EARLY DEVELOPMENT OF THE LONGHORN SCULPIN, *MYOXOCEPHALUS OCTODECEMSPINOSUS*[1]

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ABSTRACT

Illustrations and descriptions of the early development of longhorn sculpin, *Myoxocephalus octodecemspinosus*, reared in the laboratory included six symmetrical cleavages, cell multiplication, blastula formation, gastrulation, eight embryonic and six larval stages, and a juvenile stage. Development at 5°C began with initial cleavage at 8 hours, proceeded to gastrulation at 132 hours, early embryogenesis at 168 hours, and hatching between 36 and 65 days, with maximum activity between 41 and 48 days. Absorption of the yolk sac was completed about 10 days after hatching, metamorphosis to the juvenile stage occurred at about 55 days, and adult pigmentation developed between 65 and 104 days.

Characters useful for the identification of longhorn sculpin eggs included egg color, egg capsule diameter, width of the perivitelline space, and appearance of the chorion. Identification of longhorn sculpin larvae and juveniles was possible utilizing size, pigmentation, meristics, and cephalic spination.

Comparison of reared longhorn sculpin larvae with descriptions of larvae collected in the Gulf of Maine and Canadian waters revealed some differences in pigmentation, development of anal and dorsal fins, and duration of retention of the embryonic finfold.

Longhorn sculpin, *Myoxocephalus octodecemspinosus*, is a common inhabitant of the coastal waters of the northwest Atlantic; it occurs north to the Gulf of St. Lawrence and is common around Prince Edward Island, the Scotian shelf (Leim and Scott 1966), and south regularly to New Jersey (Bigelow and Schroeder 1953). It is found from very shallow water out to at least 50 fathoms (Huntsman 1922; Vladykov and McKenzie 1935).

In Block Island Sound, R.I., longhorn sculpins move inshore to spawn from November through February, and maximum spawning occurs from mid-December to mid-January (Morrow 1951). They deposit demersal egg masses of various colors (Morrow 1951; Bigelow and Schroeder 1953; Leim and Scott 1966).

Little is known about the early life history of this species. Chenoweth (1973) believed that three species of *Myoxocephalus* utilize the estuaries near Boothbay Harbor, Maine, as primary spawning and nursery areas because larval longhorn sculpins, shorthorn sculpins, *M. scorpius*, and grubbies, *M. aenaeus*, are abundant in the upper reaches of estuaries in late winter and early spring. Herman (1963) reported that *Myoxocephalus* spp., which are the predominant larvae in January and March ichthyoplankton collections in Narragansett Bay, R.I., are mostly longhorns. Khan (1971) stated that longhorn sculpin larvae are common in the Gulf of St. Lawrence and the Gulf of Maine in late winter and early spring. Pearcy and Richards (1962) and Wheatland (1956) believed that *M. aenaeus* larvae are predominant in the Mystic River, Conn., estuary and Long Island Sound and that longhorn sculpin larvae are rare or absent.

Little detailed information on the early development of *M. octodecemspinosus* is published. Morrow (1951) described gametogenesis and ripe ovarian eggs and stated that longhorn sculpins mature in their third year, at about 24 cm TL (total length), and an average female produces about 8,000 eggs annually. Khan (1971) provided illustrations and descriptions of longhorn sculpin larvae from ichthyoplankton collections. This paper presents a complete description of the early development of *M. octodecemspinosus*.

MATERIALS AND METHODS

Ripe longhorn sculpins were obtained during December 1980 and maintained at ambient temperature in continuous-flow aquaria. Eggs were artificially fertilized on seven occasions in 20 cm glass fingerbowls containing about 1,000 ml of filtered seawater. Eggs were kept in 20 cm fingerbowls and 4,000 ml glass beakers in either a temperature-controlled water bath at 5.0° ± 0.5°C or at ambient temperature in a bath of running seawater. Water in the closed system was initially changed two or three times weekly, but was changed daily after the presence of bacterial contamination was detected in some containers.

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Samples were preserved in 5% neutral Formalin[3]. Eggs were cleared over glycerin according to the method of Galat (1972). All developmental rates are at 5°C. Larvae were fed wild plankton which were obtained with a #20 mesh net, and after a month brine shrimp nauplii were added to the diet.

Drawings and descriptions are from all series. All drawings were done with the aid of a camera lucida.

RESULTS AND DISCUSSION

The egg of the longhorn sculpin was spherical and adhesive. The chorion was leathery and translucent. Egg color was variable but consistent within a single female. Eggs were green, red, and reddish brown. Morrow (1951) reported variable coloration of longhorn eggs. Lund and Marcy (1975), Bigelow and Schroeder (1953), and Westin (1968) described various egg colors of *M aenaeus*, *M. scorpius*, and *M. quadricornis*, respectively. Egg color remained constant throughout development. Subsequent statements refer to morphological changes.

