DESCRIPTION OF EGGS AND LARVAE OF SCALED SARDINE, *HARENGULA JAGUANA*[1, 2]

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ABSTRACT

Eggs and larvae of scaled sardine, *Harengula jaguana*, were described from specimens reared in the laboratory. Meristics, morphometrics, osteology, and pigmentation were examined as development proceeded. Transformation of larvae to the juvenile stage was complete at 22 to 24 mm standard length. During transformation outstanding features included forward movement of the dorsal fin, shortening of the gut, and forward movement of the anal fin. Eggs and larvae of scaled sardine were compared with those of other clupeids that may occur in the same areas. An illustrated series of scaled sardine eggs and larvae, including details of the caudal fin, was presented to show changes that occur during development.

Scaled sardines, *Harengula jaguana* Poey, are common clupeids in the tropical western Atlantic (Rivas, 1963). Until recently they were known as *H. pensacolae* Goode and Bean, 1879, but Whitehead (1973) has concluded that the correct name for the species is *Harengula jaguana* Poey, 1865. Scaled sardines prefer coastal habitats and have been reported from New Jersey to Brazil; they are abundant in the Gulf of Mexico (Briggs, 1958; Rivas, 1963; Berry, 1964b). Despite their common occurrence, larvae have not been described. Matsuura (1972) has described artificially fertilized and planktonic eggs of this species. Fecundity, maturation, and spawning of scaled sardines recently were reported by Martinez (1972). Eggs have been collected in south Florida, and the larvae reared to juvenile sizes in the laboratory (Houde and Palko, 1970; Detwyler and Houde, 1970; Saksena and Houde, 1972). Eggs and larvae from these experiments have provided us with material to describe early development.

Scaled sardines support a small bait fishery in south Florida and are important forage for predatory fishes like Spanish mackerel, *Scomberomorus maculatus* (Klima, 1959). They are caught for human consumption throughout the West Indies and are canned in Cuba and Venezuela (Rivas, 1963). Scaled sardines are one of the clupeid species that may have potential to support reduction fisheries in the tropical Atlantic.

Eggs and larvae of other species attributed to the genus *Harengula* have been described. Uchida et al. (1958) described larvae and juveniles of *H. zunasi* from Japan, and Takita (1966) described eggs and newly hatched larvae of that species. Whitehead, Boeseman, and Wheeler (1966) stated that this species is in fact a *Sardinella*, based on skeletal characters. Marchal (1967) included *H. rouxi* in his key to some west African clupeid eggs and larvae. Berry (1964a) and Berry and Whitehead (1968) restricted the genus *Harengula* to members having paired hypomaxillary bones. Neither *H. rouxi* nor *H. zunasi* have hypomaxillaries, and both species presumably belong in the genus *Sardinella*.

METHODS

Eggs were collected in surface tows of plankton nets near Miami Beach and in Biscayne Bay, Fla. during 1969 through 1971. A total of 10 embryos and 165 larvae from rearing experiments were preserved in 5% Formalin[6] to describe

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development. Rearing methods have been described (Houde and Palko, 1970; Saksena and Houde, 1972). Scaled sardines can be reared successfully at temperatures from 21° to 33.5°C (Saksena, Steinmetz, and Houde, 1972), and salinities have ranged from 29 to 37‰. Larvae and juveniles up to 38.7 mm standard length are included in this description, but we have reared scaled sardines to more than 100 mm in some experiments.

Morphometrics

Eggs and larvae were measured with an ocular micrometer in a dissecting microscope. The following measurements were made:

Total length (TL)—Tip of snout to end of caudal fin.

Standard length (SL)—Tip of snout to tip of notochord on small larvae, before notochord flexure; tip of snout to base of hypural plate on larger larvae, after notochord flexure. Unless otherwise noted, all references to lengths of larvae in text refer to standard lengths.

Preanus length—Tip of snout to anus, measured along midline. This measurement is equivalent to preanal fin length for specimens that have the anal fin developed.

Predorsal length—Tip of snout to origin of dorsal fin, measured along midline of body.

Prepelvic length—Tip of snout to origin of pelvic fins, measured along midline of body.

Head length—Tip of snout to posterior margin of otic capsules in yolk-sac larvae; tip of snout to opercular margin in older larvae.

Snout length—Tip of snout to anterior margin of eye.

Eye diameter—Horizontal distance between anterior and posterior edges of the fleshy orbit.

Body depth—Vertical height of the body at the pectoral symphysis.

Meristics

Fin rays were counted in each of the developing fins (Table 4). Myomeres were counted and designated as follows:

Total myomeres.

Preanal myomeres: number anterior to the anus.

Postanal myomeres: number posterior to the anus.

Predorsal myomeres: number anterior to the dorsal fin origin.

Postdorsal—preanal myomeres: number between the posterior insertion of the dorsal fin and the anus.

Osteology

Sequence of ossification was determined from a total of 16 specimens ranging in length from 4.8 to 22.4 mm. They were cleared with trypsin and stained with alizarin using the method of Taylor (1967). Development of the caudal fin bones was examined in detail. Ossification of fin rays, vertebrae, and head bones also was examined.

DESCRIPTION

Description and Occurrence of Embryos

Ten fertilized eggs from plankton collections were spherical, ranging from 1.55 to 1.78 mm in diameter (mean = 1.66 mm). They had a single, light yellow oil globule ranging from 0.07 to 0.10 mm in diameter (mean = 0.09 mm). Measurements did not differ from artificially fertilized eggs described by Matsuura (1972). Embryos were well developed when preserved (Figure 6A), and yolk diameters ranged from 0.63 to 0.72 mm at that time. The perivitelline space was wide, averaging 58% of the egg diameter for the 10 preserved specimens. In living embryos, the yolk is clearly segmented, but segments are difficult to see in preserved specimens. The chorion is thin, unpigmented, and unsculptured; it is fragile and easily broken compared to most teleost eggs. Preserved embryos had no discernible pigment. Living embryos, just prior to hatching, had tiny melanophores, which were difficult to see, in a paired dorsolateral series near the dorsal midline.

Embryos that were collected from mid-May through July were well developed by noon when our collections were examined (Figure 7). Surface water temperatures were 28°C or higher in the spawning area. Spawning presumably occurs only at night because embryos are all at similar stages of development when collected in the morning. Hatching usually began by late after-

noon, less than 24 h after the presumed spawning time.

The spawning season extends from February through July near Miami, based on our collections of planktonic eggs. Spawning may occur within Biscayne Bay from late February through early May but is confined to more offshore areas later in the season. Biggest egg collections were made about 4 km east of Miami Beach during May and June. Martinez (1972) confirmed the spawning season of scaled sardines by determining gonad indices and examining ovarian maturation of adults collected throughout the year from south Florida.

Description of Larvae

Body Shape

Larvae were 2.4 mm at hatching. The head was bent over the large, nearly spherical yolk sac. Yolk was absorbed and the body axis straightened during the next 12 h at 26° to 28°C. By 12 to 15 h after hatching, larvae were typically clupeoid (Figure 8A). They were elongate, thin larvae averaging 4.4 mm at 15 h after hatching. The gut was a long straight tube at this stage. Little growth occurred during the first 3 days after hatching. Thereafter, growth was rapid and temperature-dependent (Saksena et al., 1972). Larvae retained the typically elongate and rodlike shape until they transformed to juveniles when they became deeper bodied and laterally compressed. Proportional measurements of larvae in relation to standard length are given in Table 1.

Yolk Absorption and Gut Differentiation

Absorption of the nearly spherical yolk mass in newly hatched larvae was rapid at 26° to 28°C. The oil globule was located ventrally and just posterior to the middle of the yolk mass in newly hatched larvae (Figure 8A). By 48 h after hatching the yolk sac and oil globule had been absorbed, and larvae were actively feeding. The gut was a straight tube at 15 h after hatching (Figure 8A), but a distinct foregut and hindgut were present at 2 days (Figure 8B). By 4 days (at about 5.0 mm) the hindgut appeared to be composed of a series of adjacent muscular rings, typical of clupeid larvae.

