DEVELOPMENT OF EGGS AND LARVAE OF THE WHITE CROAKER, *GENYONEMUS LINEATUS* AYRES (PISCES: SCIAENIDAE), OFF THE SOUTHERN CALIFORNIA COAST

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ABSTRACT

Eggs and larvae of the white croaker, *Genyonemus lineatus*, were collected near the San Onofre Nuclear Generating Station in 1978 and 1979. A developmental series based on 59 eggs and 168 larvae and early juveniles was assembled.

Live *G. lineatus* eggs are pelagic, transparent, and spherical, averaging 0.85 mm in diameter with a single oil droplet of 0.23 mm. Preserved, newly hatched larvae average 1.57 mm SL and are not well developed. Larval development is a gradual process. Notochord flexion begins at ca. 5.4 mm SL and is complete by ca. 6.4 mm SL. Dorsal and anal fin anlagen appear at ca. 5 mm SL and the full complement of rays is present in each fin by ca. 8.2 mm SL. Pelvic differentiation begins at ca. 5.3 mm SL and is finished by ca. 8.6 mm SL. Pectoral rays begin to develop at ca. 7.8 mm SL and all are present by ca. 13 mm SL.

Larval pigmentation is largely restricted to the dorsum at hatching, but migrates to the ventral midline during early development. Melanophores are restricted to the ventrum and gut through much of the subsequent larval period. A barred pattern develops during transition to the juvenile stage.

Genyonemus lineatus larvae are distinguishable from similar cooccurring species by the presence of a nape melanophore and larger melanophores in the midventral trunk series at myomeres 9-10 and 16-18.

The sciaenid genus, *Genyonemus*, is represented by a single species, *G. lineatus* (Ayres), the white croaker. It occurs along the west coast of North America from central Baja California to southern British Columbia (Miller and Lea 1972), although its numbers are reduced north of San Francisco, Calif. (Frey 1971). In southern California the white croaker is a common inshore species of modest sport and commercial value (Skogsberg 1939; Frey 1971). Its larvae rank second in abundance only to those of the northern anchovy, *Engraulis mordax*, among the inshore ichthyoplankters off San Onofre, Calif. (Walker et al. 1980[2]).

Despite its abundance in southern California, the early life history of *G. lineatus* is poorly known. Seasonal spawning cycles are described based on gonadal studies (Goldberg 1976), and the duration of the egg stage is mentioned by Morris (1956), who reared *G. lineatus* from field-collected eggs through 19-d-old larvae. Larvae are not described, although Morris (1956) gives dimensions of the egg.

Beginning in January 1978, Marine Ecological Consultants of Southern California initiated a study of the inshore ichthyoplankton off San Onofre (Fig. 1) for the Marine Review Committee of the California Coastal Commission (Barnett and Sertic 1979[3]). During this study approximately 48,000 *G. lineatus* larvae were sorted from the samples, providing an opportunity to construct a developmental series through the early juvenile stage. Live plankton samples provided eggs for rearing purposes. This paper describes the egg and larval development of *G. lineatus* as determined from these series.

MATERIALS AND METHODS

Egg and larval descriptions are based on detailed observation of 59 eggs, 29 reared larvae,

[1]Marine Ecological Consultants, 533 Stevens Avenue, Solana Beach, CA 92075.

[2]Walker, H. J., A. M. Barnett, and P. D. Sertic. 1980. Seasonal patterns and abundance of larval fishes in the nearshore Southern California Bight off San Onofre, California. Marine Ecological Consultants of Southern California, 533 Stevens Ave., Solana Beach, CA 92075, 16 p.

[3]Barnett, A. M., and P. D. Sertic. 1979. Preliminary report of patterns of abundance of ichthyoplankton off San Onofre and their relationship to the cooling operations of SONGS. Marine Review Committee Document 79-01, p. 1-1 to 4-5. Marine Review Committee of the California Coastal Commission, San Francisco, Calif.

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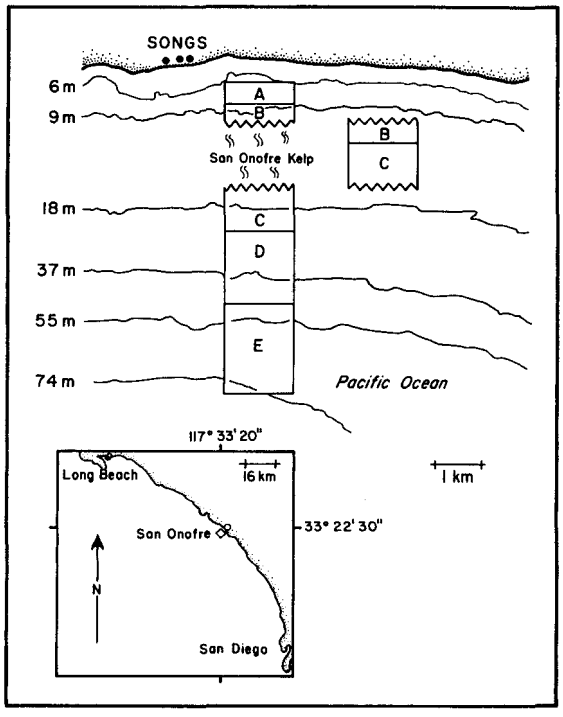

FIGURE 1.—Chart of the sampling area and its position off the southern California coast. SONGS = San Onofre Nuclear Generating Station.

and 139 field larvae. These were collected in 1978 and 1979 between the 6 and 20 m isobaths near the San Onofre Nuclear Generating Station (Fig. 1; Barnett and Sertic footnote 3).

Eggs used only for egg description were maintained at ambient air temperature (ca. 20°C) while those reared for larval description were maintained near their collection temperatures (13.4°-14.3°C). The sequence of developmental events in reared specimens was confirmed by comparison with field specimens.

Plankton samples were preserved in the field in 5% seawater-Formalin[4] and specimens later sorted in the laboratory. These were stored in 2.5-5% seawater-Formalin. Reared specimens were preserved in 2.5% seawater-Formalin.

Because reared *Genyonemus* larvae often are more heavily pigmented than field specimens, the latter were used as the principal descriptive source. Yolk-sac larvae were primarily reared specimens, owing to the difficulty of obtaining undamaged field specimens of this size. Twenty field specimens from the early larval stage through transition to the juvenile were cleared and stained with alizarin following the method of Hollister (1934) to determine the sequence of skeletal ossification.

Measurements were made to the nearest 0.03 mm at 25× using a binocular dissecting microscope equipped with an ocular micrometer. Drawings were made with the aid of a camera lucida. Pigmentation illustrated for yolk-sac larvae represents fresh material; the pattern is largely lost after several weeks of preservation.

Developmental stages follow the terminology of Ahlstrom and Ball (1954), except that the transitional period between the larval and juvenile stages is considered to begin when the first scales appear and to end when scalation is essentially complete. All fin rays and myomeres (preanal plus postanal) were counted on each specimen, when distinguishable. Dimensions measured were body depth, eye diameter, head length, preanal length, preanal fin length, snout length, and standard length. These dimensions are defined in the literature (e.g., Saksena and Richards 1975; Powles 1980).

EMBRYONIC DEVELOPMENT

The *G. lineatus* egg is pelagic, spherical or nearly so, and transparent, with an unsculptured chorion and unsegmented yolk (Fig. 2). It usually contains a single colorless to slightly yellowish oil droplet, although in the early stage it may contain two or three oil droplets which later coalesce. Thirty-eight live eggs collected from the plankton averaged 0.85 mm (SD = 0.02 mm) in diameter, with a single oil droplet of 0.23 mm (SD = 0.02 mm). The perivitelline space was very small (<0.04 mm). These dimensions are similar to those given by Morris (1956) for *G. lineatus* eggs collected from the plankton: egg diameter 0.9 mm and oil droplet diameter 0.2 mm. Twenty-one eggs preserved for 111 d in 2.5% seawater-Formalin were slightly oval, averaging 0.84 by 0.83 mm (SD = 0.02 mm) in diameter, with a single oil droplet of 0.21 mm (SD = 0.01 mm) and a perivitelline space of 0.05 mm (SD = 0.02 mm).

