LARVAL DEVELOPMENT OF BLUE GRENADIER, *MACRURONUS NOVAEZELANDIAE* (HECTOR), IN TASMANIAN WATERS

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ABSTRACT

The development of *Macruronus novaezelandiae* is described and illustrated from both reared specimens and larvae from Tasmanian waters. Eggs of *M. novaezelandiae* are pelagic, spherical (1.08–1.18 mm diameter), and have a single oil droplet (0.36–0.42 mm diameter). Eggs hatch after 55–60 hours at 14°–19°C. Larvae are 2.2–2.3 mm at hatching. Characteristic pigmentation, a myomere count of 78–80, and the sequence of fin development separate *M. novaezelandiae* from other known gadiform larvae. Development is direct, with no marked change in body morphology. Fin development proceeds in the sequence: second dorsal, anal, first dorsal, pelvic, caudal, pectoral. However, adult fin complements are reached in the sequence: first dorsal, pelvic, anal, second dorsal, caudal, pectoral.

Caudal development is late in *Macruronus*. Flexion begins at 20 mm and is not complete until 28 mm. The caudal fin is based on two ural centra, four hypurals, two epurals, and a parhypural. X and Y bones are present although they are not readily distinguishable from dorsal and anal pterygiophores.

The genus *Macruronus* comprises four nominal species, which occur in southern temperate continental shelf and slope regions. Two species, *Macruronus novaezelandiae* and *M. magellanicus* support commercial fisheries. The blue grenadier, *M. novaezelandiae*, forms the basis of fisheries in New Zealand and Australia where total annual catches range up to 97,750 and 1,100 t respectively (Patchell 1982; Wilson 1981, 1982). *Macruronus magellanicus* is fished commercially off South America. The remaining species, *M. maderensis* and *M. capensis*, are known only from a limited number of specimens (Svetovidov 1948; Cohen 1986). Despite their economic importance and widespread distribution, very little is known of the early life history of any member of the genus. Patchell (1982) identified winter spawning grounds on the west coast of the South Island for New Zealand populations of *M. novaezelandiae* and similarly Wilson (1981, 1982) has suggested a winter spawning, on the west coast of Tasmania, for Australian *M. novaezelandiae*. This paper presents the first published information on the larvae of *Macruronus*.

In 1984, the Division of Fisheries Research of the Commonwealth Scientific and Industrial Research Organization established a multidisci-plinary program to investigate the biology and ecology of blue grenadier in Tasmanian waters. An integral part of this program was a study of larval ecology. As such, it was first necessary to establish criteria for the identification of blue grenadier larvae. This paper describes the larval development of *M. novaezealandiae* from Tasmanian waters.

MATERIALS AND METHODS

Specimens were obtained from samples collected aboard the CSIRO Fisheries Research Vessel *Soela* between April 1984 and September 1985. Details of sampling strategies, locations, and procedures will be described in a subsequent manuscript. Larvae were obtained by sampling with a rectangular midwater trawl (RMT 1+8; Baker et al. 1973), a 1 m diameter ring net (500 μm mesh), and free-fall, vertical drop nets of 64 μm and 200 μm mesh (Heron 1982). Juvenile specimens were obtained with an Engels 352 pelagic trawl fitted with a 10 mm liner.

Newly hatched larvae were reared from eggs stripped and fertilized at sea. Eggs and milt stripped from ripe adults trawled from 500 m were mixed in 1 L plastic jars filled with seawater. Despite the jars being located in a seawater bath, incubation temperatures varied considerably (14°–19°C). On return to the laboratories at Hobart, the eggs were transferred to 2 L glass jars and placed in a constant temper-

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ature incubation chamber set at 14.0° ± 0.2°C. Incubation jars were not aerated, and no attempt was made to feed the larvae.

All specimens used for description were fixed in a 10% formalin-seawater solution buffered with sodium β-glycerophosphate and later transferred to a 5% solution.

This description is based on a series of 74 larvae, 2.2–34.2 mm in length, although comments on pigment and meristic variability stem from routine examination of several hundred specimens. A representative series of larvae is deposited with the South Australian Museum, Adelaide, South Australia.

Developmental terminology follows Ahlstrom et al. (1976). Body measurements follow Matarese et al. (1981). Length measurements are reported as notochord length, NL (i.e., from the snout tip to the end of the notochord) in preflexion and flexion larvae, and standard length, SL (i.e., from the snout tip to the posterior margin of the superior hypural elements) in postflexion larvae and juveniles. Larvae were measured under a dissecting microscope fitted with an ocular micrometer and a camera lucida. Juveniles were measured with vernier calipers.

Meristic counts and examination of ossification sequences were made on specimens cleared and stained using Alizarin Red S-KOH-glycerine (Hollister 1934). Caudal osteology follows Inada (1981), Marshall and Cohen (1973), and Monod (1968).