Total Length and Standard Length

Standard length was used to examine development of scaled sardine larvae with respect to other morphometric data. The relation between standard length and total length (Table 1, Figure 1) was not linear over all sizes of larvae that were available. Standard length decreased relative to total length as larvae grew. Standard length was about 97% TL for larvae between 4 and 8 mm TL but decreased to 85% TL for larvae between 8 and 25 mm TL. The ratio averaged about 83% TL for individuals longer than 25 mm TL. The observed decrease between 8 and 25 mm TL was related to development of the caudal fin, particularly notochord flexure and hypural plate development.

Preanus Length

Preanus length averaged 83% SL at 15 h after

TABLE 1.—Summary of relationships between total lengths (TL) and standard lengths (SL), and proportional measurements relative to standard lengths for larvae used to describe *Harengula jaguana* development. Proportions are from data fitted by eye to relationships in Figures 1 to 5.

TL (mm)	SL (mm)	SL:TL	Preanus length: SL	Predorsal length: SL	Body depth: SL	Head length: SL	Snout length: SL	Eye diameter: SL	Prepelvic length: SL
4.3	4.2	0.977	0.833	—	0.064	0.119	0.017	0.045	—
6.2	6.0	.968	.867	—	.067	.133	.025	.042	—
8.2	8.0	.978	.888	0.680	.064	.138	.031	.041	—
10.8	10.0	.926	.890	.648	.081	.157	.036	.041	—
13.0	12.0	.923	.900	.626	.087	.167	.040	.043	0.440
15.4	14.0	.909	.864	.600	.100	.185	.047	.050	.447
18.5	16.0	.865	.838	.556	.125	.204	.052	.056	.466
20.8	18.0	.865	.822	.517	.142	.217	.057	.057	.467
23.1	20.0	.866	.780	.478	.162	.240	.066	.064	.462
25.6	22.0	.859	.764	.441	.184	.264	.072	.073	.465
29.0	24.0	.828	.775	.417	.219	.262	.072	.075	.482
31.5	26.0	.825	.758	.404	.236	.260	.072	.077	.485
33.6	28.0	.833	.750	.408	.245	.257	.071	.075	.481
36.0	30.0	.833	.750	.410	.252	.257	.071	.074	.482
38.5	32.0	.831	.750	.409	.262	.250	.071	.073	.482

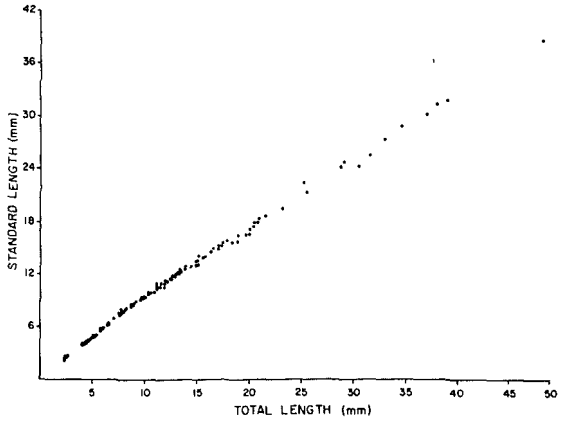

FIGURE 1.—Relation between standard length and total length for larvae of *Harengula jaguana*.

hatching and increased to about 90% SL when larvae were 12 mm (Table 1, Figure 2). A gradual decrease in preanus length occurred in larger larvae. At 22 mm, preanus length was 76% SL; juveniles 28 to 32 mm had preanus lengths that averaged 75% SL. Decreasing preanus length in larger larvae was caused by shortening of the gut during transformation to the juvenile stage.

Head Length

Head length increased relative to standard length from 12% at 4.2 mm to 26% at 22.0 mm (Table 1, Figure 3). The ratio was constant at 25 to 26% SL for specimens between 22 and 38.7 mm, which falls within the range of variation in head lengths reported for juvenile and adult *H. pensacolae pensacolae* (Rivas, 1950).

Eye Diameter

Eye diameters averaged 4.0 to 4.5% SL for specimens 4.2 to 12 mm (Table 1, Figure 4). A rapid increase in eye diameters from 4.3 to 7.3% SL occurred in specimens 12 to 22 mm. Eye diameters on specimens longer than 22 mm varied, but no increasing trend relative to standard length was observed. A 38.7-mm specimen had an eye diameter of 7.8% SL. Eye diameters were variable for larvae of a given length (Figure 4); for example, at 12 mm, eye diameters varied from about 3.5 to 5.5% SL. Rivas (1950) and

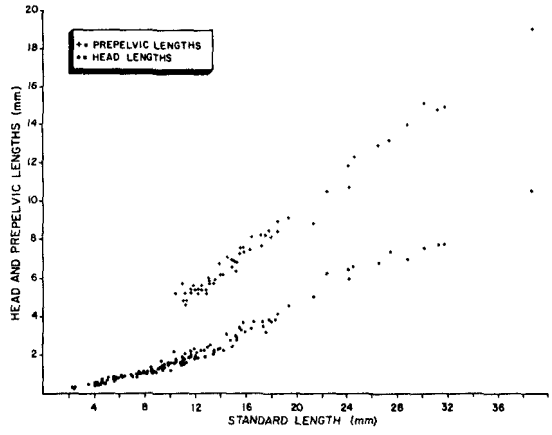

FIGURE 3.—Relation of head length and prepelvic length to standard length for larvae of *Harengula jaguana*.

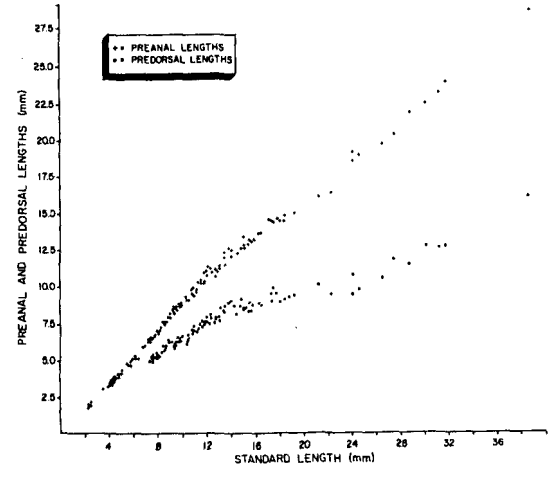

FIGURE 2.—Relation of preanal length and predorsal length to standard length for larvae of *Harengula jaguana*.

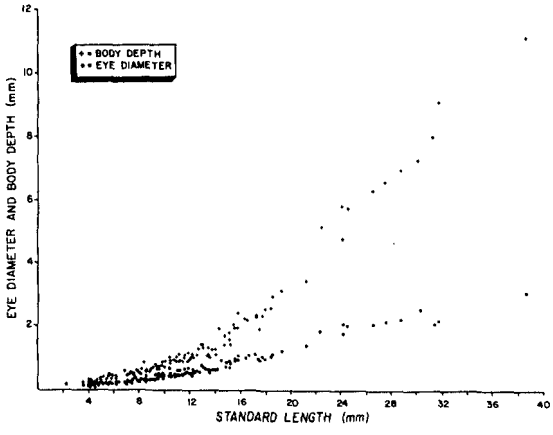

FIGURE 4.—Relation of eye diameter and body depth to standard length for larvae of *Harengula jaguana*.

Storey (1938) found eye diameters to be variable for juvenile and adult *H. pensacolae*.

Snout Length

Snout length increased from 1.7 to 7.2% SL for larvae between 4.2 and 22.0 mm (Table 1, Figure 5). It remained constant for longer larvae at about 7.2%, which is within the range of variation for juvenile and adult *H. pensacolae* (Rivas, 1963). Like eye diameters, snout lengths varied considerably for larvae of a given size; for example, at 12 mm, snout length varied from about 3.1 to 4.8% SL.

