to conceal them in float-

ing *Sargassum* and potentially other floating marine plants. Quick development and the lack of a distinct metamorphosis implies that perhaps the optimum survival strategy to the juvenile stage would be an inshore transport of eggs and larvae and retention of juveniles near the spawning location. Unless associated with floating objects or plants, large *L. maximus* larvae would be at a distinct disadvantage in the pelagic realm. The life history of *L. maximus* implies that the postlarvae become benthic in an inshore location near sea grass beds and subsequently move to offshore reefs (Davis 1976). From the present study there seems no control of spawning condition which would produce an inshore dispersal of eggs (currents, winds, tides, or wave action) and except for seasonal differences, it seems eggs are simply broadcast randomly without the influence of environmental conditions which would influence their ultimate destination.

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