LARVAL DEVELOPMENT OF THE SCUP, *STENOTOMUS CHRYSOPS* (PISCES: SPARIDAE)[1]

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ABSTRACT

Larval scup, *Stenotomus chrysops* (Linnaeus 1766), were reared from eggs hatched in an aquarium. Measurements of morphological features for 88 specimens from 2.0 to 16.9 mm SL indicate that growth is gradual and continual with no well-defined changes in relative body proportions. Twenty-four myomeres are present in larvae, agreeing with published reports of vertebrae numbers in adult scup. Ossification begins first in the skulls of 6.1 mm SL larvae, and by 7.0 mm SL the vertebrae, neural spines, and fin rays are beginning to ossify. Ossification is nearly complete in 18.7 mm SL juveniles. Three preopercular spines are present in 4.1 mm SL specimens; the numbers of spines increase and by 16.9 mm SL the preopercular margin is serrate. Median fin development occurs at 4.1 mm SL, all fins are present in 8.8 mm SL larvae, and a full complement of rays are observed by 12.8 mm SL. Larvae are completely scaled by 13.0 mm SL.

Scup, *Stenotomus chrysops* (Linnaeus 1766), the only common sparid in southern New England waters, is a popular sport and commercial fish in spring and summer. Their range is from South Carolina to Sable Island, Nova Scotia, although they are uncommon north of Cape Cod (Breder 1948; Bigelow and Schroeder 1953; Leim and Scott 1966). Scup move inshore in schools in early April in the Chesapeake Bay area and in May north to Cape Cod. Most scup spend the summer in bays or within 8-10 km of the coast where they spawn from May to August with a peak in June in Narragansett Bay (Perlmutter 1939; Bigelow and Schroeder 1953; Wheatland 1956; Herman 1963). In late October scup begin to move offshore to depths of 40-100 m. Commercial catches between January and April indicate that many scup winter off Virginia and North Carolina (Neville and Talbot 1964; Smith and Norcross 1968).

Despite the commercial importance and abundance of this species, only one description of the eggs and larvae exists (Kuntz and Radcliffe 1917). This description, which has been paraphrased several times, and the accompanying illustrations, which have been reprinted several times, provide no information on osteological development nor do they present meristic and morphometric data. Consequently we undertook to rear larvae from laboratory-spawned eggs to provide specimens for a more complete description which would be useful for identification of wild larvae.

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METHODS

Adult fish captured by trawl in Narragansett Bay, R.I., were held in a 58 m^3 aquarium until they spawned naturally. Fertilized eggs were collected from the aquarium with plankton nets and incubated in 40 l aquaria at 18° and 21°C in 31‰ salinity. The postincubation series for this study was reared at 18°C. After hatching, the larvae and juveniles were fed zooplankton and brine shrimp nauplii. Larvae were removed regularly for our studies and preserved in 4% buffered Formalin[4] and Formalin with Ionol added as a color preservative. Specimens up to 19.5 mm standard length (SL) are included in this description, but scup were reared to >40 mm in some of our experiments. Eighty-eight larvae from 2.0 to 16.9 mm SL were measured with an ocular micrometer. The data were pooled for all fish of the same SL, and all measurements converted into percentages of SL and summarized in Table 1. The following measurements were made:

Total length (TL): Tip of snout to end of caudal fin or finfold.

Standard length (SL): Tip of snout to end of notochord in larvae prior to and during notochord flexure; tip of snout to base of hypural plate once it is formed. All references to length or size in the text refer to SL unless otherwise noted.

Postanal length: Anus to end of notochord measured along midline of body.

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

TABLE 1.—Summary of nine morphological features of specimens of *Stenotomus chrysops* as shown by their percentages of standard length.