Body Depth

Body depth at the pectoral symphysis was constant at about 6.5% SL for larvae from 4.2 to 9.0 mm. Body depth then increased rapidly from 7.0 to 21.9% SL for specimens between 9.0 and 24.0 mm SL. A slow increase continued to occur for larger individuals (Table 1, Figure 4).

Predorsal Length

Predorsal lengths, as measured from the snout to the first developing ray in the dorsal fin, were recorded on specimens 7.5 mm and longer, when the rays began to develop. The dorsal fin moves forward as development proceeds, causing predorsal length to decrease from 68.0% SL to 41.7% SL for larvae between 7.5 and 24.0 mm (Table 1, Figure 2). Predorsal lengths averaged 41% SL for specimens longer than 24.0 mm.

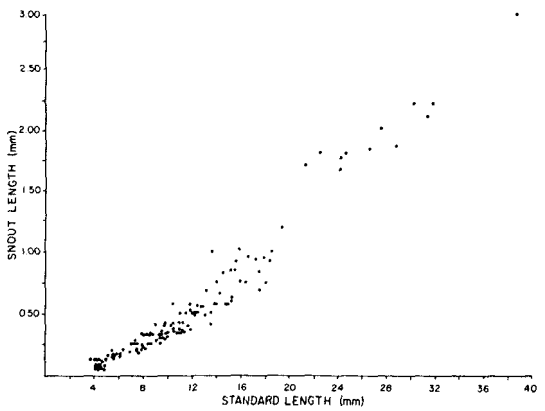

FIGURE 5.—Relation of snout length to standard length for larvae of *Harengula jaguana*.

Prepelvic Length

Prepelvic lengths were measured on larvae that had pelvic fin buds or fins. At 11 to 12 mm, prepelvic lengths averaged about 44% SL, increasing to 46% SL for larvae up to 22 mm (Table 1; Figure 3). Prepelvic lengths averaged 48% SL for specimens between 24 and 38.7 mm. Pelvic fins moved slightly posterior as larvae transformed to juveniles, causing the observed small increase in prepelvic length.

Meristics

Myomeres

Total numbers of myomeres ranged from 39 to 42; most larvae had 40 or 41. Numbers of myomeres and distribution of myomeres in relation to other body parts can be useful for identifying clupeid genera (Ahlstrom, 1968). Total myomeres could be counted accurately on 144 of our larvae. Frequencies were as follows:

Number of myomeres	39	40	41	42
Frequency	2	68	67	7

The mean number of myomeres was 40.56 ($S_{\bar{x}} = 0.2861$).

Distribution of myomeres in relation to the dorsal fin and anus was examined for larvae in 2-mm size classes (Table 2). Preanal myomeres decreased as larvae grew from about 35 for the smallest larvae to 27 at transformation. Postanal myomeres increased from a mean number of 5.7 for the smallest larvae to more than 12 for transformed specimens. Shortening of the gut during development accounted for the observed changes in preanal and postanal myomere counts. Mean numbers of predorsal myomeres decreased rapidly from about 25 to 10 as development proceeded, reflecting the anterior movement of the dorsal fin. Considerable variation in predorsal myomere numbers was present for larvae of a given length (Table 2). Postdorsal-preanal myomeres ranged from 5 to 7 for larvae of all sizes, but the mean number tended to decrease as larvae grew from 8 to 22 mm.

Fin Development

Newly hatched larvae had a fin fold that invested much of the body and which persisted in

TABLE 2.—Distribution of myomeres relative to other body parts for *Harengula jaguana* larvae.

Size class (mm. SL)	Preanal myomeres			Postanal myomeres			Predorsal myomeres			Postdorsal-preanal myomeres		
	Number of specimens	Mean	Range	Number of specimens	Mean	Range	Number of specimens	Mean	Range	Number of specimens	Mean	Range
4.0- 6.0	34	34.85	34-36	36	5.67	5-7	—	—	—	—	—	—
6.1- 8.0	16	35.00	34-36	17	5.53	5-7	11	24.82	23-26	12	6.67	5-7
8.1-10.0	22	34.68	33-36	22	6.09	5-7	22	23.41	22-25	22	6.50	5-7
10.1-12.0	18	33.72	32-35	18	6.89	6-8	18	21.61	20-24	18	6.00	5-7
12.1-14.0	15	33.47	32-35	15	7.20	6-8	15	21.07	20-23	15	5.67	5-7
14.1-16.0	12	32.08	30-34	12	8.25	7-9	12	18.75	16-22	12	5.42	5-6
16.1-18.0	6	31.67	31-33	6	8.50	8-9	6	17.17	16-19	6	5.50	5-6
18.1-20.0	4	31.00	31	4	9.25	9-10	4	15.25	15-16	4	5.50	5-6
20.1-22.0	1	29.00	29	1	11.00	11	1	13.00	13	1	5.00	5
>22.0	4	27.25	26-28	4	12.75	12-14	4	10.00	8-11	4	6.25	6-7

part until larvae were about 16 mm. Pectoral fin buds were present at hatching (Figure 8A), but no other fins were developed at this stage. An opaque area in the fin fold was the first indication of median fin development. Rayed fins developed in the following sequence: dorsal, caudal, anal, pelvics, pectorals. Fin rays first develop as cartilaginous structures; thus, the sizes of larvae at which full complements are present may be smaller than the sizes at which rays are fully ossified. Tables 3 and 4 summarize fin development sequence of scaled sardine larvae, and details are discussed in the osteological development section.

Median fin development usually was completed at 16.0 mm. Dorsal fin rays first appeared between 7.0 and 7.5 mm. A full complement of 17 to 19 rays was present at 14.0 to 17.0 mm. Principal caudal rays were first seen at 7.4 to 8.0 mm, and the full complement of 19 usually was attained at 10.0 mm. Some specimens as small as 8.5 mm had the full complement of principal caudal rays; a few specimens did not have a full complement until they were longer than 11.0 mm. Secondary caudal rays developed at 10.8 to 12.8 mm, and the full complement of 8 or 9 dorsal and 7 ventral secondary caudal rays was present at 16.5 to 19.0 mm. Notochord flexure, which occurs during caudal fin development, began at the same size that principal caudal rays first developed. Anal fin rays usually began to develop at 9.0 to 9.3 mm, but two specimens 8.5 to 9.0 mm had some anal rays. A full complement of 17 or 18 anal rays was present at 13.0 to 15.0 mm. Although principal caudal and anal fin rays began to develop after dorsal fin rays, the dorsal was the last median fin to attain its full ray complement.

Paired fins began to develop after median

TABLE 3.—Summary of fin development sequence in larvae of *Harengula jaguana*.

Fin	Standard length (mm)[1]			Number of rays in fully developed fin
	Buds first appear	Rays first appear	Full complement of rays	
Dorsal	—	7.0 to 7.5	14.0 to 16.0	17 to 19
Caudal				
Principal	—	7.4 to 8.0	8.5 to 11.0 (most by 10.0)	19
Secondary	—	10.8 to 12.8	16.5 to 19.0	8 or 9 dorsally 7 ventrally
Anal	—	9.0 to 9.3 (rarely at 8.5 to 9.0)	13.0 to 15.0	17 or 18
Pelvic	11.0-12.0 (rarely at smaller size)	13.0 to 14.0 (rarely at <13.0)	14.6 to 17.8 (most by 15.5)	7 or 8 (usually 8)
Pectoral	<4.0	15.0 to 16.0 (rarely at smaller size)	18.5 to 19.5	14 to 16

[1]Rays were present at the tabulated lengths, but not necessarily ossified at those sizes.

TABLE 4.—Some meristic characters of larval and juvenile *Harengula jaguana*.