The embryo is unpigmented through gastrulation (Fig. 2a, b). During eye capsule formation the first few small melanophores appear on the distal side of the oil droplet and on the yolk adjacent to the oil droplet (Fig. 2c). Midlateral, middorsal, and a few scattered dorsolateral trunk

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

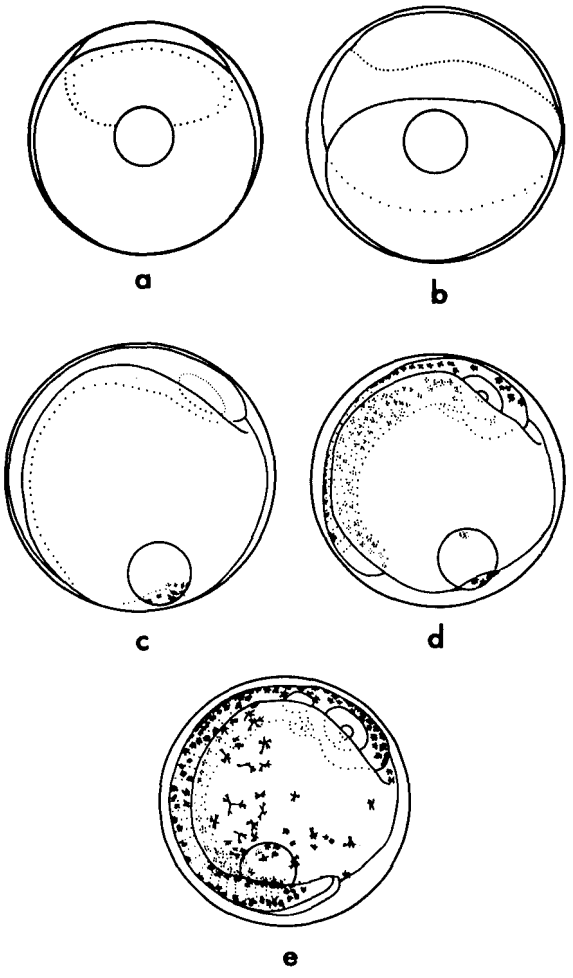

FIGURE 2.—Development of the *Genyonemus lineatus* egg: a) blastula stage, 0.78 mm diameter; b) gastrula stage, 0.86 mm diameter; c) early embryo just prior to blastopore closure, 0.90 mm diameter; d) tail bud stage, 0.84 mm diameter; e) late stage, 0.84 mm diameter. All illustrations are of live eggs. Note that oil droplets are somewhat smaller than average in this group of eggs.

melanophores appear shortly thereafter. About 5 h after eye capsule formation (at 20°C) small melanophores surround the trunk and are scattered dorsally on the head (Fig. 2d). A few melanophores occur on the yolk adjacent to the tail bud at this stage. As development continues the dorsal head pigmentation increases and trunk melanophores become situated primarily dorsally and dorsolaterally. Yolk melanophores increase in number until they nearly surround the yolk just before hatching (Fig. 2e).

The oil droplet is located opposite or adjacent to the embryo through gastrulation (Fig. 2a, b). During the latter part of the egg stage the tail of the developing embryo grows past the oil droplet, which ultimately is situated adjacent to the embryo just anterior to the anus (Fig. 2e).

Optic capsules develop almost simultaneously with blastopore closure and just prior to somite development. Lens development begins at about the four myotome stage.

Somite differentiation begins just behind the head and continues posteriorly. Kuppfer's vesicle first becomes apparent near the tip of the tail bud at about the 4 somite stage and persists to the 18 somite stage. Heart and finfold development are initiated at about the 18 somite stage and the tail first separates from the yolk shortly thereafter. By the end of the egg stage the embryo has 25-26 myomeres, otic capsules with at least the sagittae developing, a simple tubular gut, wide finfold, and functional heart.

Preserved eggs collected from the plankton at 1900 PST on 29 January 1979 were largely in the two, four, and eight cell stages. Live eggs from the same sample began gastrulation after 20-22 h of incubation (ca. 20°C) and eye capsules developed at about 26-28 h. The 18 somite stage was reached at about 38-40 h and the full somite complement attained by 43-45 h. All larvae had hatched by 52 h.

YOLK-SAC LARVAE

Pigmentation

The pigmentation of newly hatched larvae closely resembles that of late stage eggs, with melanophores concentrated primarily dorsally and dorsolaterally on the head and trunk (Fig. 3a). Additional pigment includes a characteristic large dendritic melanophore extending upward from the nape to the margin of the finfold, a large midventral melanophore about halfway between the anus and tip of the tail (one or two small lateral melanophores may occur here as well), and one to three small middorsal and midventral melanophores near the tip of the notochord. One or two melanophores usually occur ventrally on the gut, near the anus. Oil droplet pigmentation is mainly proximal. A few melanophores are usually scattered on the yolk sac. The nape, oil droplet and gut, and midtail pigment appears as three distinct bands in live larvae. Only the nape and midtail melanophores may be expected to survive prolonged Formalin preservation.

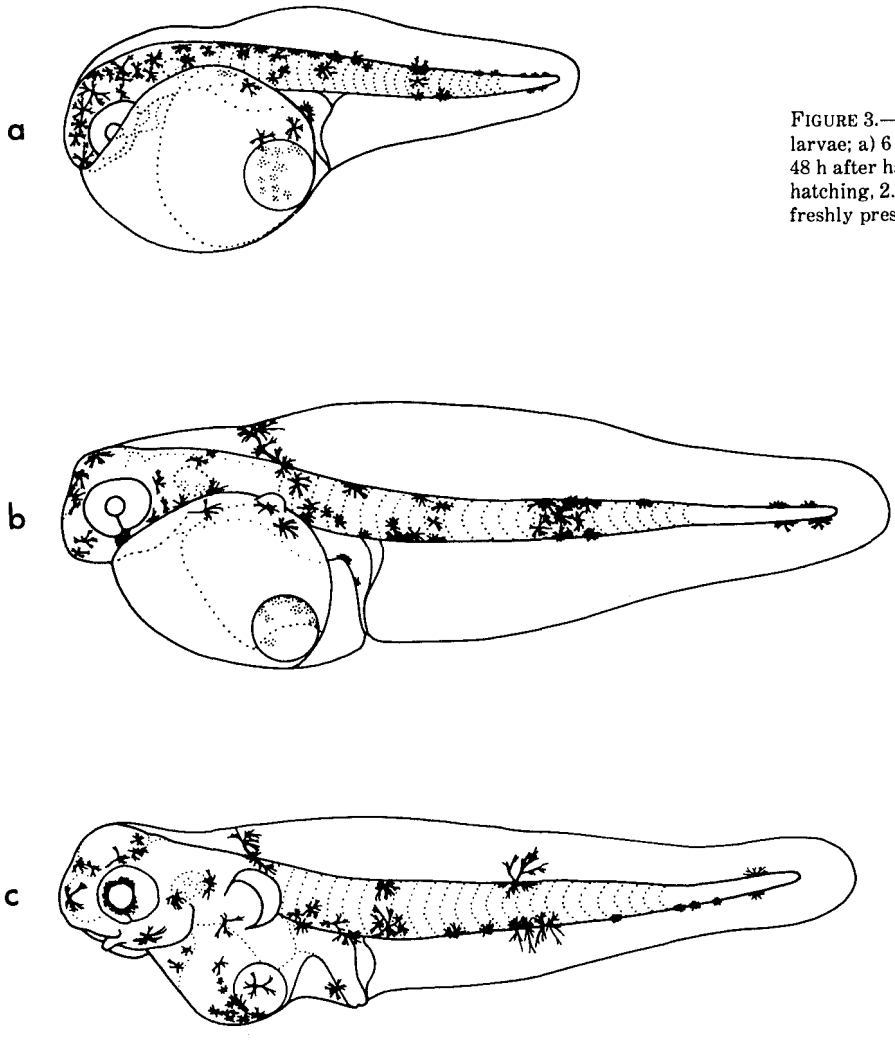

FIGURE 3.—*Genyonemus lineatus* yolk-sac larvae; a) 6 h after hatching, 1.54 mm; b) 48 h after hatching, 2.48 mm; c) 68 h after hatching, 2.36 mm. All illustrations are of freshly preserved reared larvae.