Unfertilized, water-hardened eggs: These eggs of longhorn sculpins were spherical with a mean diameter of 2.21 mm and a range of 2.1-2.3 mm. Mean yolk diameter was 2.10 mm (range 2.0-2.2 mm). The number of oil droplets was variable; some eggs had several small droplets scattered throughout the yolk, whereas others had only two or more large droplets. Perivitelline space was less than one-tenth of the egg capsule radius. Surface of the yolk capsule was slightly irregular. Chorion was colorless, translucent, and leathery (Fig. 1A).

Two-cell stage: Initial cleavage was meroblastic and was first observed at 8.0 h. Most eggs had cleaved by 8.5 h. Blastomeres were about equal in size and slightly elevated. Egg capsules had a mean diameter of 2.18 mm (range 2.1-2.3 mm). Yolk capsule had a mean diameter of 2.06 mm (range 1.9-2.1 mm). The number of oil droplets was variable. Perivitelline space was about one-tenth of the radius of the egg capsule. Yolk surface was slightly corrugated (Fig. 1B).

Four-cell stage: Second cleavage was perpen-

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

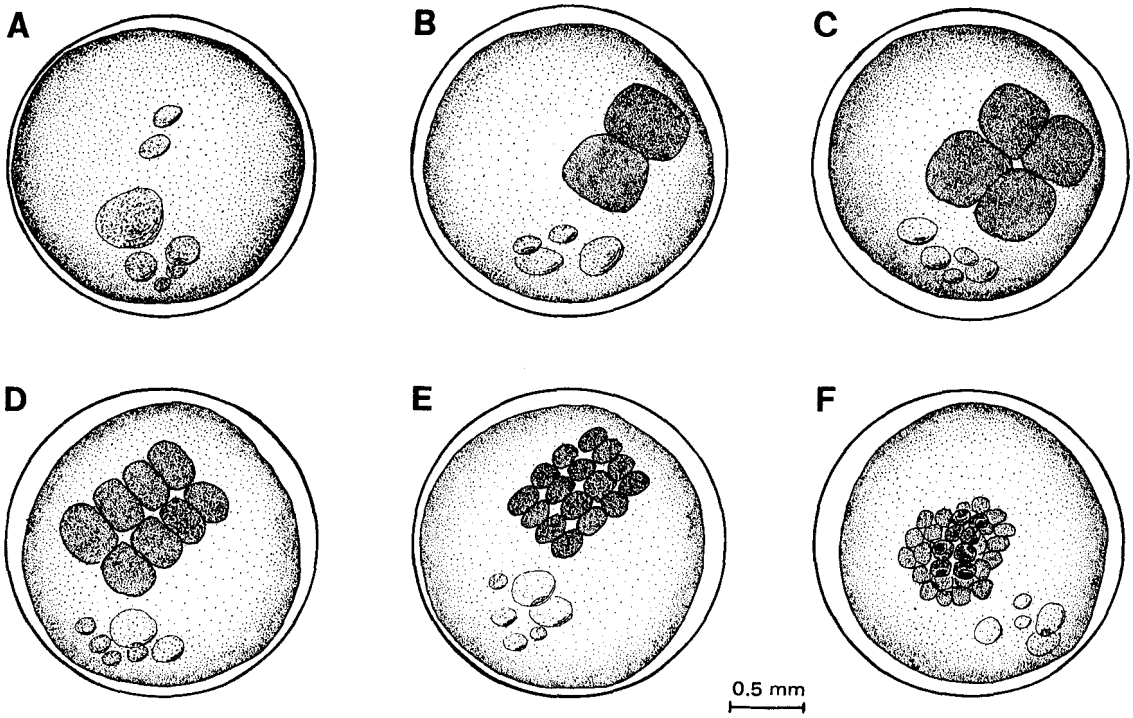

FIGURE 1.—Early development of the eggs of the longhorn sculpin, *Myoxocephalus octodecemspinosus*, artificially propagated in the laboratory: A) unfertilized water-hardened egg, 2.21 mm; B) fertilized egg, 2.19 mm, 2-cell stage (8.5 h); C) 4-cell stage, 2.15 mm (10.5 h); D) 8-cell stage, 2.22 mm (14.0 h); E) 16-cell stage, 2.15 mm (20.0 h); F) 32-cell stage, 2.21 mm (24 h); scale = 0.5 mm. Measurements refer to mean egg capsule diameters.

dicular to the first. Four blastomeres were about equal in size. This stage was first observed at 10.0 h; most eggs had reached this stage by 10.5 h (Fig. 1C).

Eight-cell stage: Third cleavage was vertical. Blastomeres were about equal in size. First observation of eggs at this stage was at 12.0 h, and all observed eggs had reached this stage by 14.0 h (Fig. 1D).