Standard length (mm)	Caudal rays	Dorsal rays	Anal rays	Pectoral rays	Pelvic rays
2.3-6.9	No elements present on 48 specimens in this size range				
7.0	—	5	—	—	—
7.3	No elements present on this specimen				
7.4	3	6	—	—	—
7.4	—	6	—	—	—
7.5	—	8	—	—	—
7.5	—	3	—	—	—
7.6	No elements present on this specimen				
7.6	—	9	—	—	—
7.7	—	7	—	—	—
7.8	2	9	—	—	—
7.9	3	8	—	—	—
7.9	5	9	—	—	—
8.0	—	8	—	—	—
8.0	2	5	—	—	—
8.1	3	6	—	—	—
8.3	6	11	—	—	—
8.5	19	14	3	—	—
8.6	6	11	—	—	—
8.6	10	11	—	—	—
8.6	—	2	—	—	—
8.9	4	8	—	—	—
9.1	15	8	—	—	—
9.1	15	12	5	—	—
9.4	8	12	3	—	—
9.4	19	12	8	—	—
9.4	19	13	5	—	—
9.4	10	9	3	—	—
9.5	15	10	—	—	—
9.5	3	9	—	—	—
9.7	19	12	8	—	—
9.7	19	12	8	—	—
9.8	19	14	6	—	—
9.8	17	13	7	—	—
9.8	19	12	6	—	—
10.0	19	14	9	—	—
10.0	8	10	—	—	—
10.4	19	14	9	—	—
10.4	18	16	15	—	—
10.5	19	15	10	—	—
10.5	19	13	10	—	—
10.9	14	11	2	—	—
10.9	19	16	12	—	—
11.0	17	14	3	—	—
11.0	17	9	3	—	—
11.2	19	14	11	—	—
11.3	19	16	12	—	—
11.3	19	15	11	—	—
11.5	19	13	10	—	—
11.7	19	17	4	—	3
11.7	19	13	9	—	—
11.9	19	14	13	—	—
11.9	19	16	15	11	5
12.0	19	14	10	—	—
12.1	19	14	8	—	—
12.2	19	16	13	—	—
12.3	19	15	9	—	—
12.4	19	14	8	—	—
12.7	19	15	12	—	—
12.8	19	15	12	—	—
12.8	19	15	10	—	—
13.0	19	17	17	9	5
13.1	19	17	16	—	2
13.1	19	17	15	—	6
13.5	19	14	11	—	—
13.6	19	15	9	—	—
13.7	19	16	12	—	—
13.9	19	17	11	—	—
14.0	19	16	12	—	—
14.2	19	16	14	—	—
14.6	19	17	17	12	7
14.9	19	16	16	—	4
14.9	19	17	16	—	6
15.2	19	17	17	—	7
15.2	19	17	17	5	6
15.2	19	18	15	—	3
15.5	19	17	15	10	8
15.6	19	18	15	10	7
15.8	19	17	17	13	7
15.9	19	17	17	—	7
16.4	19	18	17	11	7
16.6	19	17	17	12	8
17.3	19	19	17	14	8
17.4	19	19	17	13	8
17.5	19	18	17	—	6
17.8	19	18	17	12	6
18.0	19	18	17	12	7
18.4	19	18	18	13	8
18.6	19	18	16	15	7
19.3	19	17	17	14	8
21.3	19	18	17	15	8
22.4	19	17	17	14	8
24.2	19	17	18	14	8
24.2	19	18	17	15	7
24.7	19	18	18	14	7
26.7	19	17	18	14	8
27.5	19	18	18	15	7
28.9	19	17	18	15	8
30.2	19	17	18	15	8
31.4	20	18	17	16	8
31.8	19	17	18	14	8
38.7	19	17	17	15	7

fins. Rayless pectoral fins were present soon after hatching, but rays usually did not develop until larvae were 15.0 to 16.0 mm. One specimen had some pectoral rays at only 11.9 mm, but this was unusual. Full complements of 14 to 16 pectoral rays were attained at 18.5 to 19.5 mm. Pectorals were the last fins to complete development. Pelvic fins first appeared as buds when larvae were 11.0 to 12.0 mm; most specimens had pelvic buds at 11.3 mm. Pelvic rays usually began to develop at 13.0 to 14.0 mm, but one 11.7-mm specimen had rays. A full complement of 7 or 8 (usually 8) pelvic rays was present at 14.6 to 17.8 mm. Most specimens had complete pelvic fins by 15.5 mm.

Scales

Scale development apparently occurred at 21 to 22 mm. No specimens from 18.5 to 21.2 mm were scaled. The illustrated specimen 21.3 mm (Figure 10C) was fully scaled as were 4 specimens from 22.4 to 24.2 mm.

Osteological Development

Sixteen cleared and stained specimens provided a record of sequence of development of skeletal structures in scaled sardine larvae. Bones stain as a result of calcification, but many bones, though unstained, were discernible before

calcification as distinct cartilaginous structures. Our four smallest specimens (4.8, 6.2, 6.5, and 8.9 mm) showed no evidence of staining and only slight indication of developing bone structures. Our first specimen to show clear evidence of stain uptake and well-formed cartilaginous structures was 10.9 mm. The only bone which was stained in this specimen was the cleithrum. The next bones to stain (an 11.5-mm specimen) were the maxillaries, dentaries, principal caudal fin rays, hypurals, and parhypural. Ossification then proceeded rapidly as larvae grew.

The Caudal Fin Complex

Clupeids have a complex caudal fin, and for descriptive purposes we follow the terminology of Nybelin (1963). The adult caudal fin has the following structures: 2 ural vertebrae, 6 hypurals, a parhypural associated with the first preural vertebra, 19 principal caudal rays (the lower and upper are unbranched, the remainder branched), 2 or 3 epurals, 3 pairs of uroneurals, 8 or 9 dorsal secondary caudal rays, 7 ventral secondary caudal rays, and a modified neural arch and spine on the first preural vertebra. In a 9.9-mm specimen the parhypural and the first four hypurals were visible (but not stained) as distinct cartilage entities (Figure 6A). A noticeable gap was present between the second and third hypural which persisted to the adult stage and separated the 9 lower from the 10 upper principal caudal rays.

The association of individual principal caudal fin rays with the parhypural and hypurals was nearly constant. Our method of counting principal caudal rays was anterior to posterior or, after notochord flexion, ventral to dorsal. The hypurals were counted similarly. The first two principal rays articulated with the parhypural, rays 3 to 7 articulated with the first hypural (in specimens larger than 15.0 mm ray 8 also associated with this hypural); rays 8 and 9 with the second hypural; rays 10 to 14 with the third hypural; rays 15 and 16 with the fourth hypural; rays 17 and 18 with the fifth hypural; and ray 19 with the sixth hypural. Rays 1 and 19 were stained deepest, and staining decreased medially indicating that rays 9 and 10 were the last to ossify although these rays were the first to develop.

In the 11.5-mm specimen (Figure 6B) there was a slight indication of ossification of the first pair of uroneurals and the neural arch of the first preural vertebra. The hypurals were all stained as was the parhypural and hemal spine of the second preural vertebra. In the 11.9-mm specimen the first uroneural pair was well stained as was the second uroneural pair, and the second ural centrum was deeply stained. The second uroneural lay just posterior to the second ural vertebra along the plane of the notochord. The first uroneural originated above an area that became the first preural centrum, but there was no indication of the centrum at 11.9 mm. The first uroneural extended along the notochord over the second ural centrum and ended midway along the second uroneural. The second uroneural extended from the second ural centrum to the origin of the sixth hypural. Two other structures were discernible but not stained at 11.9 mm—the hemal spines of the second and third preural vertebrae and the posteriormost ventral secondary caudal fin ray.