Vertebral counts include the first vertebrae, the neural spine of which is fused to the supraoccipital crest (Marshall 1966), and both ural centra. Vertebral centra were counted as ossified only when a complete band of stain connected both neural and haemal spines.

RESULTS

Identification of *M. novaezelandiae* larvae was based on their typical gadiform morphology (large head, compact gut, tapering body form), myomere count, and the development of confluent dorsal-caudal-anal fins (see section on Distinguishing Features). Identification of field-collected specimens was confirmed by comparison with reared larvae.

Distinguishing Features

Prior to median fin development, myomere counts are useful in separating *M. novaezelandiae*

larvae (78–80) from similarly pigmented morid (41–72), macrourid (10–16 + 70 > 100), gadid (39–64) and other known merlucciid larvae (48–58) which they superficially resemble (Marshall and Iwamoto 1973; Fahay and Markle 1984; present study).

Both *M. novaezelandiae* and most morid larvae show moderately pedunculate pectoral fins, a feature common in gadiform larvae with delayed caudal development (Fahay and Markle 1984). Macrourid larvae, in contrast, have very prominently stalked pectorals and can further be separated from *M. novaezealandiae* and most morids by precocious development of the pelvic fin.

Size at caudal flexion and the sequence of fin development are also useful in separating *M. novaezelandiae* from all *Merluccius* species. In *Merluccius*, notochord flexion generally begins at about 9 mm and the caudal fin is the first to form (Dunn and Matarese 1984; Fahay and Markle 1984). *Macruronus novaezelandiae* larvae do not begin caudal flexion until approximately 20 mm, and the caudal fin is the second last to form.

Macruronus novaezelandiae larvae have 1–3 prominent melanophores along the ventral midline of the tail (although variable in appearance, see section on Trunk and Tail Pigmentation) and a double series of dorsal melanophores. When expanded, melanophores in these two regions coalesce to give the appearance of a broad postanal band. Postanal banding patterns are widespread in gadoid larvae (Fahay and Markle 1984); however, unlike many gadoid larvae, *M. novaezelandiae* lacks pigment at the notochord tip.

At larger sizes *M. novaezelandiae* larvae develop long-based dorsal and anal fins confluent with the caudal fin. Other gadoid larvae with this configuration have markedly different pigmentation (see Fahay and Markle 1984 for details). Ophidiiform larvae have confluent dorsal, caudal, and anal fins but can be separated from *M. novaezelandiae* by their lack of a separate first dorsal fin and general lack of body pigment (see Gordon et al. 1984).

Development

Embryonic development has not been treated in detail here as it is the subject of a manuscript in preparation by G. Patchell (Fisheries Research Centre, Wellington, New Zealand).

The pelagic eggs of blue grenadier are spherical, with an unsegmented yolk and a smooth cho-

rion. Late-stage eggs are 1.08–1.18 mm in diameter with a single oil droplet of 0.36–0.42 mm diameter (Fig. 1A). Reared larvae hatch at 2.2–2.3 mm after 55–60 hours (14°–19°C). Newly hatched larvae have a posteriorly positioned oil droplet and adopt a head down position in rearing containers. Yolk absorption was incomplete in specimens reared to 3.7 mm (6 days posthatch), although the smallest field-collected larvae (3.6 mm) had already completed yolk absorption. The anus opened laterally to the right in all reared larvae and 95% of field-collected larvae. The anus becomes symmetrical by 5.1 mm. A lateral anal opening in *M. novaezelandiae* is consistent with the developmental pattern reported for other gadiform species (Marak 1967; Matarese et al. 1981; Fahay and Markle 1984; Dunn and Vinter 1984).

Field-collected larvae are moderately elongate with the greatest body depth (16–22% body length) occurring at or near the pectoral fin base (Table 1). Head length as a proportion of body length (BL) remains relatively constant at about 22% BL throughout the larval phase, decreasing to about 17% BL in juveniles. Eye diameter decreases from 9% BL in preflexion larvae to 4% BL in juveniles. Depth at anus remains relatively constant at about 13% BL in larvae and juveniles. Distances from the snout tip to the first dorsal fin and from the snout tip to the anal fin decrease slightly during development from about 27% BL to 21% BL and 51% BL to 46% BL respectively.

in the number of melanophores and their degree of expansion. Although Badcock and Merrett (1976) suggested the appearance of melanophores can change on a diurnal rhythm, in the blue grenadier larvae examined, there was no conspicuous relationship between time caught and melanophore expansion.