SL (mm)	TL (mm)	SL:TL	Postanal length: SL	Preanal length: SL	Head length: SL	Snout length: SL	Prepectoral length: SL	Prepelvic length: SL	Eye diam.: SL	Body depth: SL
2.0	2.1	95.2	45.0	40.0	10.0	2.5	—	—	7.5	30.0
2.1	2.3	91.3	46.7	40.5	11.0	3.8	—	—	7.7	29.0
2.2	2.4	91.7	46.6	42.7	12.5	3.4	—	—	7.6	26.0
2.3	2.5	92.0	43.5	38.0	10.9	4.3	—	—	7.6	25.0
2.6	2.8	92.9	42.3	36.5	17.3	3.8	19.2	—	7.5	24.0
2.7	2.9	93.1	41.0	36.6	18.2	5.4	21.5	—	7.7	21.0
2.8	3.0	93.3	40.8	36.0	18.6	5.5	20.8	—	6.2	24.0
2.9	3.1	93.5	41.4	36.6	18.5	4.1	21.6	—	6.9	20.7
3.0	3.2	93.8	42.8	37.8	17.8	5.0	21.1	—	7.6	22.4
3.2	3.4	94.1	43.8	37.5	18.8	4.7	21.9	—	8.1	22.6
3.4	3.6	94.4	42.6	38.2	19.1	5.1	23.5	—	8.1	22.6
3.5	3.7	94.6	41.4	37.1	18.1	4.3	22.4	—	8.8	28.1
3.6	3.8	94.7	40.7	37.0	18.5	5.6	21.8	—	8.8	20.6
3.7	3.9	94.9	41.9	37.2	18.9	5.4	21.6	—	8.8	22.9
3.9	4.1	95.1	43.6	38.5	17.9	5.1	20.5	—	8.1	28.4
4.1	4.3	95.3	43.9	39.0	17.1	4.9	22.0	—	8.3	24.4
4.3	4.6	93.5	46.5	41.9	20.9	4.7	22.1	—	8.2	29.5
4.6	4.9	93.9	45.7	41.3	21.2	4.9	23.9	—	8.2	29.5
4.8	5.1	94.1	45.7	41.7	20.8	6.3	25.0	—	8.9	30.0
4.9	5.2	94.2	44.9	40.8	21.9	5.6	25.5	—	8.7	30.4
5.4	5.6	96.4	51.9	48.1	22.2	5.6	25.0	—	9.5	23.8
5.5	5.9	93.2	51.9	46.7	23.9	7.3	27.6	—	10.9	38.2
5.6	6.2	90.3	48.2	44.6	23.2	5.4	26.8	—	9.5	22.4
6.1	6.9	88.4	53.0	48.1	25.1	7.7	30.1	—	9.8	29.5
6.4	7.4	86.5	56.3	50.0	25.0	9.4	29.7	—	10.0	25.8
6.6	6.6	86.8	54.5	50.0	25.8	7.6	31.8	—	9.8	30.3
7.1	8.0	88.8	54.9	50.7	25.4	7.0	31.0	—	9.9	21.1
7.9	9.2	85.9	53.2	49.4	24.7	7.6	29.7	—	9.5	25.3
8.5	10.3	82.5	57.1	52.9	25.3	7.1	28.8	35.3	9.4	27.1
9.2	10.9	84.4	55.4	51.1	26.1	7.6	29.3	38.0	9.2	27.2
9.9	11.8	83.9	54.5	50.5	24.2	9.1	32.3	33.3	9.1	27.3
10.0	12.0	83.3	58.5	52.5	27.5	9.0	30.5	37.0	9.5	26.0
12.0	14.5	82.8	56.7	50.8	25.8	9.2	30.0	35.8	9.2	26.7
12.6	15.4	81.8	55.6	50.0	26.2	8.7	31.0	34.1	8.7	25.4
13.1	15.6	84.0	56.5	51.9	28.2	8.4	32.1	35.9	10.7	30.5
13.5	16.3	82.8	56.3	[1]52.6	21.5	8.1	30.4	34.1	8.9	29.6
14.6	17.0	85.9	54.8	50.0	25.3	8.9	32.2	35.6	9.6	26.0
14.9	17.1	87.1	54.4	48.3	25.5	8.1	30.9	34.2	8.7	26.8
15.9	18.8	84.6	59.1	54.7	25.2	8.2	31.4	38.4	7.5	32.7
16.9	20.6	82.0	62.1	59.2	30.2	11.2	35.5	42.6	10.7	33.7

[1]Notochord flexion.

Preanal length: Tip of snout to anus measured along midline of body.

Head length: Tip of snout to posterior margin of otic capsules in young larvae; tip of snout to cleithrum once it is apparent.

Eye diameter: Horizontal distance between anterior and posterior edges of orbit.

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

Body depth: Vertical height of body at pectoral axis.