In the 12.0-mm specimen, little change occurred. In the 12.4-mm specimen, all the structures mentioned above were more deeply stained, and the neural and hemal spines of the second preural vertebra (though this vertebra is undifferentiated) were stained (Figure 6C). Of particular interest in this specimen was the marked similarity of the hemal spine of the second preural vertebra to the parhypural. Nybelin (1963) considered the parhypural to be a hemal spine, and our observation bears this out in as much as the caudal artery goes through this bone rather than over it. Monod (1968) has referred to the hemal spine of the first preural centrum as the parhypural bone and Hollister (1936) considered this bone to be a hypural. We use the term parhypural because it has characteristics of both a hypural bone and a hemal spine. During its development, it closely resembles a hypural and in fact is joined to the first hypural (see Figure 6D), and it bears two principal caudal rays. Both spines of the two preural vertebrae are flattened bones with developing hemal arches between the spine base and the notochord. In the 14.0-mm specimen, the first preural centrum and the two ural centra were stained as was the lower portion of the second preural centrum. The posteriormost ventral secondary caudal ray was stained. A neural arch was visible, though unstained on the first pre-

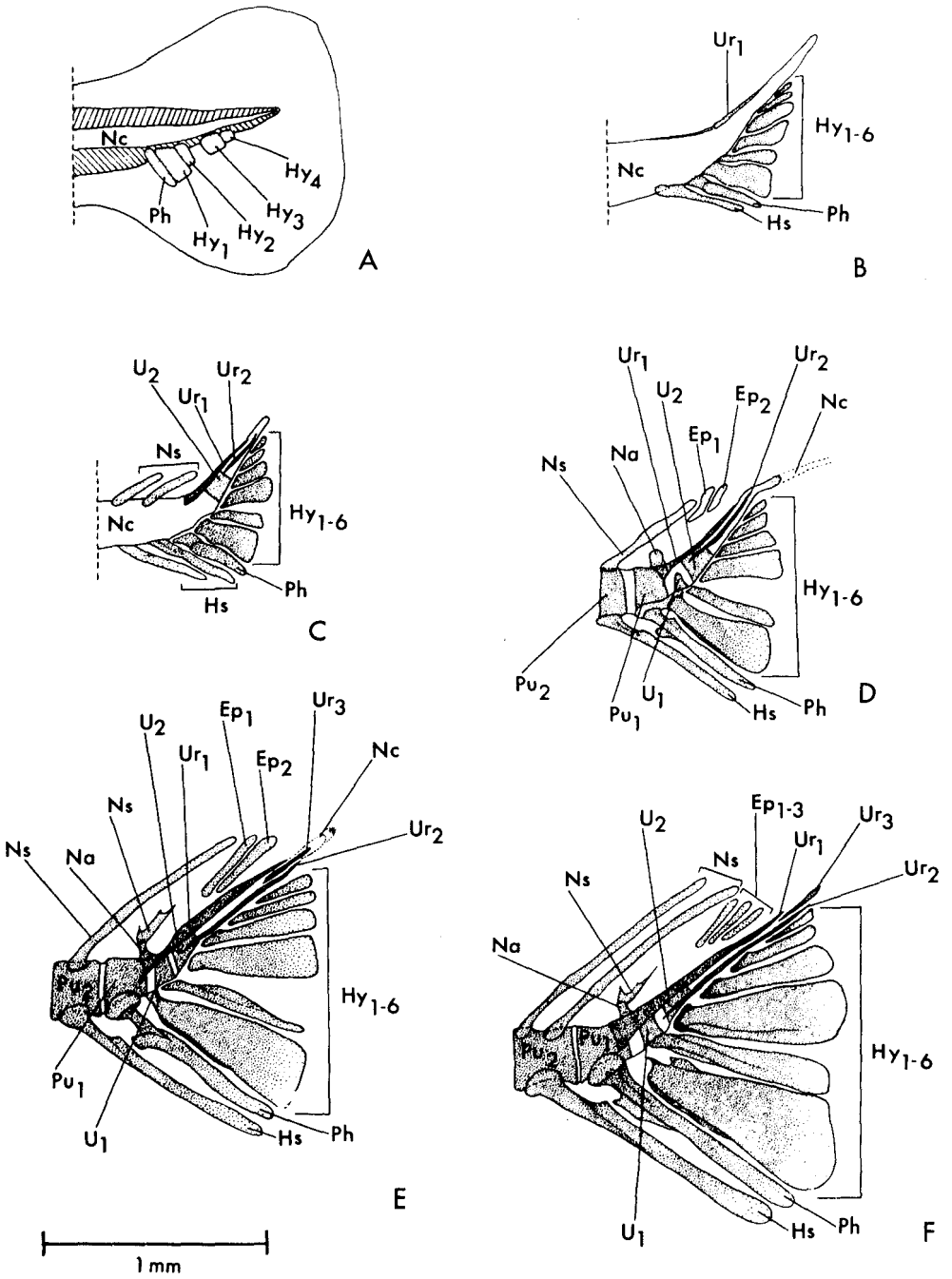

FIGURE 6.—Development of the caudal fin structures in larvae of *Harengula jaguana*. Fin rays are omitted from the illustrations to show the supporting structures more clearly. Standard length of specimens: A, 9.9 mm; B, 11.5 mm; C, 12.4 mm; D, 14.9 mm; E, 18.0 mm; F, 19.3 mm. Abbreviations: HY_{1-6} = hypurals, Ep_{1-3} = epurals, U_1 and U_2 = ural vertebrae, P_{u1} and P_{u2} = preural vertebrae, Hs = hemal spine, Nc = notochord, Ur_1-Ur_3 = uroneurals, Ns = neural spine, Na = neural arch, Ph = parhypural.

ural centrum and was not connected to the first uroneural base.

In the 14.9-mm specimen major features included an ossified area on the notochord posterior to the sixth hypural (Figure 6D). This structure apparently was temporary; it was not the third uroneural and it was not as clearly observed in larger specimens. Four upper secondary caudal rays were visible though only the posteriormost was stained. Three lower secondary caudal rays also were present with only the posteriormost stained. Two epurals were barely discernible and were not stained. The "hemal archlike" bone of the parhypural changed shape and appeared as a forked bone which received the spine of the parhypural between its forks. This small hemal archlike bone also supported the first hypural and abutted the first preural centrum, the notochord between the first preural centrum and the first ural centrum, and the first ural centrum itself. The third hypural abutted the second ural centrum, and the remaining hypurals abutted the notochord. At this stage, it was obvious that the first uroneural was fused to the first preural centrum. The second uroneural was free and never fused with any bone.

In the 15.6-mm specimen, seven upper secondary caudal rays and four ventral secondary caudal rays were stained. Two epurals were visible but weakly stained. An anteriorly directed flange or expansion had developed on the base of the parhypural. Its supporting hemal arch structure was distinct and not fused with the flange. The neural arch on the first preural vertebra was beginning to ossify. In the 16.6-mm specimen, the third uroneural was visible, lying lateral to the second uroneural. It was shaped like the second uroneural but was much smaller and appeared as a well ossified splintlike bone. The ossified area above the sixth hypural that was noted in the 14.9-mm specimen was not present. Three epurals were visible but not ossified. The full complement of secondary caudal rays was present—eight upper, seven lower.

In the 18.0-mm specimen, several significant changes were evident (Figure 6E). First, only two epurals were present, and they were slightly stained. This probably was the result of individual variation since three were observed in the 16.6-mm specimen. The neural arch of the first preural vertebra had developed an upward projecting spinelike process. This neural arch lay over the posterior dorsal surface of the first preural centrum between the bases of the left and right first uroneural. We did not verify that the dorsal nerve passes through this arch; thus this neural arch and spine of the first preural vertebra could be some other bone. Fusion had not taken place between the neural arch and the first uroneural bases in this specimen. The first hypural no longer touched the first preural centrum, and a remnant of its hemal archlike base remained between the vertebra and the hypural. The first or anteriormost upper and lower secondary caudal fin rays lay parallel to the body axis rather than slightly vertical as in smaller specimens. The third uroneural lay immediately above and posterior to the second uroneural.

Little difference was noted between the 19.3-mm and the 18.0-mm specimen except for the complete absence of the hemal archlike support of the first hypural in the larger specimen (Figure 6F). Three epurals were present but were still only faintly stained. Without doubt, these were the last components of the caudal fin to ossify. In this specimen, there were nine upper and seven lower secondary caudal rays. The second preural vertebra had the anomalous condition of bearing two neural spines.