Head Pigmentation

Newly hatched larvae (2.2–2.3 mm) have melanophores concentrated in front and behind the eye (Fig. 1B). Melanophores increase in number and extend over the sides of the head and snout by 3.3–3.5 mm (reared larvae, Fig. 1C). Melanophores migrate dorsally to the top of the head by 3.6 mm (Fig. 1D). Eyes become pigmented at this size in reared larvae. By 4.5 mm, the dorsal pigment on the head consists of a group of 3–11 melanophores scattered over the hindbrain and posteriorly to above the cleithrum. Pigment gradually extends over the midbrain, with 1 or 2 melanophores usually present between the eyes by 5.3 mm. Melanophores develop externally over these initial mid- and hindbrain spots and extend posteriorly as a double row to the dorsal fin anlage by 7.2 mm. Dorsal pigment gradually intensifies: melanophores increase in number and form a cap over mid- and hindbrains by 16.0 mm. Melanophores extend down between the eyes to the tip of the maxilla by 12.0 mm. Internal

TABLE 1.—Body proportions of larvae and juveniles of *Macruronus novaezelandiae* (expressed as percentage NL or SL): mean, standard deviation, range.

| Body proportions sample size	Preflexion 42			Flexion 4			Postflexion 4			Juvenile 2		
	X	SD	range	X	SD	range	X	SD	range	X	SD	range
length (mm)	8.9	4.5	(3.6–19.0)	23.5	2.3	(20.6–26.1)	30.0	2.9	(27.6–34.2)	189.0	1.4	(188.0–190.0)
head length	22.7	1.7	(18.3–24.7)	23.7	1.0	(22.3–24.7)	22.3	1.4	(20.5–23.6)	17.6	0.4	(17.3–17.9)
eye diameter	9.2	0.7	(8.1–10.3)	7.9	0.4	(7.3–8.3)	7.3	0.7	(6.5–8.0)	4.2	0.4	(4.4–5.2)
snout length	6.1	0.9	(4.6–7.7)	6.2	0.6	(5.7–7.0)	5.9	0.5	(5.4–6.5)	4.9	0.1	(4.8–5.0)
depth at pectoral	22.3	1.7	(21.0–24.4)	17.9	0.6	(17.2–18.5)	16.6	2.0	(13.7–18.5)	13.1	0.1	(13.0–13.2)
depth at anus	12.0	2.4	(8.2–15.2)	13.1	0.3	(12.6–13.4)	13.0	0.8	(12.3–13.8)	12.7	0.6	(12.3–13.1)
snout to first dorsal fin	27.5	1.3	(25.2–29.3)	26.6	0.8	(26.0–27.7)	25.3	0.8	(24.2–26.0)	20.7	0.2	(20.6–20.9)
snout to anal fin	51.4	0.9	(50.0–52.6)	50.4	0.5	(49.6–50.6)	46.6	1.5	(45.0–48.4)	46.5	1.2	(45.7–47.4)

Pigmentation

Although pigmentation in *M. novaezelandiae* is variable, certain features persist that, when combined with meristic and morphometric information, enable identification. Variation in the appearance of pigmentation is a result of differences

pigment expands over the forebrain in larvae from 9.0 to 15.0 mm.

Ventral pigment on the head first develops in 4.2 mm larvae as 3–5 melanophores between the dentaries. The number of melanophores increases to 10–12 by 12.0 mm.