Prepectoral length: Tip of snout to axil of pectoral fin, or its anlage, measured along midline of body.

Prepelvic length: Tip of snout to axil of pelvic fins, measured along midline of body.

Meristics: Fin rays and spines were counted as they became apparent. Myomeres (total, precaudal, and caudal) were counted. Seventeen specimens were cleared and stained by Hollister's method (Hollister 1934) to determine the ossification sequence of developing skeletal elements to verify counts of bony structures.

DESCRIPTION

Eggs

The scup egg is spherical, buoyant, and transparent. The shell is unsculptured and the yolk unsegmented. It has one gold-colored oil globule that is posterior in the yolk sac and bears black pigment. The yolk is about 78% and the oil globule about 21% of the egg diameter. The average diameter of the 97 eggs we measured was 0.93 mm (range 0.81-1.00 mm). They hatched in 70-75 h at 18°C and in 44-54 h at 21°C. These measurements and the incubation time are similar to those found by others for this species (Kuntz and Radcliffe 1917; Perlmutter 1939; Bigelow and Schroeder 1953; Wheatland 1956).

Larvae

Newly hatched larvae average 2.0 mm SL. The eyes are not pigmented and the mouth is not functional. The head is bent slightly over the elliptical yolk sac. Yolk sac and oil globule are absorbed and gut differentiation occurs between 48 and 72 h after hatching at 18°C. During this period the eyes become pigmented, the mouth functional, and the larvae begin to feed. Larvae ranging in size from 2.0 to 18.7 mm are shown in Figure 1.

Yolk Absorption and Gut Differentiation

At hatching the gut is a tube with a constriction at its posterior end that extends to the ventral edge of the finfold, but by 48 h (2.7 mm) a foregut and hindgut