Sixteen-cell stage: Another vertical cleavage resulted in 16 cells in a single layer. In some eggs, the shape of the cells and the lines of cleavage appeared irregular. This stage was first observed at 18.0 h and all eggs were in this stage by 20.0 h (Fig. 1E).

Thirty-two-cell stage: A horizontal cleavage produced a central double layer of cells, with peripheral cells in a single layer. Cells were irregular in shape. This cleavage was first noted at 23.0 h; all observed specimens had attained this stage by 24.0 h (Fig. 1F).

Sixty-four-cell to multicell stage: Eggs classified as this stage were first seen at 27.0 h. By 52 h, all eggs were considered to be at this stage. The blastodisc became raised, but did not yet begin moving over the yolk. This long stage was characterized by continued increase of cell number and decrease of cell size (Fig. 2A, B).

Blastula stage: This stage was initially observed at 86.0 h, and all observed eggs had reached this stage by 110.0 h. Blastoderm began to expand over the yolk. Periblast was visible at the periphery of the blastoderm. Blastocoel was flattened out over the yolk (Fig. 2C).

Gastrula stage: Epiboly proceeded. Germ ring was first noted at 132.0 h (5.5 d). Embryonic shield was most easily viewed on the horizon of the egg (Fig. 2D).

Early embryogenesis: Eggs with clearly discernible embryos were first observed at 168.0 h (7.0 d). Blastopore was reduced to a small opening. Oil droplets were aggregated near the opening. Neural groove was apparent and extended less than one-half way around the yolk. From a dorsal view, rudiments of the optic vesicles were visible (Fig. 2E).

At 196.0 h (7.75 d), closure of the blastopore was first seen. Optic vesicles were larger, and visible to direct view. Slight cephalic swelling was apparent. Oil droplets were coalescing (Fig. 2F).

Middle embryogenesis: Differentiation of the main divisions of the brain had begun by 250.0 h (10.4 d). Cephalic and caudal swelling were present. Optic cup and lens of the eye were best seen in dorsal view; the

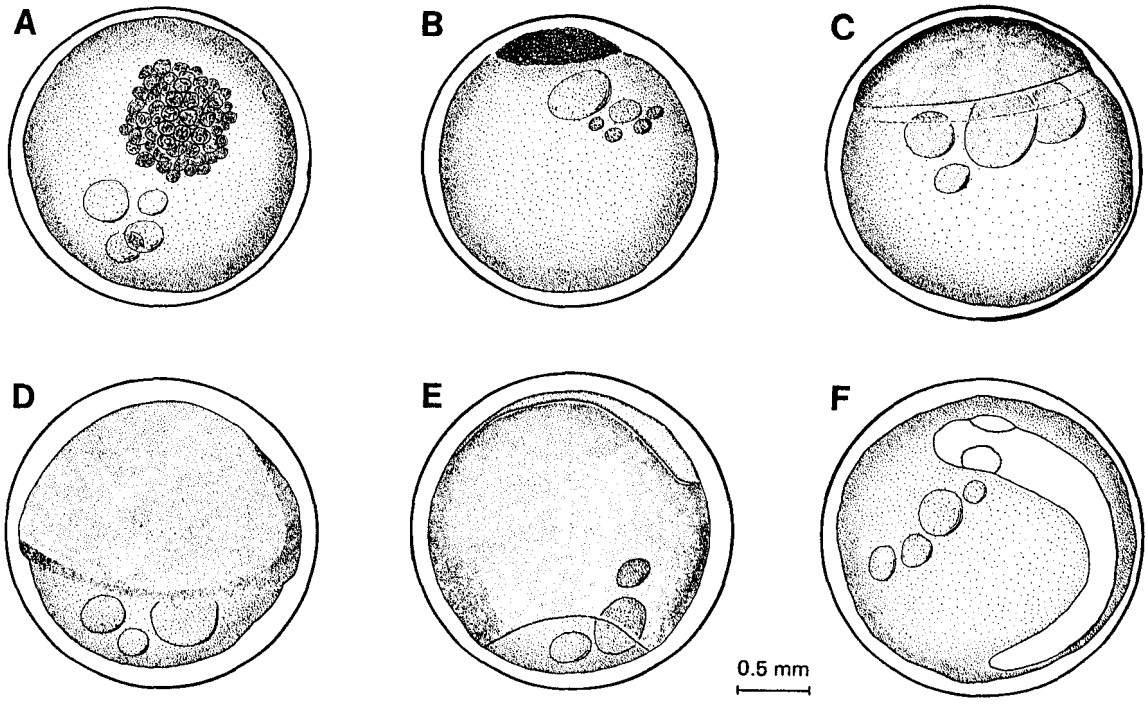

FIGURE 2.—Development of the eggs of the longhorn sculpin, *Myoxocephalus octodecemspinosus*, artificially propagated in the laboratory: A) 64-cell stage, 2.19 mm (27 h); B) multicell stage, 2.19 mm (52 h); C) blastula stage, 2.22 mm (86 h); D) gastrula stage, 2.15 mm (132 h); E-F) early embryonic stages, 2.19 mm (168 and 186 h); scale = 0.5 mm. Measurements refer to mean egg capsule diameters.

lens was not bulging out of the cup. In most specimens, one or two large oil droplets were near the cephalic region. Embryos extended slightly more than one-half way around the yolk (Fig. 3A).