FIGURE 1.—Development of *Macruronus novaezelandiae:* A) Late stage egg 1.08 mm diameter, oil droplet 0.37 mm diameter, B) 2.2 mm.; C) 3.5 mm.; D) 3.6 mm.; E) 5.3 mm.; F) 7.2 mm.; G) dorsal view of above; H) 12.0 mm.; I) 24.2 mm. postanal myomeres omitted. A-C reared specimens, D-I field-collected.
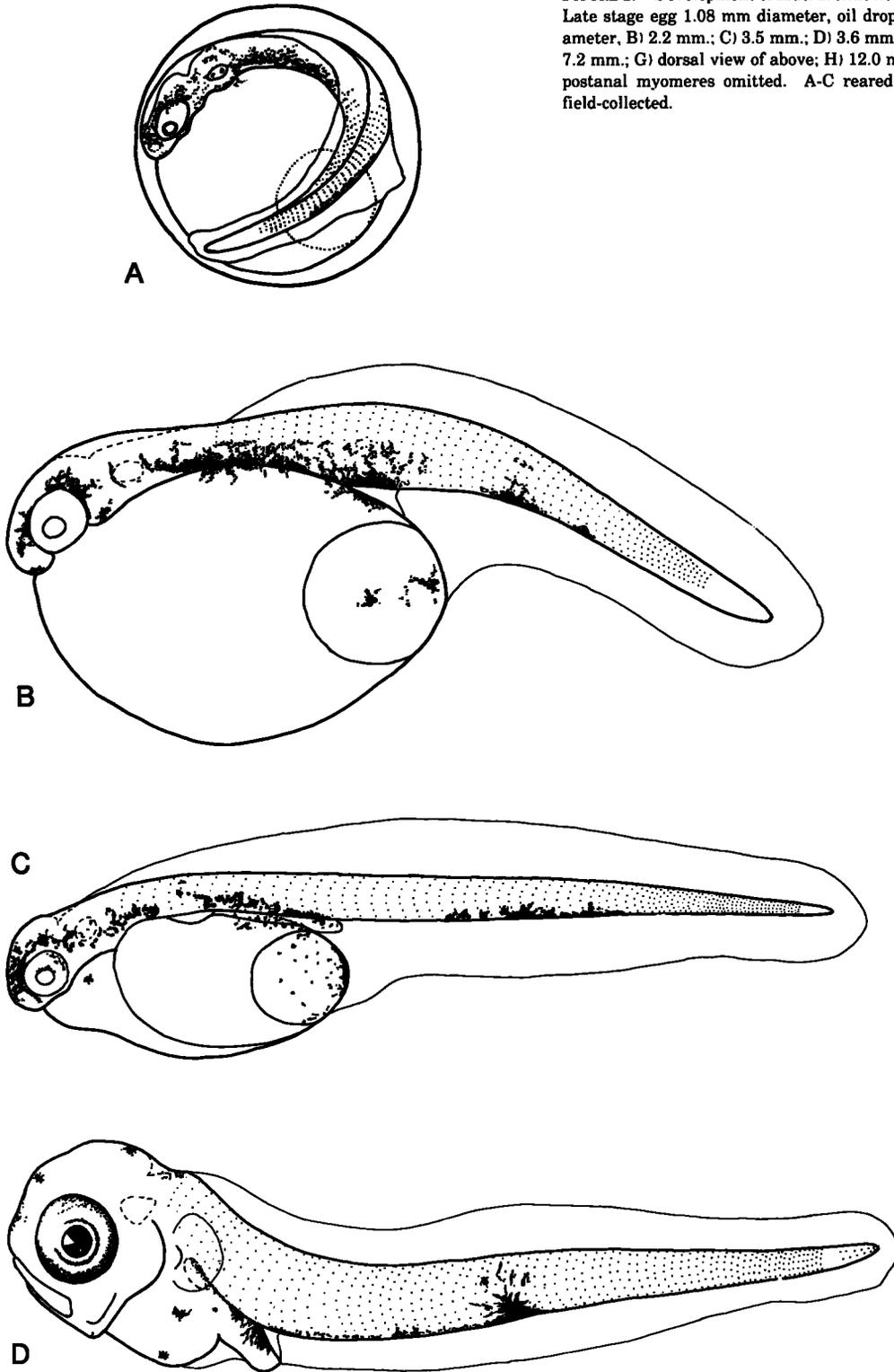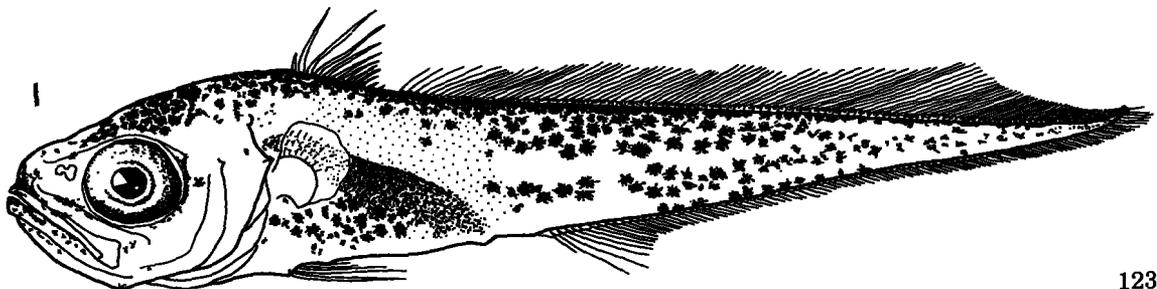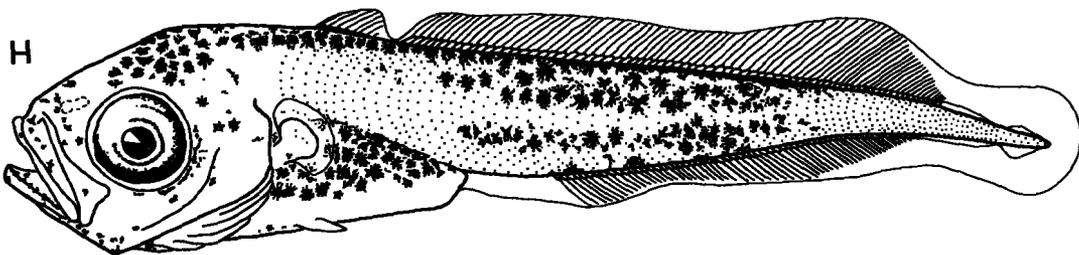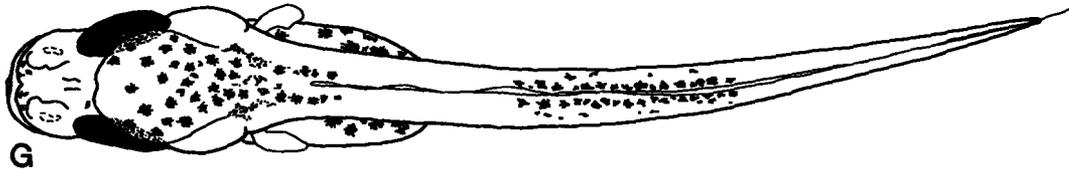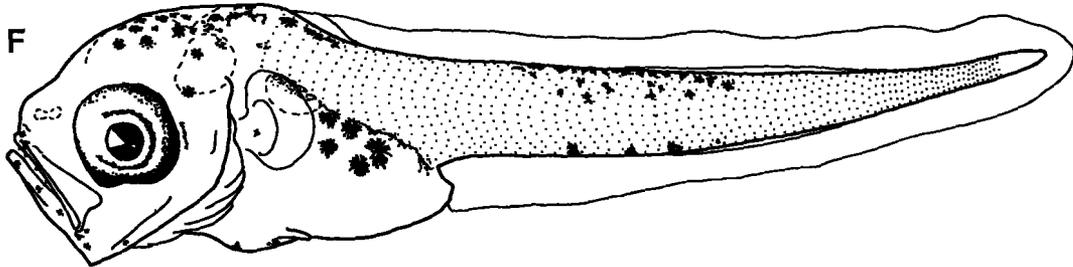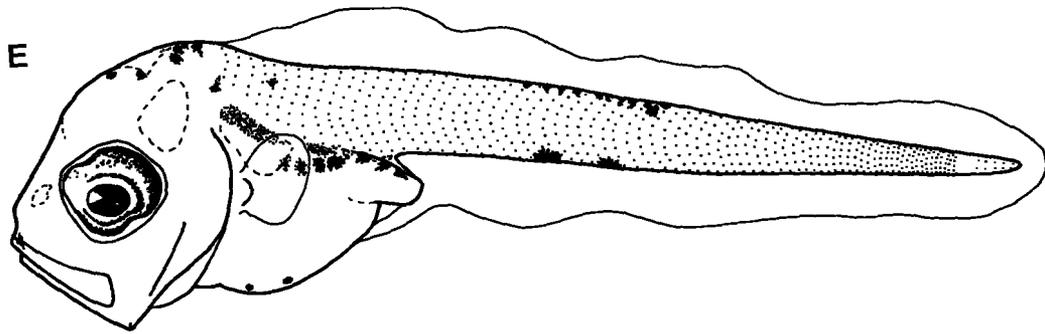
The onset of dentary pigment is variable; no pigment may be present on some larvae as large as 7.0 mm. Most larvae develop 1 or 2 melanophores over the posterior section of the dentary by 5.3 mm and add melanophores anteriorly along its length, with 5 or 6 usually present by 7.1 mm.