Head pigment changes little during the first 60 h (ca. 13°C). After this it condenses to a few melanophores over the forebrain and midbrain. These melanophores may be lost by the end of the yolk-sac stage except for one or two melanophores on the otic capsule. A small melanophore first appears at the angular bone just at the end of the yolk-sac stage. Eye pigmentation begins at about 60 h (Fig. 3c) and is complete by 120 h after hatching (ca. 13°C).

During the first 24 h after hatching the dorsal trunk melanophores begin to migrate ventrally, condensing into bands at the nape, the anus, and midtail at myomeres 16-18 (Fig. 3b). This pattern persists but becomes indistinct as melanophores continue to migrate ventrally.

By the end of the yolk-sac stage dorsal trunk pigment consists only of the large nape-finfold melanophore, one or two smaller melanophores near the level of the anus, one in the region of myomeres 16-18, and one or two near the tip of the notochord. Lateral melanophores may persist in these same areas, although more often they do not. Midventral trunk pigment increases to a series of 8-10 melanophores, with those at myomeres 9-10 and 16-18 usually larger.

Oil droplet and yolk-sac pigment changes only by condensing as the yolk is consumed. The ventral hindgut melanophores persist through the yolk-sac stage with the lower migrating to a position adjacent to the anus. A single small melanophore usually moves to the dorsal midline of the hindgut where the hindgut turns downward at the fifth or sixth myomere. After about 60 h one

or two melanophores may overlie the gut at the level of the soon-to-inflate swim bladder at myomeres 1 and 2.

Morphology

Genyonemus lineatus larvae hatch in a relatively undifferentiated state with unpigmented eyes, otic capsules usually with sagittae, a functional but simple tubular heart, straight tubular gut, large yolk sac, and posterior oil droplet. No mouth, branchial apparatus, or other viscera are apparent.

Pectoral buds appear during the second day after hatching and pectoral membranes are present on the third. The mouth opens and the operculum becomes discernible during the third day. Gut differentiation begins at this time. Yolk exhaustion and swim bladder inflation occur on the sixth day. Feeding, and consequently the end of the yolk-sac stage, is initiated during the sixth or seventh day after hatching (at ca. 13°-14°C).

Larvae lengthen during the yolk-sac stage, from a preserved hatching length of 1.57 mm ($n = 4$, SD = 0.02 mm) to 2.41 mm ($n = 4$, SD = 0.02 mm) at yolk exhaustion. Yolk-sac length declines from 0.86 mm ($n = 4$, SD = 0.04 mm) at hatching to zero. Head length, preanal length, and eye diameter change little during the yolk-sac stage.

LARVAE

Pigmentation

Genyonemus lineatus larvae are quite variable in degree of pigmentation (e.g., midwinter larvae often are more lightly pigmented than spring larvae), although the basic pattern is conservative. Because of this variability, pigmentation is described more fully than might otherwise be warranted. Illustrations are of typical (i.e., late winter) specimens.

The head typically is moderately pigmented at the beginning of the larval stage (Fig. 4a). Single small melanophores are nearly always present on the snout and at the angular bone, as many as four or five may be scattered over the fore- and midbrain regions, and one or two are often located in the floor of the otic capsule. Some specimens have an elongate melanophore laterally on the mandible.

The snout melanophore is lost soon after yolk absorption and the snout remains unpigmented throughout larval development. Small melanophores begin to appear between the nostrils at ca. 17 mm and rapidly proliferate to form a band which persists until becoming obscured by the increasing head pigmentation in the juvenile stage.

The melanophore at the angular bone persists through the juvenile stage. Mandibular pigment typically is absent until the beginning of transition at ca. 13 mm, when a pair of melanophores appears at the center of the mandible. The number increases to six or eight by the beginning of the juvenile stage (ca. 17 mm). Premaxillary pigmentation begins shortly before transition, with a pair of melanophores at the center of the upper jaw. Four to six more melanophores are added by the beginning of the juvenile stage. Some small specimens may have one or two melanophores in the central gular region. These rarely persist beyond ca. 5 mm.

Pigment on top of the head declines rapidly early in the larval stage, and is absent after ca. 2.8 mm. During the transitional period melanophores again appear on the head, beginning with a pair over the midbrain region at ca. 14.8 mm. Melanophores rapidly proliferate to form bands over the midbrain by the beginning of the juvenile stage.

Opercular pigmentation is acquired just before the juvenile stage, with a pair of melanophores under the central opercular region. One or two external melanophores develop on the upper operculum at ca. 17.2 mm and quickly increase in number to form a dark patch.

Otic floor pigment is most often present in larvae <4 mm and absent in larger specimens. At ca. 9.5 mm a melanophore appears under the anterior hindbrain, followed by an anterolateral melanophore on each side at ca. 10 mm. A second ventrolateral melanophore is acquired here during transition (ca. 13 mm) and by the beginning of the juvenile stage the anterior hindbrain is usually surrounded by a heavy pigment band.

At the beginning of the larval stage dorsal trunk pigment includes one or two nape-finfold melanophores, usually a single middorsal melanophore between myomeres 16 and 18, often a middorsal or dorsolateral melanophore between myomeres 6 and 8, and occasionally one or two small middorsal melanophores near the tip of the notochord (Fig. 4a). Lateral trunk pigment which persists into the larval stage is located at myomeres 6-8 and 16-18. This usually is lost by 2.8 mm although an occasional specimen of any