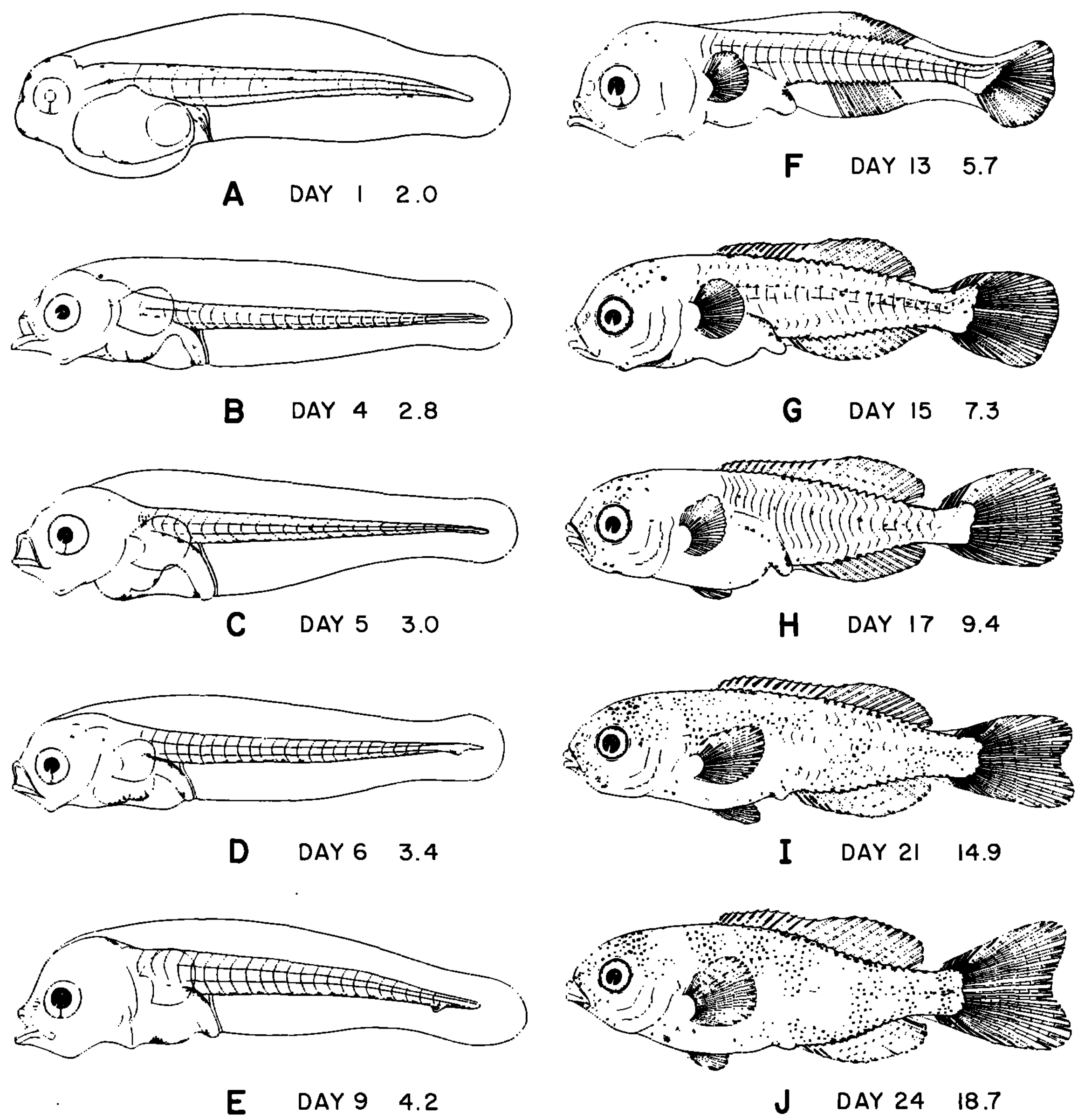

FIGURE 1.—Development of *Stenotomus chrysops*. Lengths (SL) are in millimeters.

can be distinguished. The hindgut appears to be muscular and remains a tube until between day 7 and day 9 (ca. 4.0 mm), when a well-defined stomach becomes apparent and the hindgut is relatively shorter.

Total Length and Standard Length

Larval growth appears to be gradual and continuous with no well-defined changes in relative body proportions. Apparent slight changes which are noticeable after notochord flexion relate to a change in measurement from an SL which is actually notochord length to one which is a true SL.

Postanal Length

Postanal length remains about 45% from 2.0 to 4.9 mm SL, when notochord flexion is occurring. A gradual increase to 62.1% in juveniles longer than 16.9 mm SL is concurrent with development of vertebrae and overall growth of the larvae.

Preanal Length

Preanal length increases relative to SL from 36.0% at 2.0 mm to 41.9% at 4.9 mm to >59% for juveniles longer than 16.9 mm. The lengthening of the body cavity during growth accounts for the increase in preanal length.

Head Length

Head length increases relative to SL from an average of 11.1% (10-12.5%) in newly hatched larvae (2.0-2.3 mm) to 17.3% in 2.6 mm larvae, then gradually increases to 30.2% in the largest juvenile specimen. In very young larvae the otic capsules are the reference structure for head measurements. However, once the cleithrum develops it is used as the reference structure for subsequent head measurements and an increase in head length percentage is observed.

Eye Diameter

The ratio of eye diameter to SL in our series is 6.2-10.9% of SL. It averages 7.5% SL in 2.0-3.0 mm larvae, and 8.5% SL (range 8.1-8.9%) in 3.2-4.9 mm larvae. In larvae >4.9 mm the average is 9.5% of SL (range 7.5-10.9%). Variation in individuals of the same size is considerable.

Snout Length

As with eye diameter, there is considerable variation among individuals of the same size. At hatching the snout length is 2.5% of SL, but this increases gradually to 9.4% of SL at 15.9 mm and 11.2% of SL in the juveniles.

Body Depth

Body depth ranges from 25 to 30% in newly hatched larvae, but once the yolk is absorbed it decreases to between 21 and 24.4% of SL (with one exception) up to 3.9 mm, and then increases to 22.4 to 33.7% of SL.

Prepectoral Length

Anlagen are present at hatching. Initially prepectoral length is about 19.2% of SL. This increases gradually during the larval and postlarval period to 35.5% of SL in the juvenile.

Prepelvic Length

Pelvic fin buds do not appear until the larvae are 8.0-8.5 mm long. Prepelvic to SL ratio is about 35.6% (range 33.3-38.4%) for larvae from 8.5 to 15.9 mm SL, but increases to 42.6% of SL in the juvenile.

MERISTICS

Scup, being typical of most perciform fish, have 24 myomeres. This agrees with Miller and Jorgenson's (1973) vertebrae numbers for adult fish.