Two melanophores are often present around the otic capsule by 7.0 mm, but they are obscured by overlying tissue in 10.0 mm larvae. Scattered melanophores develop over the pterotic region by 25.0 mm, but the operculum and preoperculum remain largely unpigmented, even in the largest specimen examined (34.2 mm).

Trunk and Tail Pigmentation

Newly hatched larvae have melanophores on the body above the yolk sac and ventrally on the tail. Some pigment is also present on the yolk sac near the developing gut and scattered over the oil droplet. Pigment forms a cap over the gas bladder by 4.2 mm. Melanophores are gradually added to the lateral surfaces of the gut throughout the larval period until the entire gut (including the ventral surface) becomes pigmented by 30.0 mm.

Dorsal pigment first appears on larvae 3.8–4.5 mm as scattered melanophores at approximately 60% NL. Melanophores rapidly increase in number and form a double row, extending from 51% to 67% NL in larvae of 5.0 mm. Lateral melanophores may also develop above the body midline in this region. Concurrently, a similar double row of melanophores appears and extends posteriorly from the head (Fig. 1G). The head and tail rows join by 10.5 mm. Melanophores appear posteriorly in the caudal region by 29.0 mm forming a twin series one either side of the developing dorsal fin. Pigment also appears internally on the dorsal surface of the vertebrae in larvae of 9.5 mm and extends anteriorly to approximately 50% SL and posteriorly to the last vertebrae by 34.0 mm.

Single melanophores appear on the dorsal fin ray bases by 14.0 mm and are present on all bases by 29.0 mm.