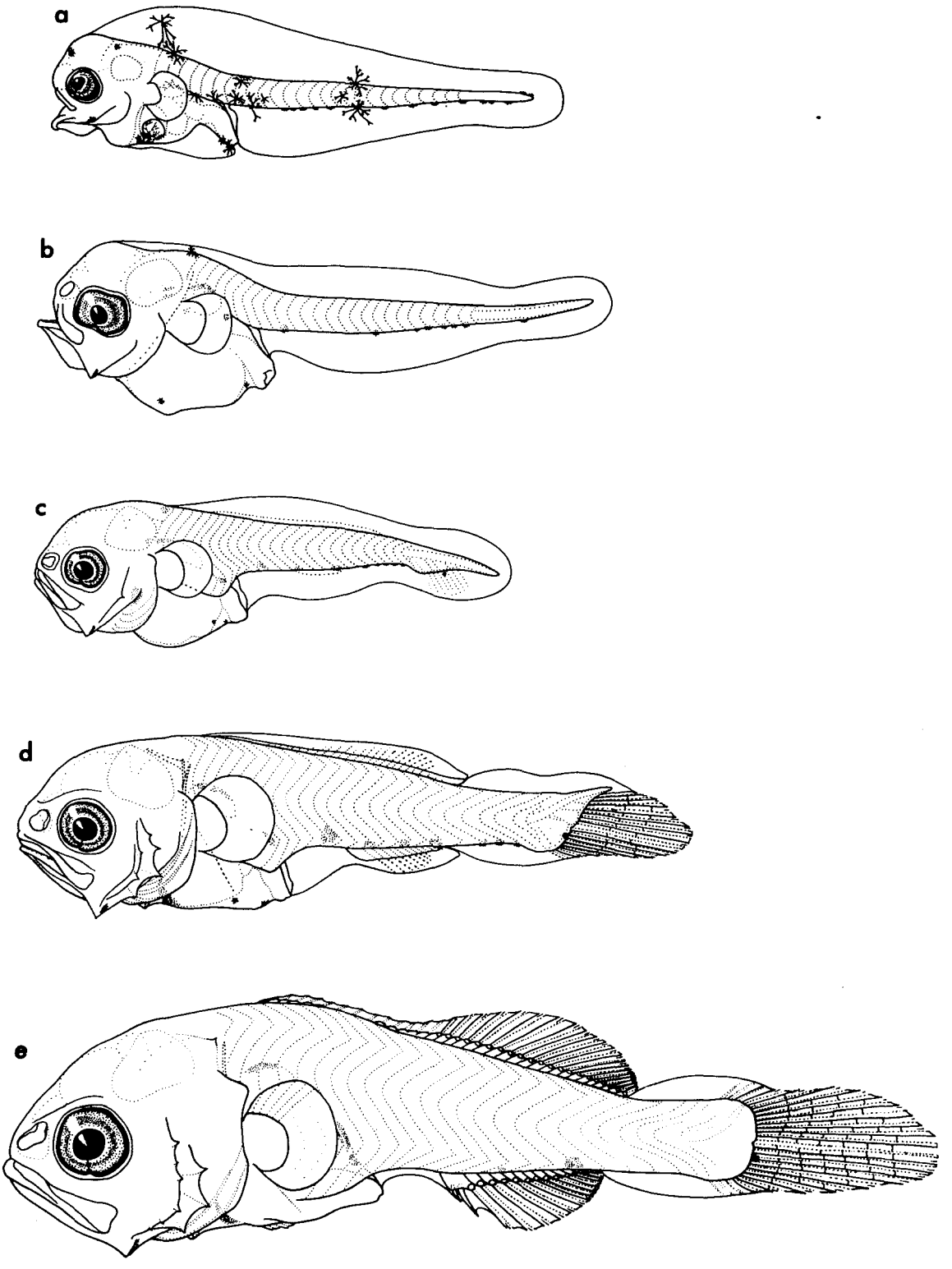

FIGURE 4.—*Genyonemus lineatus* larvae: a) 2.73 mm; b) 3.04 mm; c) 5.15 mm; d) 6.18 mm; e) 8.16 mm. All illustrations are of field specimens.

size may retain a midlateral melanophore in the myomere 16-18 region. The ventral midline melanophore series increases quickly from 8 to 10 late in the yolk-sac stage to 15-21 by ca. 2.6 mm. The melanophores at myomeres 9-10 and 16-18 remain largest.

The dorsal notochord tip melanophores and those at myomeres 6-8 are lost by ca. 2.8 mm (Fig. 4b). The melanophore at myomeres 16-18 often persists to 5 mm, and may continue until 6 mm in some specimens. The nape melanophore migrates internally and is obscured by the overlying tissue as early as ca. 2.5 mm or as late as ca. 6.1 mm, but most often between 4.8 and 5.6 mm. Following the internal migration of the nape melanophore the trunk remains unpigmented dorsally and laterally through the larval and transitional periods. Early in the juvenile stage a barred pattern develops (Fig. 5). At 17.2 mm a short bar crosses the nape and may extend laterally to the level of the supracleithral spine. A second bar extends to the midlateral line from dorsal spines VII-X, a third and fourth from dorsal rays 5-10 and 16-21, and a fifth crosses the peduncle. Six to nine bars ultimately develop in the juvenile stage, counting the snout and cranial bars. Trunk melanophores in these bars are principally myoseptal.

The midventral trunk melanophores number between 15 and 21 at the beginning of the larval stage. They begin coalescing immediately, but from 7 to 19 remain through 4.5 mm. By the beginning of caudal flexion (ca. 5.5 mm) they decline to between 2 and 12, and thereafter number between 2 and 6. The melanophore between myomeres 16 and 18 is always largest and persists through the larval stage (Fig. 4e). This melanophore lies at the posterior end of the anal fin in older larvae. The second largest midventral melanophore, which initially lies between myomeres 9 and 10, shifts one to three myomeres posteriorly and migrates internally by the time of anal fin anlage formation (Fig. 4c, d). It often persists through the larval stage, lying near the anal fin origin in older specimens. One to three small melanophores may also remain in the ventral midline between myomeres 20 and 25 through the larval period. One small melanophore usually persists near the end of the notochord, becoming located at the central distal margin of the developing hypural complex during flexion. As the caudal fin rays ossify, one to a few melanophores develop along the central and lower fin ray bases. During transition internal melanophores begin to appear along the urostyle and lower hypurals, and a band of pigment develops along the distal one-third of the caudal rays.

Soon after anal fin completion melanophores develop at the anal fin ray bases. These occur first on either side between anal soft rays 1 and 4, and proceed both anteriorly and posteriorly. The number of melanophores is variable—usually three or fewer in larvae <9 mm and five or fewer in larger specimens.

The gut region is moderately pigmented at the beginning of the larval period: a single external melanophore normally lies on each side just behind the upper pectoral insertion; one to three pairs of melanophores occur on top of the swim

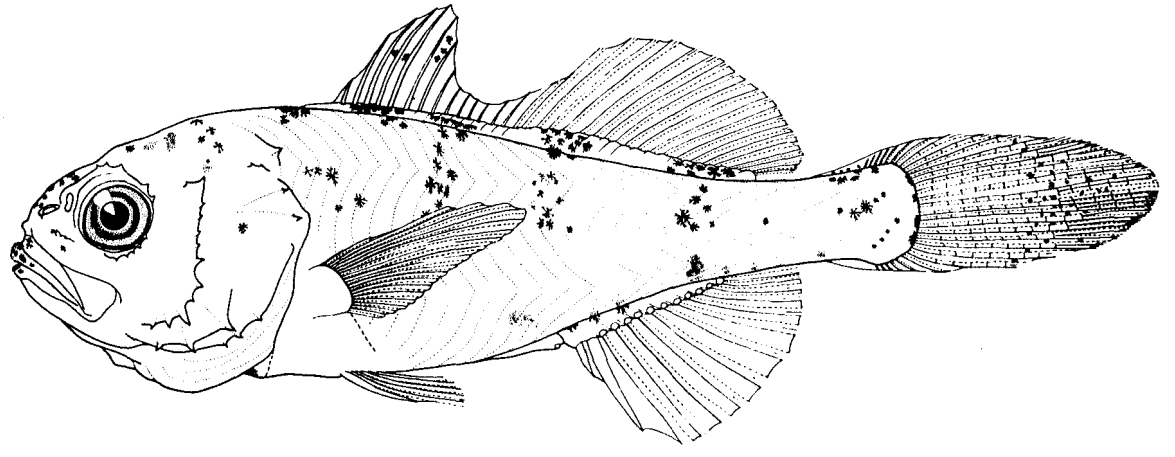

FIGURE 5.—*Genyonemus lineatus* early juvenile, 19.20 mm.

bladder; as many as two lie on the middorsal surface on the gut just behind the swim bladder; one small melanophore usually lies on the dorsal hindgut just where it turns downward at myomere 5 or 6; a larger melanophore lies adjacent to the hindgut just anterior to the anus, one rather large melanophore may lie on the anterior midline of the visceral mass just below the level of mideye; none to several small melanophores are scattered ventrally and ventrolaterally over the anterior gut.

Gut pigment generally decreases during larval development. The melanophore behind the pectoral base rarely persists beyond 5.2 mm. Swim bladder pigment increases but remains restricted to its dorsal surface through the larval period. All other dorsal gut pigment except the melanophore on the hindgut is lost by ca. 3 mm and usually does not reappear until ca. 11.2 mm, near the end of the larval stage. The dorsal melanophore on the hindgut is present more often than not (present in 63% of the larvae examined) and is nearly always quite small in specimens smaller than ca. 8 mm. In larger specimens it is nearly always present (in 95% of the larvae examined) and increases in size (occasionally others are added as well) to nearly cover the dorsal surface on the hindgut by ca. 11.2 mm (Fig. 5). In older specimens melanophores begin to fill in between the swim bladder and hindgut, so that in early juveniles the dorsal gut cavity is often entirely pigmented.