At 302.0 h (12.6 d), the divisions of the brain were more clearly differentiated. The mid- and hindbrains had increased in size. Lens of the eye protruded from the optic cup. Otic vesicles, Kupffer's vesicle, pectoral buds, and notochord were present. Toward the caudal end of the embryo, clearly distinguishable somites were first observed and ranged in number from 12 to 14. The embryo reached about two-thirds way around the yolk (Fig. 3B).

Embryos in the tail-free stage were first noted at 424 h (17.7 d). Kupffer's vesicle was deeper. The olfactory placode was visible. Somites had increased in number to 16 or 17. The embryos stretched about three-fourths way around the yolk (Fig. 3C).

Late embryogenesis: Darkly pigmented eyes were first visible at 472.0 h (19.7 d). All observed embryos had dark eyes and a pulsating heart by 520.0 h (21.7 d). Lens of the eye was large. Head was large and rather flattened. Brain ventricles were apparent in dorsal view. Otoliths were present. The rudiment of the lower jaw was visible. Pectoral fins were spread over the yolk sac. Finfold was apparent. Tip of the tail was curved around past the mouth. There were about 25 somites. Most specimens had a single large oil globule located beneath the head (Fig. 3D, E).

Embryo movement within the eggs was first observed at 545.0 h (22.7 d). The tail passed well over the hindbrain on the lateral flexion. The lower jaw became more developed, but the mouth was not yet open. Opercular margin was well defined. The anal vent was visible. The circulatory system became functional along the length of the tail; this was first noted at 800.0 h (33.3 d), and all observed embryos had noticeable circulation by 825.0 h (34.4 d).

Prehatching stage: Embryos in this stage were characterized by silvered eyes and by the onset of pigmentation of the body. Most embryos were in this stage at about 850.0 h (35.4 d). Contracted melanophores densely covered the dorsal surface of the yolk sac. A few large stellate melanophores were present behind the head. Evenly spaced melanophores were present from near the vent along the ventral line of the tail. Yolk sac was much reduced in size. Tail was wrapped about 1½ times around the