Pigment along the ventral midline of the tail appears in newly hatched larvae as a diffuse region that extends posteriorly from the yolk sac to 75–82% NL. This contracts to 1–3 melanophores (most commonly 2) located 52–65% NL in larvae of 3.8–4.0 mm. Additional melanophores (up to 6) may appear later, but the initial 1–3 melanophores persist throughout the larval period. In larvae larger than 7.0 mm, the initial 1–3 melanophores appear internally above the anal fin ray bases and are gradually obscured by both overlying musculature and external melanophores. These ventral melanophores on the tail are a useful diagnostic character, although their appearance varies, depending on their degree of expansion. This variability in melanophore appearance is particularly evident in small larvae where expanded ventral melanophores may extend over the lateral surfaces of the body to almost the dorsal area (Figs. 1D, 2).

Lateral pigment gradually intensifies throughout the larval period, excepting the area immediately above the gut, which remains largely devoid of pigment even in the largest specimen (34.2 mm).

Morphological Variability

Macruronus novaezelandiae larvae showed some size variation in development. In general, specimens captured in ring net and RMT samples appeared to develop features at slightly smaller sizes than those taken from drop net samples. This is likely a result of differential shrinkage of specimens caught by the different capture systems. Hay (1981) reported that considerably more shrinkage occurred in Pacific herring when larvae were killed prior to fixation and that shrinkage increased with tow length. Ring net and RMT tows varied in duration from 15 to 110 minutes, with most larvae dead by the time the net was retrieved and the catch fixed. Drop net sampling, in contrast, lasted for, at most, 3 minutes duration, and many larvae were still alive on fixation. Some variability in development can also be expected in field-collected larvae as a reflection of past history (e.g., feeding success), although it is unlikely such variations would account for the observed differences between larvae caught by different techniques.

Meristics and Osteology (Table 2)

Head and Axial Skeleton

In laboratory-reared larvae, jaw development was first visible after 3.5 days (posthatch) with a functional mouth present in larvae of 5.5 days (3.7 mm). Pigmentation of the eyes also occurred at this time suggesting that larvae were ready for first feeding. The smallest larva stained was a field-collected specimen 3.7 mm NL. The maxilla, premaxilla, dentary, and cleithrum were all ossified in this specimen.
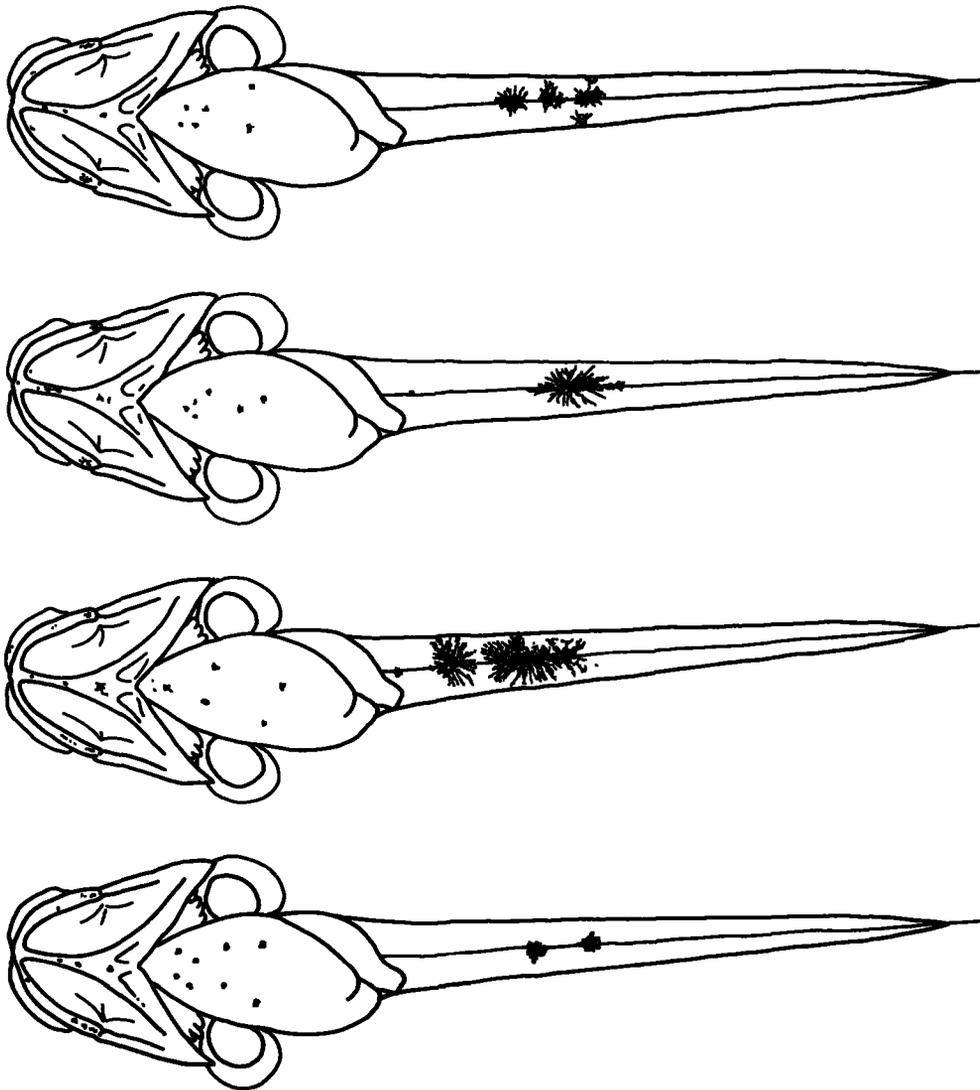
FIGURE 2.—Variability of ventral pigment on the tail in 4.9 mm larvae of *Macruronus novaezelandiae*.