The melanophore just anterior to the anus usually persists through ca. 6 mm but is rarely present in larger specimens. Other ventral gut pigment is quite variable early in the larval period, ranging from one to several melanophores typically on the anterior half of the gut. The ventral midline of the gut often remains unpigmented throughout larval life. Only a single melanophore just anterior to the cleithral symphysis commonly remains after 5 mm (present in 64% of the larvae examined). During the transitional period one or two additional melanophores develop to form a series along the midline of the isthmus. After completion of the pelvic fin (ca. 9 mm) a single melanophore may appear between the pelvic bases. During transition a ventral midline series of two or three melanophores may arise behind the pelvic fin bases.

The large internal melanophore located anteriorly on the upper visceral mass migrates ventrally as larval development proceeds: when present it is nearly always on the upper visceral mass in larvae smaller than ca. 4 mm, is most frequently located halfway down between 4 and 6 mm (Fig. 4c), and is nearly always present at the lower anterior margin of the visceral mass in specimens larger than ca. 6 mm (Fig. 4d).

Fin Development

At the beginning of the larval period *G. lineatus* larvae have only a broad medial finfold and pectoral fin without rays. Subsequent fin development follows a typical sciaenid sequence (e.g., Powles 1980; Pearson 1929).

The caudal fin is first to develop. The caudal anlage appears at ca. 3.8 mm and the central four to six principal rays begin to ossify at ca. 4.8 mm. Notochord flexion begins at ca. 5.4 mm and is complete at ca. 6.4 mm. The full complement of 9+8 principal caudal rays is ossified by the end of flexion. Further development includes the addition of secondary caudal rays (15 to 17 total by the early juvenile stage), branching of the central principal rays and lengthening of the fin. The central rays are longest throughout larval development.

Anal and dorsal fin anlagen appear nearly simultaneously at ca. 5 mm. The anal fin anlage is short, usually extending between myomeres 13 and 18. Differentiation begins with the most anterior anal soft ray bases just after the anlage first appears, and proceeds posteriorly. The sequence of anal fin ray differentiation follows that of the ray bases, beginning with the first soft ray at ca. 6 mm and proceeding posteriorly. All anal soft rays are discernible by ca. 6.7 mm, at which time the second anal spine begins to ossify. The first anal spine completes the anal fin ray complement at ca. 7.2 mm. Subsequent larval development consists of lengthening of the rays and ossification of the pterygiophores.

The dorsal anlage initially lies between the tenth and fifteenth myomeres and lengthens to myomeres 3-21 by ca. 6 mm. As in anal fin development, the anterior soft ray bases differentiate first, beginning at ca. 5.4 mm, and the soft rays ossify from the first ray posteriorly beginning at ca. 6 mm. The posterior 8 to 10 bases are undifferentiated as the first soft rays begin ossifying. Dorsal spine bases begin differentiating anteriorly at ca. 6.4 mm and the anterior spines appear at ca. 7.2 mm, about the time of acquisition of the full complement of dorsal soft rays. The dorsal spines ossify posteriorly, reaching the adult complement of 12 to 15 by 8.0-8.5 mm. The

dorsal fin is continuous, with the first dorsal much lower than the second initially. As growth continues the anterior spines (except the first) lengthen faster than the others, so that the dorsal fin is deeply notched by the beginning of the transitional period.

Pelvic fin buds first appear between 5.3 and 5.9 mm and the first one or two elements become visible at ca. 7.2 mm. Differentiation of rays proceeds toward the midline. The full complement of one small spine and five rays usually is attained by ca. 8.6 mm.

Pectoral rays first develop at ca. 7.8 mm, beginning from the upper pectoral base and proceeding downward. Five to nine upper rays are present by ca. 8.6 mm and the full complement of one small spine plus 17 to 18 rays is attained by ca. 12.7 mm, just before the transition to the juvenile stage. The upper pectoral rays lengthen much more than the lower rays as the fin grows, changing its outline from rounded to bluntly pointed.

Head Spination

Genyonemus lineatus acquires a number of small spines on the head during larval development. First among these is the spine at the angle of the preopercle at ca. 3.5 mm. A second spine is added just above the angle and a second row of preopercular spines begins developing at ca. 4.5 mm. Preopercular spination subsequently increases to between five and eight short spines in each row by the end of the larval period. Early juveniles may have as many as 12 spines in each row. An interopercular spine develops at ca. 5.5 mm. Interopercular spines vary in number between one and four throughout larval development. A subopercular spine develops at ca. 10.5 mm; as many as two or three may be present at the beginning of the juvenile stage. An opercular spine first appears at ca. 10.5 mm and remains throughout subsequent development.

A minute supracleithral spine emerges at ca. 6.6 mm. Up to three additional supracleithral spines may develop during the transition to juvenile.

The first supraocular spine becomes apparent at ca. 7.2 mm and is joined by an additional one or two spines by ca. 9.2 mm. As many as eight small supraocular spines may be present by the end of the transitional period.

Ossification

Initial skeletal ossification in *G. lineatus* begins with the cleithra. This is soon followed by the jaws and associated bones, some of the branchiostegals, opercular apparatus, and branchial apparatus, and the posterior skull. Premaxillary teeth appear next, followed by the first pharyngeal teeth. Dentary teeth arise later, about the beginning of vertebral and principal caudal fin ray ossification. Initiation of dorsal and anal soft fin ray and hypural ossification follows (Table 1). Anal fin spines precede the dorsal fin spines, which are followed by pelvic and then pectoral fin rays. All fin rays begin to ossify before their respective supporting structures. Somewhat more detailed descriptions of ossification follow.

In the smallest larva cleared (2.6 mm) the only stained structures are the cleithra and basioccipital. By ca. 4 mm the posterior parasphenotic has begun to ossify; parasphenotic ossification is complete and the exoccipitals begin to ossify at ca. 4.6 mm. Exoccipital ossification is essentially complete and posttemporal ossification is beginning at ca. 5.1 mm. Ossification of the frontal bones initiates at ca. 5.6 mm. The lacrimal ap-

TABLE 1.—Meristics of cleared and stained *Genyonemus lineatus* larvae. Larvae smaller than 4.64 mm are not included since fin rays and vertebrae are not ossified below this size. Specimens between dashed lines are undergoing notochord flexion.

Standard length (mm)	Vertebrae	Caudal rays		Dorsal rays	Anal rays	Pectoral rays	Pelvic rays	Branchiostegal rays (left side)	Gill rakers
		Primary	Secondary						
4.76		4						4	
5.12		4						5	0+0+5
5.56	11	10						7	(not ossified)
6.00	15	13						7	0+0+5
6.12	17	13						7	0+0+5
6.28	18	13						7	0+0+6
6.64	24	17		10	5			7	0+0+9
7.97	25	17	4	XII, 21	I, 11	4		7	3+1+9
10.46	26	17	6	(dam.), 22	II, 11	8	4	7	3+1+12
14.49	26	17	16	XIII, 22	II, 12	17	I, 5	7	4+1+15
32.00	26	17	17	XIV, 21	II, 11	I, 17	I, 5	7	(damaged)

pears at ca. 6.6 mm. By 8 mm additional bones ossified include the epiotic, sphenotic, supraoccipital, parietal, nasal, and the first circumorbital. The skull is essentially complete by ca. 14.5 mm.

None of the bones of the splanchnocranium are ossified at the beginning of the larval stage. By 4 mm they are all ossifying. Teeth first appear at ca. 4.3 mm; four are present on the premaxillary. Four to six dentary teeth are acquired by 5.6 mm; 18 premaxillary teeth are present at this size. Numbers of teeth increase through subsequent larval development: an 8 mm specimen has 26 premaxillary and 18-20 dentary teeth while a 14.5 mm specimen has 60 and more than 30, respectively.

Bones of the suspensorium begin ossifying at ca. 4.2 mm; the hyomandibular and symplectic are first. The ectopterygoid begins to ossify at ca. 6 mm and the quadrate at ca. 6.1 mm. The metapterygoid is next (8 mm). The suspensorium is essentially complete by 14.5 mm.