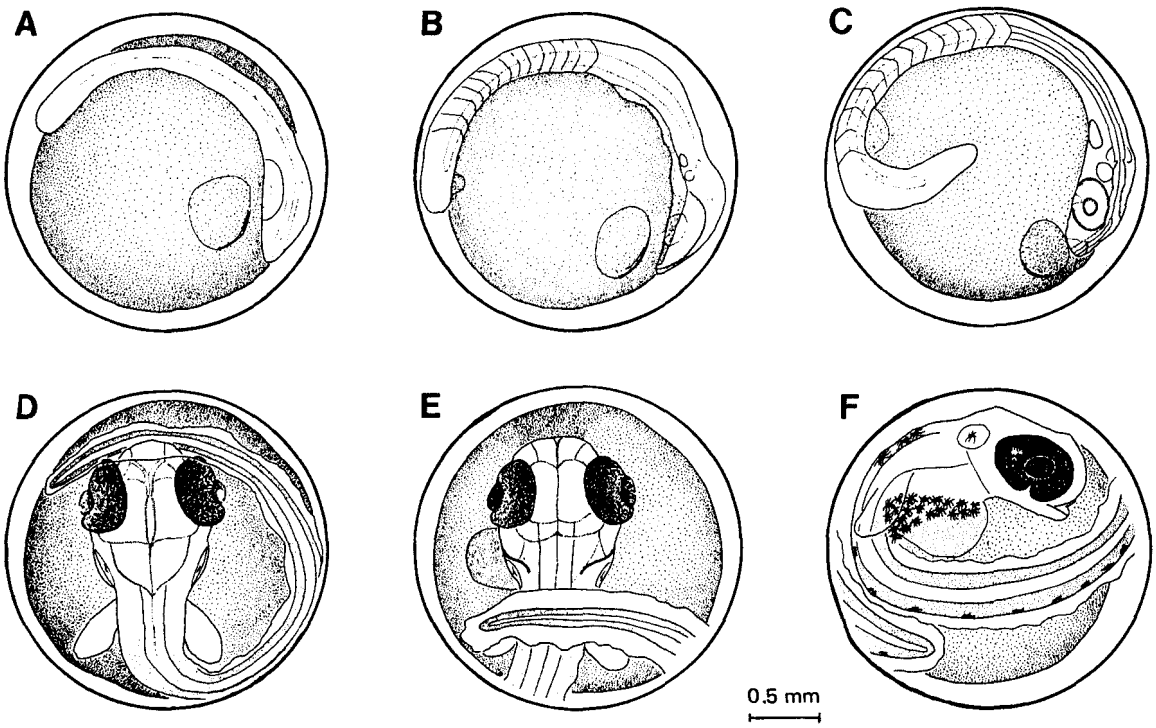

FIGURE 3.—Later development of the eggs of the longhorn sculpin, *Myoxocephalus octodecemspinosus*, artificially propagated in the laboratory: A-C) middle embryonic stages, 2.16 mm (250-424 h); D-E) late embryonic stages, 2.16 mm (578-780 h); F) prehatch stage, 2.18 mm (880 h); scale = 0.5 mm. Measurements refer to mean egg capsule diameters.

yolk sac. Pectoral fins were larger and were first seen to make intermittent fluttering motions. Mouth was open. Embryos exhibited considerable movement within the eggs, including complete rotations (Fig. 3F).

Hatching of eggs occurred between 36 and 65 d after fertilization. Newly hatched longhorn sculpin prolarvae ranged from 6.2 to 7.8 mm TL (mean 6.8 mm) and 6.0 to 7.2 mm SL (mean 6.4 mm). Yolk sac averaged 1.2 mm (range 1.1-1.3 mm). Oil droplet was 0.4 mm (range 0.3-0.5 mm) and transparent. Eye was darkly pigmented, and choroid fissure was apparent. Bulging of the lens could best be seen from the dorsal view. Mouth was wide open in some specimens, but did not yet appear well developed. A pair of olfactory buds flanked a deep pit located on the midline anterior to the eyes. Auditory vesicles were large and could be seen to protrude when viewed from above. A few stellate chromatophores were present above and behind the auditory vesicles. Some specimens had a single large stellate melanophore at the anterior end of the yolk sac near the oil globule. Dorsal surface of the yolk sac was densely covered by contracted chromatophores. A series of spots were present along the ventral line of the tail and ranged in number from 18 to 28. Larvae had 37 or 38 myomeres. Anus was situated just anterior to the ventral origin of the finfold. Dorsal finfold originated posterior to the auditory vesicles and had a smooth margin; its caudal portion was lunate. Pectoral fins had broad bases and were approximately as deep as they were wide (Fig. 4A).

Absorption of the yolk sac was completed about 10 d after hatching. Postlarvae averaged 7.7 mm TL (range 7.1-8.3 mm). Although reduced in size, a remnant of the oil globule was present. The mouth was well developed. In most specimens, a pair of small head spines and 3 or 4 preopercular spines were visible. A pair of nostrils flanked the nasal pit. The eyes retained the fissure. Most specimens had a single large stellate chromatophore above and posterior to the uppermost cheek spine. The other major change in pigmentation was the approach of dense contracted chromatophores toward the anus. Pectoral fins increased in size and were deeper than wide. Larvae had 37 or 38 myomeres. Stomach and liver were visible. Finfold was smooth and continuous (Fig. 4B).

Absorption of the oil globule was completed at about 15-20d, when larvae averaged 8.7 mm TL (range 8.3-9.1 mm). Larvae at this stage exhibited large stellate melanophores scattered over the top of the head, and on the midline above and between the nostrils. Several stellate chromatophores were present on the isthmus. Additional stellate melanophores developed almost down to the anus, beyond the extent of the contracted chromatophores. Several contracted chromatophores were posterior and parallel to the cleithrum. Margins of the pectorals were ragged in appearance. In most specimens, incipient rays of the caudal fin became visible. Four preopercular spines were present on each cheek. One pair of spines was well developed on the crown of the head above the auditory vesicles. Nostrils appeared slightly larger. Fissure of the eye remained visible. Ventral spots on the tail ranged in number from 16 to 24. Finfold was smooth and continuous (Fig. 4C).

Among larvae which were 25-30 d old, the head was more densely pigmented, including the presence of some contracted chromatophores on the crown and a few stellate chromatophores within the auditory vesicles. Pigmentation was also increasing posterior to the auditory vesicles. There were four spines along the operculum and one pair of spines on the crown of the head. Fissure of the eye was difficult to see. Caudal rays were more clearly visible. Pectoral fins appeared more thick and fleshy at their bases, where 1-3 stellate chromatophores were located. Some specimens had incipient pectoral rays. Pelvic buds were present. The margin of the finfold was slightly ragged (Fig. 4D).