Ossification of branchiostegals begins in larvae of 4.6 mm, with the full complement of 7 ossified by 11.5 mm. Gill rakers are first discernible in larvae of 9.4–9.9 mm with the full complement of 7 + 22 − 23 present by 28.9 mm.

Ossification of neural and haemal spines generally precedes that of the vertebral centra. Ossification of centra, neural spines, and haemal spines occurs sequentially from anterior to posterior proceeding slowly in larvae less than 9.0 mm in length and then more rapidly until the full complement is ossified by 23.2 mm. Elements associated with the caudal complex are the last to ossify.

Fins

Completion of fin development in *M. novaezelandiae* occurs in the sequence: first dorsal and pelvic (almost simultaneously), anal, second dorsal, caudal, pectoral.

Pelvic fins first appear in larvae of 5.7–5.8 mm as slight swellings either side of the gut. They do not form distinct buds until 6.9 mm. Ossification

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TABLE 2.—Meristic counts from cleared and stained larval and juvenile *Macruronus novaezelandiae*. Specimens between dashed lines are undergoing notochord flexion.   a = specimen damaged; b = juveniles not stained.

Length (mm)	Fin rays				Branchi-ostegal rays	Gill rakers			Total centra	Neural spines	Haemal spines	Caudal elements
	dorsal	anal	pectoral	pelvic		upper	lower	total				
3.7	—	—	—	—	—	—	—	—	—	—	—	—
3.9	—	—	—	—	—	—	—	—	—	1	—	—
4.2	—	—	—	—	—	—	—	—	—	1	—	—
4.6	—	—	—	—	1	—	—	—	—	2	—	—
4.8	—	—	—	—	1	—	—	—	—	2	—	—
5.2	—	—	—	—	3	—	—	—	—	2	—	—
6.0	—	—	—	—	3	—	—	—	—	3	—	—
7.4	—	—	—	—	5	—	—	—	5	6	—	—
9.4	4 + 28	18	—	3	6	—	8	8	42	55	37	—
9.9	0 + 19	4	—	—	6	—	6	6	38	54	34	—
11.5	9 + 74	60	—	4	7	—	12	12	55	58	42	—
16.3	12 + 84	73	4	8	7	1	15	16	70	70	55	3
17.4	12 + 86	76	4	8	7	3	15	18	71	70	55	3
19.8	13 + 87	86	3	8	7	5	15	20	73	74	57	4
23.2	12 + 100	90	9	8	7	5	17	22	76	74	57	5
26.1	13 + 99	90	13	8	7	5	21	26	76	74	57	5
28.9	13 + 99	91	9	8	7	7	22	29	78	76	57	a
188	13 + 94	90	20	8	7	7	22	29	b	b	b	b
190	13 + 96	90	20	8	7	7	23	30	b	b	b	b

may start as early as 9.4 mm with the full complement (8 rays) present by 16.3 mm. Ossification proceeds from the outer to the innermost rays.

The second dorsal fin anlage is visible in larvae of 5.7 mm. Bases are first visible by 6.9 mm, with ray ossification commencing by 7.3 mm. Although the anal fin anlage does not form until 6.9 mm, complete ossification is reached before that of the second dorsal. Distinct anal fin bases are first visible in 7.2 mm larvae and ossification has consistently begun by 9.9 mm. The full complement of anal rays is present by 21.0 mm and for the second dorsal, by 23.2 mm.

The first dorsal starts development slightly later than the second dorsal, although it is the first fin to complete ossification. The full complement of 12 or 13 elements is present by 16.3 mm.

Pectoral buds were first observed in larvae 4.5 days posthatch (3.2 mm). However, the pectoral fin is the last to complete development. Ossification of pectoral rays starts by 16.3 mm; a 34.2 mm specimen had only 15 ossified rays, still short of the 20 rays of juveniles. Sequence of ossification is from upper to lower.