The opercular apparatus begins ossification at ca. 4 mm with the opercular and preopercular bones. The subopercular is added at ca. 4.2 mm and the interopercle at ca. 4.3 mm. Subsequent development consists of spination and further ossification of these bones.

Ossification of the branchial apparatus commences by 4 mm with the ceratobranchials of the outer two arches. By ca. 4.3 mm the ceratobranchials of four arches are ossified and the hypobranchials are just beginning to ossify. Two pairs of pharyngeal teeth appear at ca. 4.4 mm although the associated pharyngobranchial bones remain unossified until ca. 8 mm. Gill rakers on the outer arch first appear at ca. 5.1 mm—5 lower rakers are present. By 8 mm the number of gill rakers on the outer arch increases to three upper + one at the angle + nine lower rakers. Epibranchials begin to ossify at this size. The basibranchial ossifies between 10.5 and 14.5 mm but the hypohyal remains unossified into the early juvenile stage. The gill raker count at the end of the larval stage is 4+1+15 on the outer arch.

The first three branchiostegal rays are ossifying by 4 mm. A fourth branchiostegal ray and the posterior part of the ceratohyal begin ossification at ca. 4.2 mm; the fifth branchiostegal follows at ca. 4.6 mm. All seven branchiostegals, the epihyal, and interhyal are present by 5.6 mm. Ceratohyal ossification is complete and urohyal ossification is beginning by 6.3 mm. The hyoid apparatus is essentially complete by 14.5 mm, except for the unossified hypohyal.

Vertebral ossification begins with the anterior centra and proceeds posteriorly. Each vertebra ossifies from its ventral midline toward its dorsal midline. Ossification is first evident in a 5.6 mm specimen in the staining of the anterior seven vertebral centra and first four neural arches. In this same specimen centra 8 through 11 are stained ventrally only. By 6 mm the first 10 centra are completely stained, the next 3 on the ventral half only, and the next 2 on the ventral midline only. At this size the first 20 neural arches and 5 haemal arches (originating at the twelfth centrum) are becoming ossified. At 6.3 mm the first 18 centra, 20 neural arches, and 7 haemal arches are stained. By 6.6 mm the anterior part of the urostyle and all except the last centrum are ossified, along with 23 neural arches and 12 haemal arches. The final complement of 25 neural and 14 haemal arches is attained by 8 mm. The first four pleural ribs and three epipleural ribs develop during the transitional period, at ca. 14.5 mm.

The cleithra are the first bones to ossify in the pectoral girdle (by 2.6 mm). The supracleithra begin to ossify at ca. 4.6 mm and the postcleithra at ca. 5.6 mm. The first pectoral radial, coracoid, and scapula begin to stain during the transition to juvenile, after most of the pectoral rays are already ossified. The basipterygia of the pelvic girdle begin to ossify at this time as well.

The general sequence of dorsal and anal fin pterygiophore differentiation is described above under Fin Development. Ossification in both fins begins after 10.5 mm and is completed during the transition to the juvenile stage.

Pterygiophores of the anal spines are fused. Except for the pterygiophores of the first and last soft rays, each successive pair lies between adjacent haemal spines (Fig. 6).

The first two dorsal pterygiophores (bearing the first two dorsal spines) fuse during ossification. The pattern of dorsal pterygiophore placement between adjacent neural spines is somewhat variable (Table 2). Three predorsal bones develop during the transitional period.

The central three hypural elements begin to ossify at ca. 6.1 mm and all hypurals are ossified by 8 mm. These are distinguishable as separate elements throughout larval development. All but one of the principal caudal rays are associated with these elements; the other is associated with the haemal spine of the penultimate vertebra

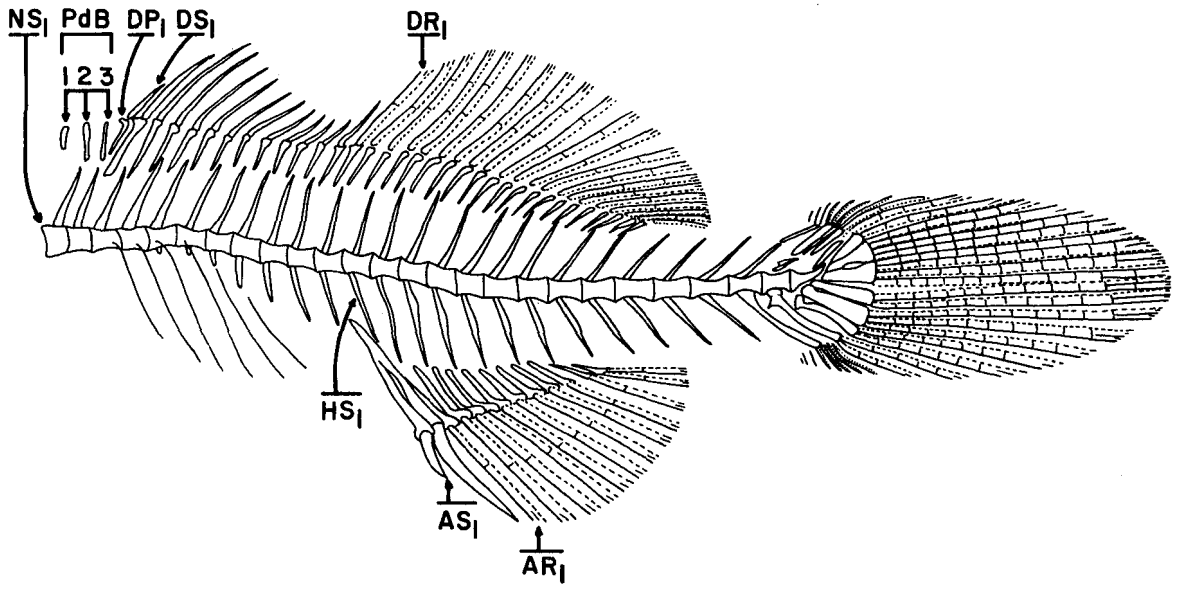

FIGURE 6.—Vertebral column and median fins of a 17.68 mm juvenile *Genyonemus lineatus*, showing typical relationships of dorsal and anal pterygiophores to neural and haemal spines. NS, first neural spine on the first vertebra; PB, predorsal bones; DS, first dorsal spine; DP, first dorsal pterygiophore; DR, first dorsal ray; HS, first haemal spine; AS, first anal spine; AR, first anal ray.

TABLE 2.—Number of dorsal pterygiophores between adjacent neural spines in *Genyonemus lineatus*.

Standard length (mm)	First dorsal pterygiophores	Second dorsal pterygiophores
32	1, 2, 1, 2, 1, 1, 2, 1, 1	1, 2, 2, 2, 2, 3, 2, 3, 2, 3
110	1, 2, 2, 1, 2, 3, 1, 2	2, 2, 2, 2, 2, 2, 2, 3, 2, 1
115	1, 2, 1, 2, 1, 2, 1, 2, 2	1, 2, 3, 2, 2, 2, 3, 2, 3
180	1, 2, 1, 2, 1, 1, 2, 2, 2	2, 2, 2, 3, 2, 2, 3, 3, 1
197	1, 2, 1, 2, 1, 2, 1, 2, 2	2, 2, 3, 2, 1, 3, 2, 3, 1

which is also associated with the first lower secondary caudal ray. Additional lower secondary caudal rays apparently are becoming associated with the haemal spine of the antepenultimate vertebra in specimens larger than 10.5 mm. The first (unossified) epural is associated with the first upper secondary ray at 8 mm. There are five supporting structures above the urostyle in specimens larger than 10.5 mm; the anterior three appear to be associating with the neural spine of the penultimate vertebra, and support five secondary caudal rays. Additional dorsal secondary rays in larger larvae are supported by the neural spine of the antepenultimate vertebra.

Proportions

Larval development of *G. lineatus* is a gradual process without rapid changes in body proportions: all body parts measured are linearly related to standard length through the larval period (Table 3). Since it is of little value to describe such growth only a summary of measurements is given (Table 4).