The onset of development of dorsal and anal fins was observed at 33-40 d, when larvae were about 9.0 mm TL. Some larvae at this stage had an anlage of the dorsal fin, whereas the larger specimens possessed the rudiments of 9 dorsal spines, 6 dorsal rays, and 13 anal rays. Pectoral fins had 15 or 16 rays, and the stellate chromatophores at the anterior margin of the fin had increased in number from 7 to 10. Caudal fin had 9-12 rays, and the hypurals were present. Pelvic fins appeared slightly larger. The crown of the head was densely pigmented with stellate and contracted melanophores. Dark vertical bars were located posterior to the auditory vesicles. Four spines were present on each cheek and two pairs of spines were present on the crown. The nostrils were beginning to constrict. The notochord was not yet flexed (Fig. 5A).

Forty-eight day larvae measured about 10.5 mm TL. They exhibited a first dorsal fin with 9 spines, and a second dorsal with 14 rays. The first dorsal was lower than the second, the two were continuous, and the finfold remained complete in the region of the caudal peduncle. Anal fin had 14 rays. Caudal fin had 13 or 14 rays, and urostyle pointed dorsally. Pelvic fins were somewhat larger, but the rays were not yet visible. Pectoral fins were large and fanlike; these had 17 or 18 rays and the bases of the fins were well pigmented. The pigmentations of the crown of the

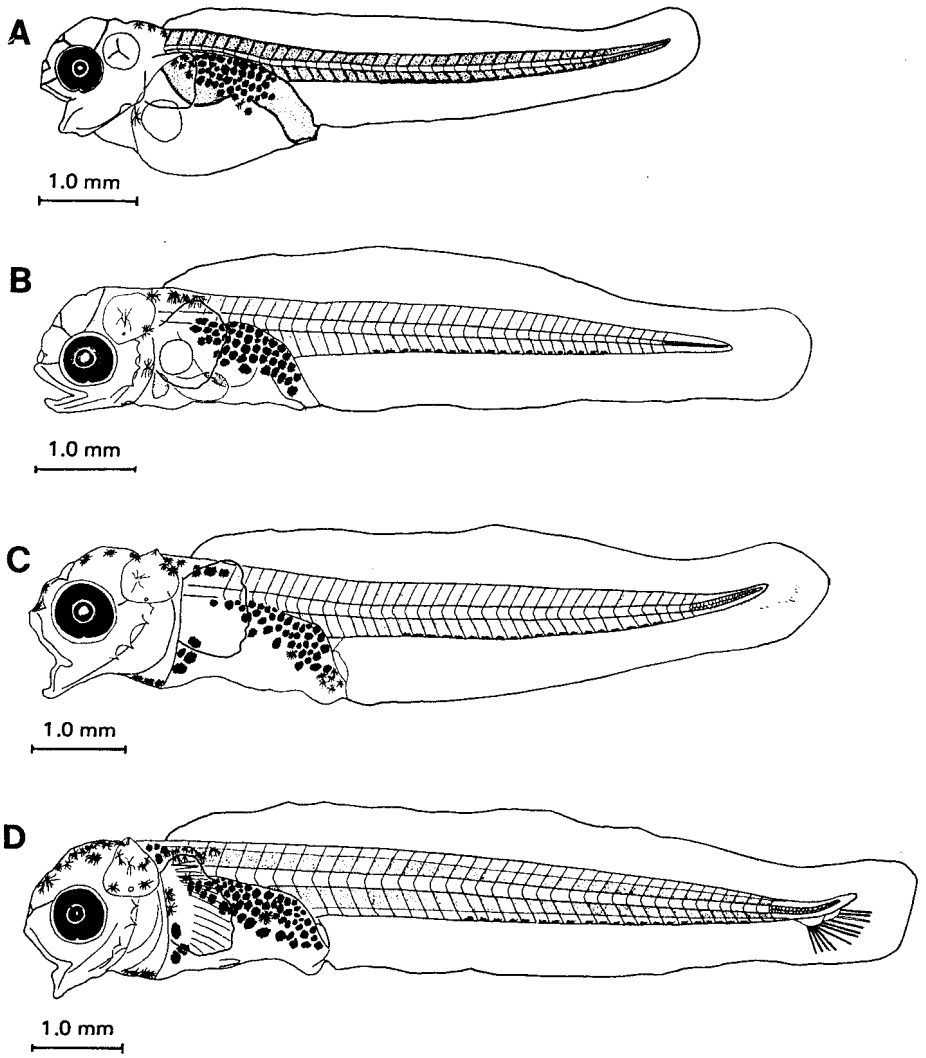

FIGURE 4.—Prolarval and early postlarval stages of the longhorn sculpin, *Myoxocephalus octodecemspinosus*, artificially propagated in the laboratory: A) newly hatched prolarva 6.8 mm TL, scale = 1 mm; B) postlarva 7.7 mm TL (10 d old), scale = 1 mm; C) postlarva 8.7 mm TL (20 d old), scale = 1 mm; D) postlarva 8.8 mm TL (30 d old), scale = 1 mm. Measurements refer to mean total length of larvae.

head and the dorsal aspect of the gut region were so dense as to produce an almost uniformly dark appearance. About 25 spots were along the ventral line of the tail, including some beyond the point of flexion. There were four preopercular spines on each side, and two pairs of head spines. The nostrils were almost completely constricted (Fig. 5B).