All three uroneurals are paired and obviously provide rigid support for the notochord as the tail develops. As a result, the first and second uroneurals are among the first tail bones to ossify. The ossified first uroneural fuses to the first preural centrum after the centrum becomes ossified. The other uroneurals were not fused to any bone in the *Harengula* we examined nor were they fused to other bones in large larvae of *Opisthonema* (Richards, Miller, and Houde, 1974).

Dorsal and Anal Fins

Ossification of dorsal fin rays was first observed in the 11.9-mm specimen. Twelve rays in the midregion of the developing fin were faintly stained. Supporting pterygiophores for these rays also were faintly stained. About eight unstained anal rays were visible, but no supporting pterygiophores were seen. In the 12.4-mm specimen, 12 dorsal rays also were stained but these were the last 12 rays of the fin. Supporting pterygiophores for these rays also were stained.

The anal fin rays showed only slight staining. The 14.0-mm specimen had 15 ossified dorsal rays and pterygiophores; the anal had 11 unstained rays and pterygiophores. At this size, the vertebrae were countable and the dorsal rays were over the 24th to 29th vertebrae. The anal fin was beneath the 34th to 38th vertebrae. In the 14.9-mm specimen, 17 ossified dorsal rays were present and were over the 20th to 27th vertebrae. The anal fin had 15 faintly stained rays and visible but unstained pterygiophores. This fin was under the 33rd through 38th vertebrae. In the 15.6-mm specimen, the anal fin pterygiophores were well ossified. Seventeen dorsal pterygiophores supported 18 rays (1 pterygiophore supported the first 2 rays), and 14 anal pterygiophores supported 15 ossified anal rays (1 pterygiophore supporting the first 2 rays). In that specimen, the dorsal fin was over the 19th to 27th vertebrae, the anal under the 33rd to 37th vertebrae. In the 16.4-mm specimen, 18 dorsal and 16 anal ossified rays were present. The first few pterygiophores of each fin were faintly stained. The dorsal fin was over the 18th to 25th vertebrae, the anal under the 32nd to 38th vertebrae. In the 18.0-mm specimen, there were two ural vertebrae in the caudal region. In the 12.0-mm specimen, the middle vertebrae were visible because the ventral portions of their centra were ossified. In the 12.4-mm specimen, 20 vertebrae anterior to the dorsal fin were ossified. Neither the first few vertebrae nor the last several were ossified. The 14.0-mm specimen had the first vertebra faintly stained, the next 36 were complete, the next 3 were visible but unstained, and the last had only the lower half of the centrum stained. In this specimen, a few neural arches near the middle of the vertebral column were lightly stained. The first 10 hemal spines also were slightly stained as were the 2 preceding the parhypural. In the 14.9-mm specimen, all neural spines and hemal spines were lightly stained. Pleural ribs were first observed in the 15.6-mm specimen on the 8th to 16th vertebrae. From density of stain, it appears that they develop in a posterior to anterior direction.

Head Bones

The many skull bones were difficult to describe. A detailed analysis of general developmental changes in skull development has been completed for the related Atlantic thread herring, *Opisthonema oglinum* (Richards et al., 1974). The maxillaries and dentaries of scaled sardines ossified at 11.5 mm. At this time, the maxillary bore five small teeth. These teeth were too small to be shown in the illustrations. Teeth were added with growth—8 teeth at 14.0 mm, 14 teeth at 14.9 mm, 17 teeth at 15.6 mm. Teeth were observed on the dentary only on the 15.6-mm specimen, where two were observed. Dentary teeth apparently are a temporary feature. Teeth also were present on the basihyal; the 15.6-mm specimen had two large teeth, and the 16.6-mm specimen had three teeth on this bone. These teeth, like the dentary teeth, apparently are temporary larval structures. They were also seen as temporary structures in the larvae of *O. oglinum* (Richards et al., 1974). The premaxillaries were first visible in the 14.9-mm specimen, and the posterior supramaxillaries were first seen in the 16.6-mm specimen. The anterior supramaxillaries and the hypomaxillaries had still not developed in our 19.3-mm specimen but were present in our 22.4-mm specimen. Berry (1964a) reported hypomaxillaries to be developed in a 16-mm specimen of *Harengula thrissina* from the eastern Pacific.

Pigmentation

Melanophore distribution on preserved scaled

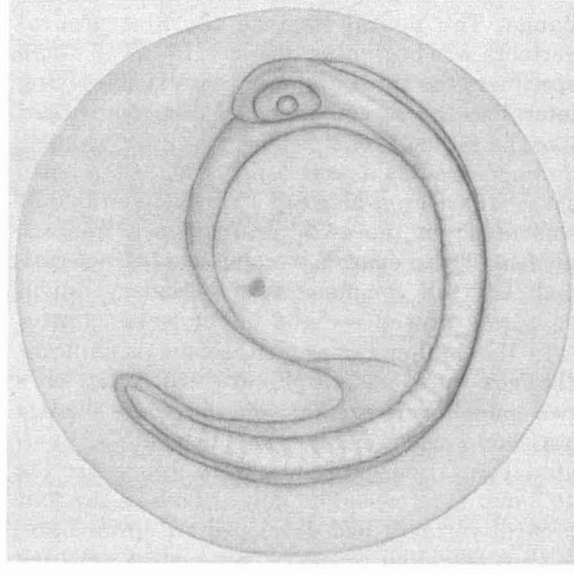

FIGURE 7.—Late stage egg of *Harengula jaguana*.

sardine larvae is similar to that of other clupeid larvae. Pigmentation varied somewhat among individuals of the same size, but a general pattern was always present. Some variation resulted because individual melanophores could be in either a contracted or expanded state. Illustrated specimens have pigmentation that is typical of most larvae of those sizes (Figures 8 to 10). In life, numerous yellow chromatophores were present, usually as internal pigmentation, but these were not illustrated.

Head Region

Pigmentation was sparse on the head of scaled sardine larvae until they attained 15 mm. Eyes became pigmented when larvae were 4 to 5 mm, at 30 to 40 h after hatching. At the same time, from two to four melanophores developed near the pectoral symphysis. These usually consisted of one just anterior to the symphysis and a pair immediately posterior to it. They were retained throughout larval development. One or two melanophores usually were present at the base of the pectoral fins when larvae were 6.5 mm or longer. From one to four stellate melanophores first appeared over the hindbrain at 7 to 8 mm. This number gradually increased as larvae grew, but some specimens had only a single melanophore at 14 mm. On specimens longer than 15 mm, melanophores became numerous over the midbrain and hindbrain. One or two deeply imbedded melanophores were visible through the otic capsules on most specimens longer than 8 mm. One or two stellate melanophores frequently appeared on the cheek when larvae were 14 mm. This number often increased to several at 15 to 18 mm. Tiny melanophores developed on the snout and lower jaw of larvae that were 14 to 17 mm. Melanophore numbers increased