The caudal fin anlage first appears on the ventral surface of the notochord just anterior to the tip in larvae of 10.4 mm. Flexion begins at 20 mm and is usually complete by 28 mm. Ossification of all caudal elements was incomplete in a 34.2 mm specimen. Insufficient material of the appropriate size was available to define the completion of caudal ossification.

The caudal complex in *M. novaezelandiae* is based on two ural centra, two epurals, a superior hypural (HP3 + 4), inferior hypural (HP1 + 2), and a parhypural (Fig. 3). Eight to nine rays articulate with these elements—one or two rays on the second epural, three rays on the superior hypural, two on the inferior hypural, and one ray each on the first epural and the parhypural. Single rays also articulate with the elongate neural and haemal spines of the first preural centrum. X and Y bones are present although they are not readily distinguishable from dorsal and anal pterygiophores. Total caudal fin ray counts are low (12 or 13).

Additional caudal structures occurred in one of the six specimens examined. This specimen had a twin haemal spine on the first preural centrum and greatly elongated haemal spines on preural centra 3–8 (1.3–1.4 times the length of corresponding neural spines, Fig. 3).

DISCUSSION

The general morphology and pigmentation of *M. novaezelandiae* larvae show broad similarities to *Merluccius* and to gadine gadids. Characteristic differences between *M. novaezelandiae* and *Merluccius* species occur in fin structure and the sequence of fin development. In *Merluccius*, the caudal fin is the first to form, followed by the pelvic. In *Macruronus*, caudal development is late with the caudal fin being the second last to
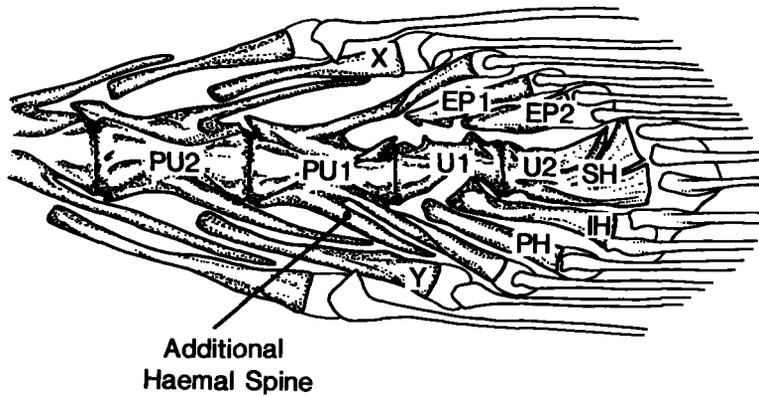
FIGURE 3.—Caudal osteology of a juvenile *Macruronus novaezelandiae* (181 mm SL). X = X bone, Y = Y bone, EP = epural, SH = superior hypural (hypurals 3+4), IH = inferior hypural (hypurals 1+2), PH = parhypural, U = ural centra, PU = preural centra.

form. The pectoral fin in *Macruronus* larvae is more markedly stalked than in *Merluccius*. Fahay and Markle (1984) suggested that this pectoral modification in larvae with delayed caudal development may be a compensatory response associated with swimming.

Although the larvae of the remaining merlucciid genera (*Lyconus* and *Lyconodes*) are currently unknown, fin structure and position should be useful in separating these from *Macruronus*. Based on adult features, pelvic insertion should distinguish *Macruronus* (pelvics inserted behind pectorals) from *Lyconus* (opposite) and *Lyconodes* (abdominal). Additionally, *Lyconus* has only a single dorsal fin and no caudal fin.

The caudal fin of *M. novaezelandiae* is similar to *Muraenolepis* in its confluence with dorsal and anal fins (Fahay and Markle 1984). This similarity extends to the undifferentiated X and Y bones and the total caudal fin ray count (12 or 13) reported by these authors. However, unlike *Muraenolepis, M. novaezelandiae* has radials fused to the spines of the first preural centrum, which is the more typical gadoid condition.

Variability in the structure and appearance of bones associated with the caudal fin has been reported for other *Macruronus* species. Marshall (1966) observed double neural arches and "supernumary elements" in *M. magellanicus*. Indeed, variability in gadiform caudal structure appears not to be unusual with examples in several taxa (Markle 1982). Unfortunately, insufficient specimens in the appropriate 35–150 mm size range were available to assess developmental

characteristics of these variations in blue grenadier.

ACKNOWLEDGMENTS

NOTE: Since the acceptance of this paper, the embryological work by A. Patchell (see section on Development) has been published in New Zealand Journal of Marine and Freshwater Research Vol. 21, No. 2. That paper includes a similar larval developmental sequence to that reported here.

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