Longhorn sculpins metamorphosed from the larval stage at 51-58 d, when they were about 12.0 mm TL. A small remnant at the caudal peduncle and incomplete separation of the two dorsals were the only relics of the embryonic finfold. There were nine spines in the first dorsal. This fin was shorter than the second dorsal and approximately equal in height; fish at this stage did not yet exhibit the higher first dorsal characteristic of adults. Second dorsal fin had 14 or 15 rays. Anal fin had 14 rays. Pelvic fin had three rays. Pectoral fins had 17 or 18 rays and extended beyond the origin of the second dorsal. Five spines were now on each cheek, and the uppermost had begun growing strongly, signalling the development of the long cheek spine characteristic of adults. Two pairs of head spines were fusing and appeared as a single large flesh-covered structure. There was one pair of

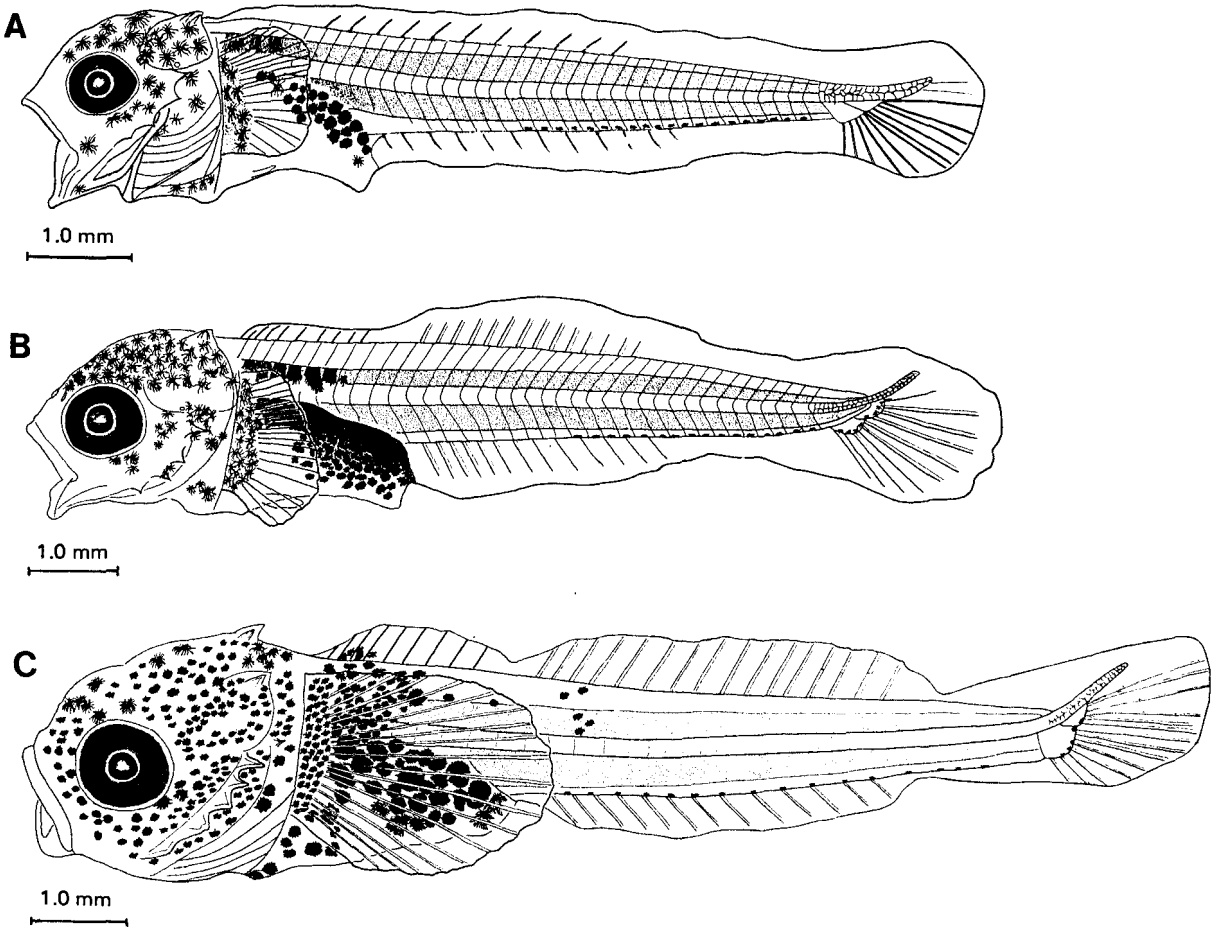

FIGURE 5.—Later postlarval and young stages of the longhorn sculpin, *Myoxocephalus octodecemspinosus*, artificially propagated in the laboratory: A) late postlarva, 9.0 mm TL (40 d old), scale = 1 mm; B) postlarva prior to transformation to young, 10.5 mm TL (48 d old), scale = 1 mm; C) transformed young, 13.0 mm TL (65 d old), scale = 1 mm. Measurements refer to mean total length of larvae and young.