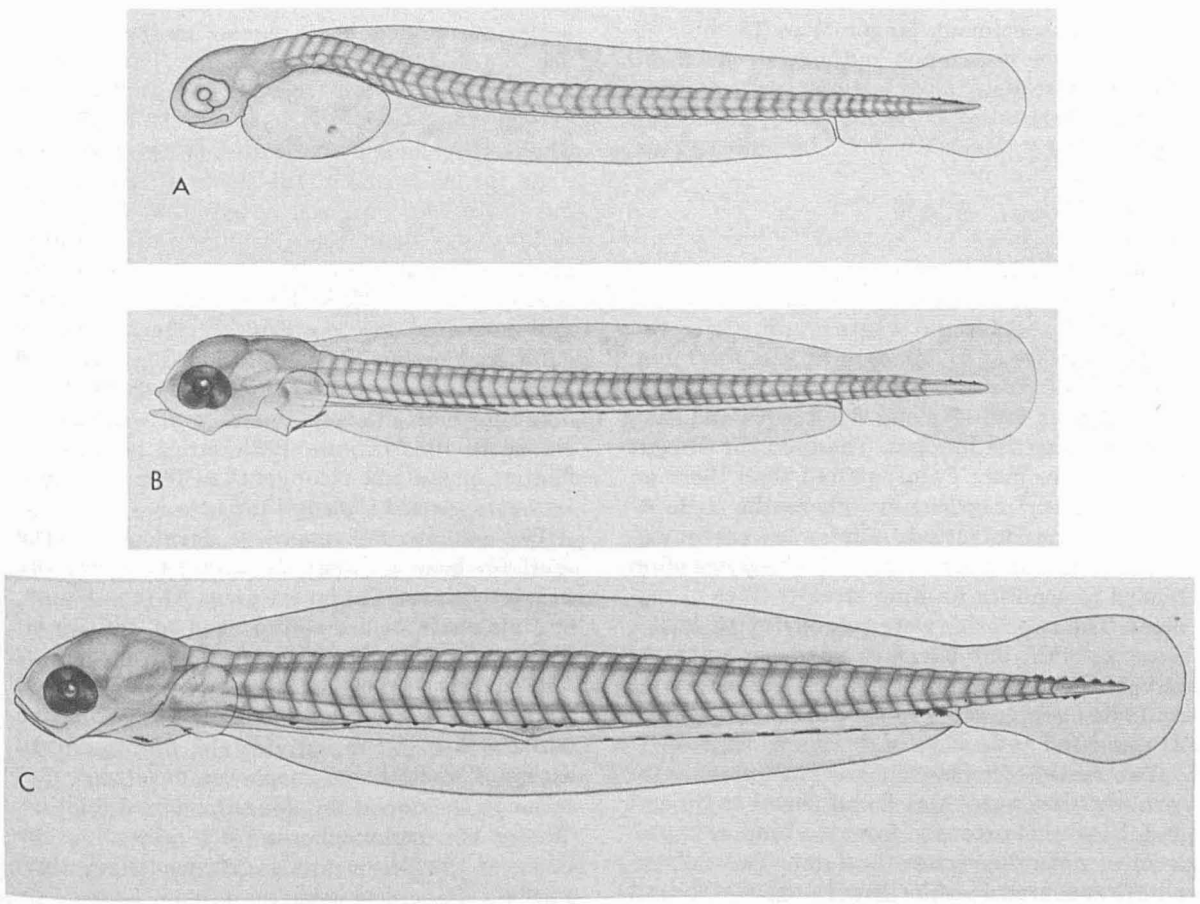

FIGURE 8.—Larvae of *Harengula jaguana*: A, 4.4 mm SL; B, 4.5 mm SL; C, 6.0 mm SL.

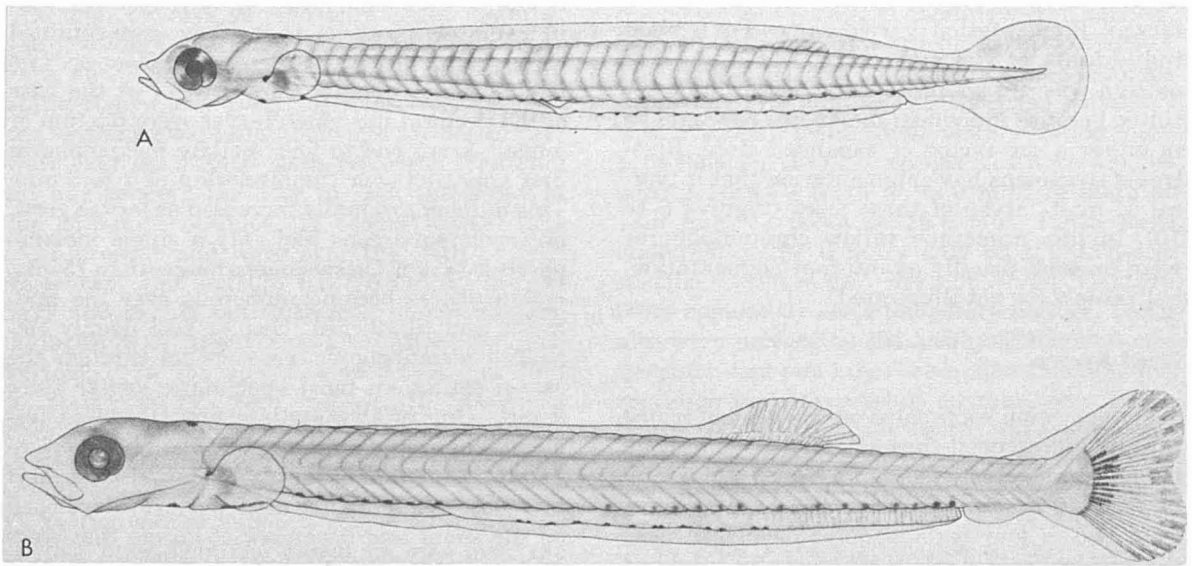

FIGURE 9.—Larvae of *Harengula jaguana*: A, 8.9 mm SL; B, 11.5 mm SL.

rapidly on specimens longer than 18 mm, although there was much individual variation. Numerous stellate melanophores were present over the brain, on the snout, jaws, and cheek region of specimens between 18 and 24 mm.

Gut and Trunk Region

Paired series of melanophores, typical of clupeid larvae, developed over the dorsolateral surface of the foregut region and along the ventral surface of the hindgut at about 4.5 mm. Numbers of pairs in the series were variable, ranging from 7 to 12 along the foregut and from 8 to 14 along the hindgut. Those on the foregut usually were more evenly paired than those on the hindgut. In specimens where the melanophores were contracted, pairs were easily distinguished, but when dispersed, the pairs often tended to coalesce forming streaky lines of pigment. The two series were retained until larvae were 21 mm, but became indistinct on some larvae between 18 and 21 mm. No distinct series could be distinguished on specimens longer than 21 mm.

Two series of melanophores were present internally. One series was found dorsal to the gut and the second extended from the hindbrain posteriorly along the vertebral column. Two melanophores appeared near the dorsal surface of the gut near the anus at 4 to 5 mm, from which the series of melanophores dorsal to the hindgut began to develop at 5 to 6 mm. The number gradually increased from as few as 2 to 5 to as many as 34 when larvae were 12 to 15 mm. The first melanophores in this series developed near the posterior of the hindgut; additional melanophores developed anterior to those. The series along the vertebral column first appeared at 10 to 12 mm, and numbers gradually increased to about 25. Melanophores in this series first appeared just posterior to the hindbrain; additional melanophores developed posterior to them. The vertebral series was difficult to distinguish in most specimens and was not included in illustrations. Both series became indistinct on specimens longer than 18 mm because larvae increased in body thickness.

Two stellate melanophores developed at the anal fin base between 11 and 13.5 mm. The number increased as larvae grew. At 14 to 15 mm, stellate melanophores appeared at the dorsal fin base, the numbers increasing from one or two to eight or more at 18 mm. Between 18 and 21 mm, a few melanophores developed in the dorsal fin of most individuals, and a paired series of stellate melanophores developed posterior to the dorsal fin along the dorsal midline. One or two melanophores were present at the bases of the pelvic fins in larvae longer than 15 mm.