FIN DEVELOPMENT

At hatching a finfold extends from the top of the head to the visceral sac interrupted only by the anus. There are no fin rays. A remnant of this persists between the anus and the first anal fin ray in a larva 9.1 mm long. Fin sequence development is given in Table 2.

Anlagen of the pectoral fins are present in most, if not all, hatchlings. These are low buds at first, but by the time the larvae are about 2.5 mm these fins have bases and blades. By removing pectoral fins from one side of some of our larvae and flattening them out, we could see 13 rays in one 4.9 mm larva and 10 rays in a 5.7 mm larva. Aside from these two, however, we could not see pectoral fin rays, even on cleared and

TABLE 2.—Summary of fin development sequence in larvae of *Stenotomus chrysops*.

Fin	Notochord or standard length (mm) Buds first appear	Rays first appear	Full complement of rays	Number of rays in fully developed fin
Dorsal		5.5-6.0	10.8	XII + 12
Caudal			10.4-10.8	32-34
Principal		4.3	5.3	Dorsal 9 Ventral 8
Secondary		5.3		Dorsal 7-8 Ventral 8-9
Anal		5.5-6.0	10.8	III + 11
Pelvic	5.7	8.8-10.0	12.8-13.2	I + 5
Pectoral	2.3	2.9-3.0	10.4-10.8	16

stained specimens until the larvae were about 8.0 mm, when the larvae had nearly the full complement of 15-16 pectoral rays.

An anlage of the caudal base can be seen in larvae as small as 3.4 mm. Some of the principal caudal rays are detectable in the finfold of larvae as small as 4.3 mm, and are the first rays of any fins to appear. Notochord flexion in our series begins at 4.7 mm. By 5.3 mm all of the principal caudal rays are present as are some of the secondary ones. Flexion is complete at about 8.0 mm and the caudal fin begins to fork at about 10 mm. Full complements of caudal rays (9-10+9+8+8-10) are present in larvae 14 mm or longer. Secondary rays develop in a posterior to anterior direction.

The soft-ray parts of the median fins first develop beginning at 5.3 mm in our series. Anal and dorsal rays develop together. In both fins, the central soft rays develop first. The development of anterior and posterior rays follows rapidly so that when the larvae in our series are >6.0 mm, full complements of 11-12 soft rays are present in these fins. Development of the spiny rays in these fins is from posterior to anterior and follows the soft-ray development. An exception is the posteriormost spiny rays in both fins that appear first as soft rays.

The last fins to appear are the pelvics. Anlagen are first seen in our series in some larvae at 5.7 mm. Other larvae are >7.0 mm long before these anlagen are visible. Development thereafter is from the distal edge medially. Full arrays of 1 spine and 5 soft rays are present in larvae 8.5 mm or longer.

Adult scup have six pairs of branchiostegals. Five pairs of these are present in a 4.2 mm larva of our series. They were visible in all of our series that were 5.0 mm or larger. The sixth pair, the median one, is not visible in some of our larvae even at 16.5 mm. The first five pairs usually appear simultaneously, but the sixth appears later.

PIGMENT

Although scup have chromatophores other than melanophores, these faded rapidly after preservation in Formalin. This account is confined to melanophore pigmentation (Fig. 1). Pigmentation other than that by melanophores is extensive on embryos and early larvae and is described and illustrated by Kuntz and Radcliffe (1917).

Head Region

Newly hatched scup have unpigmented eyes. Two rows of stellate melanophores, one on either side, extend from the snout back over the eyes and continue as part of a lateral series on the trunk. At a length of about 2.5 mm there is a hiatus in this series that extends from mideye level to over the visceral sac.

At 4.0-5.0 mm length, the pattern that will culminate in that of the juvenile has begun to appear. There are few, usually no, melanophores on the dorsal and lateral parts of the head anterior to the middle of the eyes. However, there are several prominent melanophores on the posterior midbrain and several on the hindbrain. Ventrally there is usually no pigment on the head. A few of our specimens have one or two small melanophores.

Development beyond this stage consists of a gradual increase of pigment on the dorsal and dorsolateral parts of the head. Most of it occurs above mideye level. A few melanophores appear on the snout and below the eye. There is a prominent melanophore, sometimes accompanied by one or two small ones as well, at the articulation of the lower jaw with the quadrate bone.