shoulder spines. Two pairs of nostrils resulted from the completed constriction. The gills had four arches and six branchiostegal rays on each side.

The earliest indication of the onset of development of adult pigmentation was apparent at about 65 d, in juveniles of about 13.0 mm TL. Dark spots were present at the base of the first dorsal and on the body beneath both dorsals. Melanophores beneath the first dorsal covered the vertical bars which had previously been visible posterior to the auditory region. The other noticeable change in the pigmentation relative to the previous stages was contraction of chromatophores located along the operculum, pectoral fin bases, and isthmus; these now had the appearance of dense, dark spots rather than large, stellate melanophores (Fig. 5C).

Juvenile fish of 92-104 d exhibited the characteristic four crossbar marks of adults. These fish averaged 16.7 mm TL (range 15.2-17.7 mm). Another change in pigmentation was the presence of a line of spots extending from the first crossbar down to and surrounding the anal vent. Many of the melanophores of the head and body were reduced in size, so that the basic coloration resulted from the presence of many densely crowded, small melanophores, rather than the large melanophores characteristic of earlier stages. Pigmentation increased at the base of both dorsals and was observed on the anal and caudal fin membranes in a 104-d specimen. A pair of well-developed ridges ran longitudinally along the crown of the head. Supraorbital spines and large head spines were located along the ridges. There were four cheek spines on each side, the uppermost being the largest and the two lowest being quite small. There

were two pairs of shoulder spines, the lower spine having emerged close above the upper margin of the pectoral fin. There was a single pair of small nasal spines. The fins had all acquired the characteristic adult shapes, including the high profile of the first dorsal. The pelvics had acquired a single spine in addition to the three rays; all other fins had the same meristic characteristics as the preceding stage. There were no longer any visible remnants of the embryonic finfold.

Descriptions of longhorn sculpin larvae from the Gulf of Maine and Canadian waters (Khan 1971) were somewhat different. Khan found that early larvae had ventral pigmentation near the anus and absorbed the oil globule prior to yolk-sac absorption, whereas ventral pigmentation along the intestine was absent and yolk-sac absorption was completed prior to oil globule absorption among larvae reared in this study. He found that anal and dorsal fins developed consecutively, whereas in this study these fins developed concomitantly. Finally, he found that juvenile longhorn sculpins retained remnants of the finfold at a larger size (ca. 15 mm) than occurred here (ca. 13 mm).

Development of eggs and larvae of *M. octodecemspinosus* was very similar to *M. aenaeus*, as described by Lund and Marcy (1975). Grubbies reared at mean temperatures between 4.6°-6.0°C underwent the stages of fertilization, cleavage, cell multiplication, gastrulation, embryogenesis, hatching, and larval development to the juvenile stage at rates which differed very little from the longhorn sculpin larvae of this experiment. Eggs of the two species were distinguishable as grubby eggs had a mean diameter of 1.58 mm and a transparent chorion (Lund and Marcy 1975), while longhorn sculpin eggs had a mean diameter of 2.19 mm and a translucent chorion. The larvae of the two species can be distinguished by size, pigmentation, and meristics.

Behavior of longhorn sculpins as observed in aquaria underwent marked changes during development. Immediately after hatching, the larvae swam toward the surface, sometimes making random turns, after which they sank to the bottom where they remained quiescent for variable periods. The longest observed continuous posthatch swim was almost 5 min, whereas other larvae swam for only a few seconds before sinking. This resting behavior was characteristic of prolarvae. Ennis (1970) reported similar behavior of newly hatched *M. scorpius* larvae.

Activity of the larvae increased considerably as absorption of the yolk sac neared completion. The larvae foraged actively near the surface. Postlarvae did rest on the bottom intermittently, but did so to a lesser extent than prolarvae. Lund and Marcy (1975) described intermittent resting of *M. aenaeus* postlarvae, particularly after a strike at prey.

The assumption of benthic behavior was considered to signify metamorphosis from the larval stage. After taking to the bottom, juvenile fish made sudden darting movements in search of prey or when disturbed, and they maintained this behavior throughout the juvenile period when the adult pigmentation was developing.

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