Stellate melanophores began to appear on the

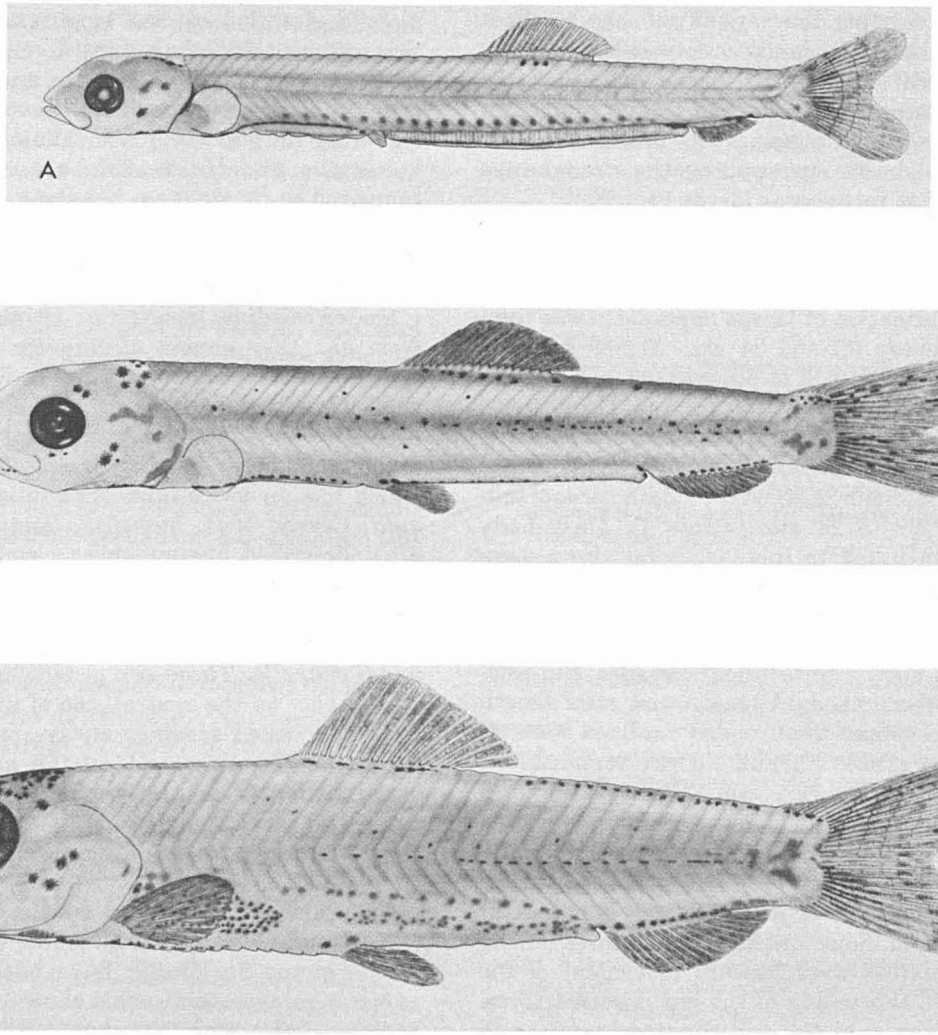

FIGURE 10.—Larvae of *Harengula jaguana*: A, 16.1 mm SL; B, 18.8 mm SL; C, 21.3 mm SL.

sides of most larvae between 16 and 17 mm. The first of these developed posterior to the dorsal fin along the lateral midline of larvae. Numbers increased as larvae grew, spreading anteriorly, dorsally, and ventrally so that most individuals had numerous melanophores scattered over their sides by 22 mm. The epaxial myomeres of specimens longer than 22 mm usually were outlined by melanophores that were concentrated along the myosepta. Silver coloration began to appear along the ventral and ventrolateral areas of the trunk at 22 to 24 mm. By 28 mm few melanophores could be discerned below the midline on sides of juveniles because of the accumulation of guanine in that area. At this stage, scaled sardines resemble large juveniles and adults because of their predominantly silver color.

Caudal Region

Newly hatched larvae, 4 to 4.5 mm, had three or four melanophores along the dorsal tip of the notochord. In the first 48 h after hatching, the number of melanophores in that area ranged from three to six. During the same time from one to three melanophores developed along the ventral tip of the notochord in some specimens. As caudal rays began to develop at 8 to 10 mm, pigment migrated from the notochord tip to the

area surrounding the rays. From one to three deeply imbedded melanophores were present near the hypural plate when larvae reached 11 to 16 mm. Larger specimens had similar pigmentation in the caudal region except that the number of melanophores surrounding the caudal rays continued to increase as larvae grew.

Transformation

Transformation of larvae apparently was complete between 22 and 24 mm. Scaled sardines of 22 mm conformed to descriptions of juveniles and adults in most respects (Storey, 1938; Rivas, 1950, 1963). Proportional measurements relating preanal length, predorsal length, head length, and eye diameter to standard length became constant at 22 to 24 mm (Table 1). Only body depth continued to increase relative to standard length for larger individuals. The slender rodlike shape of larvae was replaced by the deeper bodied, laterally compressed shape of juveniles during transformation. Also, the relation between standard length and total length became constant when scaled sardines were 22 to 24 mm (Table 1). Full fin ray complements were present by 19.5 mm (Table 3), slightly before the dorsal and anal fins had completed their movements during transformation. Scales first developed at 21 to 22 mm, and the typical silvery coloration of juveniles was apparent at 22 to 24 mm. Some outstanding features during transformation were forward movement of the dorsal fin, shortening of the gut, forward movement of the anal fin, and relative increases in head length, snout length, eye diameter, and body depth.

COMPARISONS

Eggs and larvae of scaled sardines can be distinguished from those of similar genera in south Florida marine waters. Houde and Fore (1973) have prepared a guide that will help to identify eggs and larvae of some clupeid fishes, including scaled sardines, from the Gulf of Mexico.

Scaled sardine eggs are larger than those of other clupeid genera from south Florida. Only scaled sardines have eggs larger than 1.50 mm diameter. Eggs of *Opisthonema oglinum, Sardinella anchovia, Brevoortia* spp., and *Etrumeus teres* rarely exceed 1.35 mm diameter. The oil globule of scaled sardine eggs is smaller than that reported for other clupeid genera. Eggs of *Etrumeus* have no oil globule and cannot be confused with scaled sardines. Two other species of *Harengula* may occur near Miami. *Harengula humeralis* and *H. clupeola* are not common compared to *H. jaguana*, but their eggs may be similar to those of scaled sardines. Eggs of *Jenkinsia* spp. are undescribed and cannot be compared to scaled sardine eggs.

Scaled sardine larvae can be distinguished from all other genera of clupeids with which they might cooccur, except perhaps for *Jenkinsia* spp., which are undescribed. Myomeres do not exceed 42 in *Harengula* larvae, but number 45 or more in other genera, except for *Jenkinsia* which has myomere numbers similar to *Harengula*. Larvae of *H. humeralis* and *H. clupeola* are undescribed, but probably are similar to those of scaled sardines. Caudal pigmentation of larvae less than 9 mm serves to separate scaled sardine larvae of those sizes from larvae of *Opisthonema* and *Sardinella*. Those two genera have melanophores only on the ventral side of the notochord tip while scaled sardines always have melanophores on the dorsal side of the notochord tip and frequently on the ventral side as well. *Brevoortia* larvae have caudal pigmentation like that of *Harengula*, but they rarely have fewer than 45 myomeres.

Eggs and larvae of two species that Berry (1964a) and Whitehead et al. (1966) would assign to the genus *Sardinella* have been described as *Harengula zunasi* (Uchida et al., 1958; Takita, 1966) and *H. rouxi* (Marchal, 1967). Eggs and larvae of *H. zunasi* from Japanese waters (Uchida et al., 1958; Takita, 1966) closely resemble those of *H. jaguana*. Egg diameters and oil globule diameters of *H. zunasi* average slightly larger than for *H. jaguana*, but the very wide perivitelline space and exceptionally small oil globule are similar in the two species. Pigmentation is present only on the ventral side of the notochord tip in *H. zunasi* larvae, thus differing from *H. jaguana*. Both *H. zunasi* and *H. jaguana* larvae have less than 45 myomeres—43 in *H. zunasi*, usually 40 or 41 in *H. jaguana*. Marchal's (1967) *Harengula* (= *Sardinella*) *rouxi* eggs and larvae also more closely resemble those of *H. jaguana* than other clupeid eggs and larvae that we have observed from Florida waters. Eggs of *H. rouxi* are smaller than *H. jaguana*,

but relative widths of the pervitelline space and the oil globule diameters are similar. *H. rouxi* and *H. jaguana* larvae have similar pigmentation at the notochord tip. Myomeres range from 43 to 45 in *H. rouxi*, which is higher than for *H. jaguana* but lower than the number observed in most other clupeids.

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