Between the head and the trunk pigmentation in the occipital region there is a gap in the dorsal pigment with relatively little pigment in it. This gap is part of the barred pattern of the juvenile.

Trunk and Tail Region

At hatching there are two dorsal rows of stellate melanophores extending from the head to beyond myomere 20. They appear to be between myomeres on the myosepta. Occasionally these rows are interrupted by "missing" melanophores. When this is so, the melanophore is usally lower down on the side of the body. A few, usually three or four, melanophores occur at various places on the anterior part of the yolk sac, and there are one or two on the oil globule. Some specimens have widely spaced melanophores on the ventral margin of the tail.

This pattern persists until the larvae are about 2.5 mm long with a gradual increase in the number of melanophores along the ventral margin of the tail. The melanophores on the yolk sac and oil globule disappear with the exception of one or two on the midventral line of the anterior part of the yolk sac.

In larvae 4.0-5.0 mm long, most of the pigment is on the peritoneum dorsal to the viscera and along the midventral line. Anteriorly there is a melanophore at the cleithral symphysis and posterior to it a large one midventrally on the anterior belly and a smaller one on the posterior belly. There is a prominent melanophore on the hindgut just anterior to the anus. Posterior to this there is a melanophore on most of the anal pterygiophores; this pattern is continued externally on the ventral myosepta. Dorsally there are several melanophores on the posterior pterygiophores of the dorsal fin. There are usually a few scattered spots on the finfold and, on some specimens, a few on the sides.

The peritoneal pigment becomes denser and more prominent in 9-10 mm larvae, however, it is often obscured because of the opacity of the thickening body musculature in preserved specimens. The hindgut is nearly covered by large melanophores. The melanophores on the midventral line are still present, usually accompanied by two or three smaller ones. The melanophore just posterior to the anus is still present, but less prominent.

The trunk and tail pigment is more extensive at 9-10 mm. There are many more pigment spots along the sides, but these are still widely spaced, especially anteriorly. There is pigment along the bases of the dorsal and anal fins that continues posterior to them to the procurrent caudal rays. A line of melanophores runs dorsoventrally at about the juncture of the caudal fin rays and caudal bones. Internally there are melanophores near the bases of the haemal and neural arches. These become increasingly obscure as the body musculature thickens.

Pigment development beyond this size is characterized by the development of the barred pattern of the juvenile accompanied by a general increase in pigment everywhere, especially above the midlateral line.

OSSIFICATION

A total of 17 fish were stained with Alizarin Red to determine where ossification began and the sequence in which the bones ossified. A summary of osteological development is presented in Table 3.

There is no dye uptake in 5.2 or 6.0 mm larvae, although the cartilaginous skeleton is easily distinguished. Cartilaginous hypural plates are present in larvae undergoing notochord flexure (5.4-5.6 mm). The first ossification occurs in skulls of 6.1 mm larvae. The premaxillary, maxillary, dentary, articular, and quadrate bones associated with the jaws, the preoperculum, hyomandibular, branchiostegal rays, and cleithrum showed varying degrees of dye uptake. There is no ossification posterior to the cleithrum.

By 7.0 mm more ossification of the skull occurs, notably the pterygoid, metapterygoid, opercular series, supracleithrum, and frontal bones. The circumorbitals, as well as the parasphenoid and the scapula, show the beginning of dye uptake. Ossification has begun in the first 10 vertebrae, the neural spines of the first 4 vertebrae, and the pectoral and caudal fin rays.

In 9.3 mm specimens the skull is further developed; teeth are visible and the lachrymal, dermethmoid, nasal, prefrontal, and urohyal bones show varying degrees of ossification. The postcleithrum is well developed and the radials, scapula, and coracoid are ossifying. The entire vertebral column is ossified with the exception of the ultral centrum and penultimate vertebrae. Both haemal and neural spines are ossified. The pleural ribs, and the dorsal and anal fin rays are beginning to ossify; hypural plates and caudal fin rays are partially ossified.

By 10.8 mm the distal vertebrae (caudal complex) have ossified and scales are present. The pelvic fin supports and rays show some dye uptake. Pterygiophores are present as cartilage. All the dorsal and anal fin rays and spines have ossified.