TABLE 3.—Summary of regressions of measurements of body parts (y) on standard length (x) of *Genyonemus lineatus* larvae.

y	n	r	Regression equation
Head length	164	0.99	$y = -0.24 + 0.32x$
Snout length	155	0.97	$y = -0.10 + 0.09x$
Eye diameter	165	0.98	$y = 0.04 + 0.09x$
Preanal length	166	0.99	$y = -0.51 + 0.59x$
Preanal fin length	85	0.97	$y = 0.20 + 0.62x$
Depth at pectoral insertion	165	0.98	$y = -0.003 + 0.30x$

COMPARISON WITH SIMILAR SPECIES

Genyonemus lineatus eggs closely resemble those of many other fish which spawn in the nearshore coastal waters off southern California. Consequently, separation to the species level is difficult and of doubtful practicality in the routine identification of ichthyoplankton samples.

Among the fish larvae commonly taken in inshore plankton samples along the southern California coast, *G. lineatus* most closely resembles

TABLE 4.—Summary of measurements (in millimeters) of *Genyonemus lineatus* larvae. The mean ($\bar{x}$), sample size (n), and standard deviation (SD) are given for each distance measured. Notochord flexion takes place in the size range demarked by dashed lines.

Size class (SL)	Head length			Snout length			Eye diameter			Preanal length			Preanal fin length			Depth		
	$\bar{x}$	n	SD	$\bar{x}$	n	SD	$\bar{x}$	n	SD	$\bar{x}$	n	SD	$\bar{x}$	n	SD	$\bar{x}$	n	SD
[1]1.51-2.00	0.48	12	0.06	—			0.20	13	0.02	.98	13	0.05	—			0.68	13	0.02
[1]2.01-2.50	0.46	10	0.03	0.10	10	0.03	0.20	10	0.01	.99	10	0.02	—			0.54	10	0.07
[2]2.51-3.00	0.49	6	0.03	0.13	6	0.02	0.22	6	0.02	1.04	6	0.06	—			0.54	6	0.06
[3]2.01-2.50	0.54	2	0.03	0.14	2	0.03	0.25	2	0.01	1.16	2	0.11	—			0.74	2	0.08
2.51-3.00	0.59	5	0.08	0.13	5	0.04	0.27	5	0.02	1.11	5	0.12	—			0.78	5	0.78
3.01-3.50	0.69	8	0.08	0.20	8	0.05	0.32	8	0.03	1.41	8	0.11	—			0.91	8	0.07
3.51-4.00	0.85	7	0.05	0.21	7	0.04	0.36	7	0.02	1.61	7	0.13	—			1.07	7	0.09
4.01-4.50	1.09	8	0.15	0.28	8	0.06	0.40	8	0.02	1.98	8	0.19	—			1.22	7	0.11
4.51-5.00	1.26	5	0.08	0.36	5	0.02	0.44	4	0.01	2.22	5	0.08	—			1.36	5	0.04
5.01-5.50	1.43	6	0.14	0.37	6	0.10	0.47	6	0.03	2.32	6	0.18	2.93	3	0.37	1.44	6	0.22
5.51-6.00	1.55	9	0.18	0.42	9	0.07	0.53	9	0.06	2.82	9	0.28	3.32	5	0.22	1.81	9	0.20
6.01-6.50	1.78	7	0.20	0.45	8	0.06	0.59	7	0.06	2.98	8	0.23	3.64	5	0.20	1.86	8	0.11
6.51-7.00	1.94	4	0.09	0.43	4	0.04	0.65	4	0.03	3.38	4	0.08	4.05	3	0.08	2.13	4	0.15
7.01-7.50	2.13	5	0.11	0.55	5	0.08	0.70	5	0.05	3.62	5	0.12	4.40	5	0.19	2.21	5	0.06
7.51-8.00	2.31	5	0.19	0.65	5	0.03	0.72	5	0.09	3.97	5	0.29	4.64	4	0.10	2.35	5	0.18
8.01-8.50	2.40	8	0.15	0.66	8	0.09	0.78	8	0.05	4.19	8	0.26	5.05	7	0.35	2.56	8	0.22
8.51-9.00	2.59	5	0.24	0.72	5	0.10	0.81	5	0.06	4.60	5	0.29	5.26	4	0.10	2.78	5	0.17
9.01-9.50	2.73	5	0.14	0.78	5	0.10	0.85	5	0.05	4.72	5	0.24	5.45	5	0.15	2.78	5	0.23
9.51-10.00	2.95	6	0.11	0.78	6	0.10	0.88	6	0.04	5.13	6	0.38	5.86	6	0.21	2.94	6	0.20
10.01-10.50	3.14	9	0.20	0.78	9	0.09	0.93	9	0.05	5.38	9	0.26	5.92	8	0.23	3.08	9	0.11
10.51-11.00	3.22	6	0.06	0.79	6	0.06	0.95	6	0.07	5.83	6	0.23	6.41	6	0.17	3.22	6	0.06
11.01-11.50	3.40	7	0.12	0.93	7	0.07	1.04	7	0.05	6.20	7	0.20	6.73	7	0.18	3.34	7	0.16
11.51-12.00	3.08	1	—	0.83	1	—	0.82	1	—	6.00	1	—	—			3.50	1	—
12.01-12.50	3.68	2	0.22	1.04	2	0.06	1.10	2	0.04	6.53	2	0.16	7.16	1	—	3.51	2	0.01
12.51-13.00	3.83	4	0.26	1.00	4	0.12	1.05	4	0.09	7.15	4	0.21	7.75	4	0.15	3.75	4	0.16
13.01-13.50	4.00	2	0.06	0.96	2	0.11	1.10	2	0.03	7.38	2	0.25	7.96	2	0	3.62	2	0.37
13.51-14.00	4.08	1	—	1.04	1	—	1.20	1	—	7.64	1	—	8.16	1	—	4.12	1	—
14.01-14.50	4.30	2	0.25	1.10	2	0.03	1.22	2	0.08	8.22	2	0.54	8.52	2	0.28	4.20	2	0.45
14.51-15.00	4.72	1	—	1.40	1	—	1.24	1	—	—			—			—		
15.01-15.50	—			—			—			—			—			—		
15.51-16.00	—			—			—			—			—			—		
16.01-16.50	5.24	1	—	1.56	1	—	1.36	1	—	9.32	1	—	10.04	1	—	4.80	1	—
16.51-17.00	—			—			—			—			—			—		
17.01-17.50	6.48	1	—	1.66	2	0.48	1.80	2	0.17	11.74	2	2.46	12.16	2	2.60	5.82	2	0.76
17.51-18.00	—			—			—			—			—			—		
18.01-18.50	4.84	1	—	1.28	1	—	1.32	1	—	8.48	1	—	8.76	1	—	4.32	1	—
18.51-19.00	5.64	1	—	1.60	1	—	1.48	1	—	11.64	1	—	11.96	1	—	5.64	1	—
19.01-19.50	5.20	1	—	1.52	1	—	1.52	1	—	10.40	1	—	10.80	1	—	5.00	1	—
19.51-20.00	5.52	1	—	1.48	1	—	1.68	1	—	11.36	1	—	11.84	1	—	5.80	1	—

[1]Reared specimens, yolk-sac stage.
[2]Reared specimens, postyolk-sac stage.
[3]Field specimens.

the sciaenids *Seriphus politus* and *Roncador stearnsii* (Moser and Butler[5]), the haemulid *Anisotremus davidsonii*, and the scombrid *Scomber japonicus*. *Genyonemus lineatus* is principally a winter spawner while the other species are principally summer spawners, but some overlap occurs in spring and fall.