Skull development and ossification of most of the bones of the skull is complete by 14.5 mm. The radials and scapula which were just beginning to ossify in the 10.8 mm fish are now complete. Pelvic fin supports are complete. The pleural ribs are

TABLE 3.—Summary of osteological development in laboratory reared larvae of *Stenotomus chrysops*.

	Notochord or standard length (mm)		
	First appearance in cartilage	First evidence of ossification (stain uptake)	All ossifying
Cartilaginous skeleton	5.2		
Hypural plates	5.4	9.3	14.5
Vertebrae and neural spines		7.0	10.8
Pectoral girdle	7.0	10.8	14.5
Pectoral and caudal fin rays		7.0	9.3
Haemal spines		9.3	9.3
Pleural ribs		9.3	14.5
Dorsal and anal fin rays		9.3	10.0
Caudal complex		10.8	10.8
Pelvic fin supports		10.8	14.5
Pelvic girdle		10.8	18.7

stained as are the pterygiophores. The hypural plates are all present and completely ossified; a few dorsal plates are still partially cartilaginous.

By the time scup are 18-19 mm long, they are juveniles. Ossification continues in the skull with the bones being joined at suture points; the pelvic girdle is complete. The pterygiophores and ribs have completed ossification.

PREOPERCULAR SPINES

Figure 2 shows the development of preopercular spines. We saw them first on a 4.1 mm specimen, which has three spines on the preopercular margin. Thereafter their number increases until there are so many on a 16.9 mm specimen that the margin is serrate. Specimens larger than about 25 mm have nearly smooth preopercular margins.

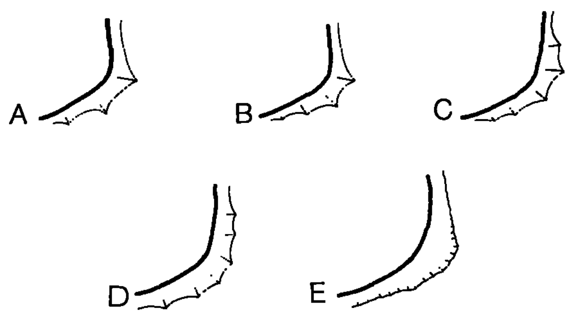

FIGURE 2.—Development of the preopercular spines of *Stenotomus chrysops*. Standard lengths in millimeters of the specimens are A) 4.1, B) 5.6, C) 8.3, D) 9.8, and E) 16.9.

SCALES

The first scales are seen between 9.9 and 10.8 mm. At 12.3-13.0 mm the larvae are completely scaled.

COMPARISONS

The geographical extent of spawning of *S. chrysops* is not known. The authors can find no record of it spawning south of the New York Bight. At least one other species of *Stenotomus*, *S. caprinus* (Bean 1882), occurs in the western North Atlantic. According to Geohagen and Chittenden (1982), the major population of this species is in the northern Gulf of Mexico and it occurs only rarely along the east coast to North Carolina. A third nominal species, *S. aculeatus* (Valenciennes 1830), said to replace *S. chrysops* south of Cape Hatteras, is of doubtful validity. Birdsong and Musik (in 1977 reprint of Hildebrand and Schroeder 1928) placed *S. aculeatus* in the synonomy of *S. chrysops*; Robins et al. (1980) did not list *S. aculeatus*. Dahlberg (1975) mentioned young stages of *S. chrysops* with crossbars (i.e., juveniles) in his account of Georgia coastal fishes, although it is not clear whether he had taken such specimens in his collections.

This issue is further complicated by lack of information about the northern extent of spawning of other sparid fishes. If their spawning ranges overlap with that of *S. chrysops*, then the younger larvae of some species will probably be confused with scup larvae, at least until the dorsal, anal, and pectoral fin rays can be counted. Except for the reference to juvenile scup on the Georgia coast by Dahlberg, the authors can find no references to such an overlap.

We have seen larval scup in collections misidentified as *Scomber scombrus*, the Atlantic mackerel, from which they can be separated at all stages by the numbers of myomeres (24 in scup and 31 in mackerel). We have also seen larval gerreid fishes misidentified as scup. Among other characters, scup differ from gerreid fishes in lacking the long premaxillary spines that extend up between the eyes in gerreids.

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