Scomber japonicus is distinct in having 30-31 myomeres versus 25-26 for the other species. Yolk-sac larvae of *A. davidsonii* are undescribed; however, yolk-sac larvae of the Atlantic haemulids *Haemulon plumierii* (Saksena and Richards 1975) and *Orthopristis chrysoptera* (Hildebrand and Cable 1930) have an anterior oil droplet in contrast with the posterior oil droplet typical of sciaenids. *Seriphus politus* yolk-sac larvae lack the dorsal pigmentation and banded pattern typical of *G. lineatus* (Moser and Butler footnote 5). *Roncador stearnsii* closely resemble *G. lineatus* until late in the yolk-sac stage (Moser and Butler footnote 5) when *G. lineatus* may be distinguished by a single (rarely two) large dendritic nape melanophore extending into the finfold rather than two or more smaller nape melanophores not extending into the finfold. *Roncador stearnsii* typically has heavier anterior gut pigment than *G. lineatus*.

Characters useful for separating *G. lineatus* from similar larvae are summarized in Table 5. The nape melanophore separates *G. lineatus* larvae from *A. davidsonii* and *S. politus* for as long as it remains visible. *Anisotremus davidsonii* may be distinguished from *G. lineatus* to at least as small as 2.6 mm by ventral pigmentation, and by dorsal fin ray counts in older specimens

[5]H. G. Moser, and J. L. Butler. Description of the early life history stages of croakers (Family Sciaenidae) occurring off California. Manuscr. in prep. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038. Pers. commun. February 1981.

TABLE 5.—Selected characters of larvae which resemble *Genyonemus lineatus*.

Species	Myomeres	Dorsal fin rays	Anal fin rays	Preanal lengths (% of SL) mean (range)	Depth (% of SL) mean (range)	Nape melano-phore	Melanophore above hindgut	Number of midventral trunk melanophores mode (range)
Anisotremus davidsonii	25-26	XI-XII, 14-16	III, 9-11	[1]48 (43-52)	22 (19-25)	No	Large	14 (12-18)
Genyonemus lineatus	25-26	XII-XV+1, 18-25	II, 10-12	[2]47 (38-53)	30 (26-34)	Yes	Small, often absent	Decreases with growth (2-21)
Roncador stearnsii	25-26	IX-X+1, 21-25	II, 7-9	[3]40 (33-49)	24 (18-31)	Yes	Large	Decreases with growth (5-29)
Seriphus politus	25-26	VII-IX+1, 18-21	II, 21-23	[4]46 (40-54)	26 (23-29)	No	Usually present, usually large	Decreases with growth (2-24)
Scomber japonicus	30-31	VIII-XI+1, 9-14+4-6	II, 9-12+4-6	[5]53 (46-59)	25 (23-27)	No	Two or more	[6]Decreases with growth (10-26)

[1]52 specimens, 2.6-8.1 mm SL.
[2]94 specimens, 2.6-9.7 mm SL.
[3]19 specimens, 2.2-4.3 mm SL.
[4]50 specimens, 3.6-9.8 mm SL.
[5]Taken from Kramer 1960, table 5. Larvae 4.00-9.99 mm SL.
[6]20 specimens, 2.2-5.5 mm SL.

(Table 5). *Anisotremus davidsonii* commonly has a uniform row of one midventral, postanal trunk melanophore per myomere after the first postanal myomere, and nearly always has a large melanophore anteriorly on the ventral midline of the gut. As many as four smaller melanophores may also be arrayed along the midline of the gut. *Genyonemus lineatus*, in contrast, rarely displays uniformity in the midventral, postanal melanophore series (those at myomeres 9-10 and 16-18 typically are distinctly larger), and the ventral gut pigmentation usually is not on the midline. *Genyonemus lineatus* is deeper bodied and its hindgut turns down at a much steeper angle than that of *A. davidsonii*.

Seriphus politus lacks the banded pattern of young *G. lineatus* larvae and usually displays an approximately uniform series of small, postanal midventral melanophores (Moser and Butler footnote 5). Shortly before anal anlage development two melanophores of the midventral series typically enlarge in *S. politus*; these lie at myomeres 11-13 and 19-21 versus 9-10 and 16-18 for *G. lineatus*. During anal fin development the anterior of these migrates internally in *G. lineatus* but remains external in *S. politus*. Specimens smaller than 8 mm are often distinguishable by the presence and size of the melanophore above the hindgut (Table 5). The melanophore on the anterior visceral mass also distinguishes these two after it has assumed its ventral position in *G. lineatus*. *Seriphus politus* larvae are somewhat more slender than *G. lineatus*. Anal fin ray counts separate older specimens.

Roncador stearnsii larvae closely resemble *G. lineatus* (Moser and Butler footnote 5). Before acquisition of fin rays *R. stearnsii* may often be distinguished by having rather heavy anterior gut pigmentation (usually light in *G. lineatus*), by the large melanophore above the hindgut, and by one to three pairs of internal melanophores along either side of the midline of the head behind the eye at the level of the floor of the otic capsule plus one or two medially under the forebrain (these often give the appearance of a stripe through the eye, lacking in *G. lineatus*). Dorsal and anal fin ray counts separate older specimens.

DISTRIBUTION

Genyonemus lineatus off southern California spawns principally from October through April (Skogsberg 1939; Goldberg 1976). This is consistent with our study off San Onofre: larvae were taken from January (initiation of our study) through early June 1978, and early October 1978 through late June 1979, with abundance peaks in March 1978 and February 1979 (Walker et al. footnote 2). Few larvae were taken in June or October.

The smallest larval *G. lineatus* were most abundant in the epibenthos (lower 0.5 m) shoreward of about 3.9 km (21 m isobath) and in the water column above the epibenthos between 2 and 3.9 km from shore (13 and 31 m isobaths). During development, they move shoreward and tend to become more strongly epibenthic. This is evidenced by the low abundance of larvae between ca. 3.8 and 6.4 mm in the water column and offshore of 3.9 km. Larvae larger than 6.4 mm are virtually absent above the epibenthos. The abundance peak for *G. lineatus* larvae larger than ca. 3.8 mm is between 1 and 2 km from shore (9 to 12 m isobaths)[6]. Brewer et al. (in press) noted a similar distribution in their study of the

[6]Barnett, A. M., A. E. Jahn, P. D. Sertic, and W. Watson. 1980. Long term spatial patterns of ichthyoplankton off San Onofre and their relationship to the position of the SONGS

ichthyoplankton from the shallow coastal waters of the Southern California Bight.

SUMMARY

1) The *G. lineatus* egg is pelagic, transparent, and spherical with an unsculptured chorion, unsegmented yolk and a single clear to yellowish oil droplet. The live egg averages 0.85 mm in diameter and the oil droplet 0.23 mm. Hatching occurs about 52 h after spawning.

2) Yolk-sac larvae hatch at about 1.8 mm in an undifferentiated state with unpigmented eyes, straight tubular gut, large yolk sac, and posterior oil droplet. Pectoral buds develop during the second day after hatching, the mouth opens and gut begins differentiating on the third, eye pigmentation is complete on the fifth, and yolk exhaustion and swim bladder inflation occurs on the sixth.

3) Yolk-sac larvae initially are pigmented primarily on the dorsum. During the yolk-sac period melanophores migrate toward the ventral midline.

4) Pigmentation is largely restricted to the ventrum and dorsal surface of the gut through much of the larval stage. A nape melanophore and the large internal melanophore on the lower anterior midline of the visceral mass are characteristic. A barred pattern develops during the transition to the juvenile stage.

5) The order of ossification (first uptake of alizarin stain) is: cleithra (2.6 mm); splanchnocranium, hyoid apparatus, opercular apparatus, branchial apparatus, skull (4 mm); caudal fin rays (4.8 mm); vertebrae (5.6 mm); second dorsal and anal fin rays and hypural complex (6 mm); first dorsal and pelvic fin rays (7.2 mm); and pectoral fin rays (7.8 mm). Each fin ray begins to ossify before its supporting structure.

6) The principal characters useful for separating *G. lineatus* from similar larvae are the nape melanophore, the anterior visceral mass melanophore when in its ventral position, the larger midventral melanophores at myomeres 9-10 and 16-18, and fin ray and myomere counts.

7) *Genyonemus lineatus* spawns mainly from October through April, with peak spawning in late winter.

8) Larvae are located principally within 4 km from shore. As they develop they tend to move shoreward and into the lower 1 m of the water column.

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