DEVELOPMENT OF EGGS AND LARVAE OF 
CARANX MATE (CARANGIDAE)1

JOHN M. MILLER AND BARBARA Y. SUMIDA2

ABSTRACT

The development of eggs and larvae of omaka (Caranx mate) is described from approximately 2 h after fertilization to day 36 after hatching. The pelagic, spherical eggs (700-740 \( \mu \) diameter) had a single oil droplet and hatched after about 26 h incubation at 24.5\(^{\circ}\)C. The average growth rate in culture was 0.44 mm/day; feeding began four days after hatching. Fin development and ossification of omaka occurred at smaller sizes, but in the same sequence as jack mackerel (Trachurus symmetricus) off California. Of the body proportions measured, body depth was most useful in separating omaka from at least two other species of carangid larvae. The pigment pattern was also of diagnostic value. Reared larvae were indistinguishable from similar-sized field specimens.

Omaka (Caranx mate) is one of the most abundant carangids in the Hawaiian Islands. The species is rather widespread throughout the Indo-Pacific, reaching the eastern coast of Africa. In Hawaii, the preferred habitats are estuaries, bays, and harbors with relatively long water residence times. Kuthalingham (1959) described the feeding habits of omaka near Madras, India. The growth rate of captive adult omaka was reported by Watarai (1973).

Omaka have a protracted spawning period in Hawaii; the eggs can be taken with fair regularity from March through September from the surface waters of Kaneohe Bay, Oahu. Little else is known of the spawning habits. However, a bi-weekly year-round fish-egg survey in Kaneohe Bay indicated three spawning peaks: one in April and May, another in September and October, and a third, smaller peak in July (Watson and Leis, 1973). During these peaks omaka eggs were by far the most abundant of any, occasionally exceeding concentrations of 10/m\(^3\) in the surface waters of south Kaneohe Bay. Larval densities, on the other hand, were found to be much lower than these egg densities, rarely reaching 0.1/m\(^3\) (Watson and Leis, see footnote 3). As is characteristic of many carangids, young are frequently seen under medusae. Large larvae and juveniles are similarly attracted to floating raffia, and have been collected in this manner. Adult omaka do not appear to make the offshore spawning movements characteristic of many of the resident fish species in Kaneohe Bay.

MATERIALS AND METHODS

Larvae used for description came from two sources: reared specimens and field specimens. Reared larvae of known age were the primary source of material; field specimens were used mainly to verify observations and conclusions based on the former. Over the past 2 yr omaka larvae have been taken in numerous plankton tows. Each time that comparisons were made between similar-sized field and reared specimens, the larvae were indistinguishable.

Larvae were obtained from two cultures (called Series A) begun in February 1971. One of these (A1) supplied larvae through day 5 (Table 1). This culture was terminated on day 6, when high mortality (of unknown cause) was experienced. Although the sizes of these larvae are included in the growth rate curve (Figure 4), they were not used in the description of developmental stages. The second (A2) was maintained for 36 days during which post yolk sac specimens (day 6 and older) were taken for description.

Two other cultures (Series B) were begun in May 1972 to provide eggs and yolk-sac larvae. The first, begun 1 May, was to determine the approximate rate of development and design a

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1Hawaii Institute of Marine Biology Contribution No. 427.
2Hawaii Institute of Marine Biology, University of Hawaii, Coconut Island—P.O. Box 1346, Kaneohe, HI 96744.

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Table 1.—*Caranx mate*—reared larvae, 22 February-31 March 1971.

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Sampling schedule. The second, begun 5 May, provided most of the specimens used in the description, although certain additional measurements (e.g., size at hatching) were made on specimens from the first culture.

**Series A Cultures**

One thousand eggs were pipetted from the washed plankton of a surface tow with a 505 μm mesh meter net in south Kaneohe Bay, Oahu, on 22 February 1971. These eggs were placed in a 78-liter fiberglass and glass aquarium which had been filled with triple CUNO4 filtered (5 μm effective pore size) bay water. The water was previously exposed to long-wave ultraviolet light for 1 min. Penicillin (to a concentration of 50 mg/liter) and Polymixin B (to a concentration of 8 mg/liter) were added before introduction of the eggs. These antibiotics have been shown to substantially reduce bacterial counts in cultures and materially increase hatching success of omaka eggs (Struhsaker, Hashimoto, Girard, Prior, and Cooney, 1973). A *Chlorella* sp. culture was added initially to an approximate cell count of 10 × 10⁴ cells/ml.

Salinity, oxygen, and temperature in the tank were usually measured daily. Salinity remained nearly constant throughout the experiment at 35%, the value in the bay at the time of collection. Oxygen values ranged from 6.1 to 9.5 mg/liter during the subsequent 36 days. The maximum range of temperature in the tank was 21.5 to 25.9°C, with a 36-day mean of 24.5°C. The bay surface temperature at the time of collection was 24.4°C.

The tank was continuously illuminated by two 40 watt fluorescent "daylight" bulbs. The light intensity at the surface of the water was approximately 6.5 × 10³ flux. The tank was aerated with a single airstone, with airflow adjusted to produce a slow single stream of bubbles.

Food was added daily from the third day after hatching. Through day 11 the food was the 75-150 μ fraction of wild zooplankton attracted to a night light suspended in the bay. On day 12 the addition of wild plankton was replaced with additions of *Artemia* nauplii. Wild plankton and *Artemia* were added each time to a concentration in the tank of 5/ml and 1/ml, respectively. No doubt the culture tank supported other (unknown) populations of plankters and microorganisms.

Usually ten larvae were captured by dipping or pipetting at about two-day intervals from hatching (the day after introduction of the eggs) until 36 days after that time (Table 1). No attempt was made to select particular sized larvae.

**Series B Cultures**

Larvae reared for yolk-sac-stage description were hatched from eggs taken from Kaneohe Bay on 5 May 1972. At the time of collection (midafternoon), eggs were found in both late middle stage and early stage, i.e., from two spawnings. Only the latter (in blastodisc stage) were selected for culture. (The exact time of fertilization is unknown; hence the duration of the early stage was estimated.) Extrapolating from the subsequent rate of development, we estimate the eggs had been fertilized for about 2 h before capture.

Two hundred eggs were placed in each of four 4-liter beakers of unfiltered seawater obtained about two miles offshore from Kaneohe Bay. This "offshore" water contained less plankton...
and, in general, was of higher quality than that found in the bay used in the Series A cultures. Salinity was always about 35°.

Water temperature in the beakers during the experiment ranged from 23.5 to 24.4°C. Bay surface temperature at the time of collection was 25°C. No food or algae was added to these cultures. Erythromycin glucosinate was added to a concentration of 9 mg/liter before introduction of the eggs. The beakers were continuously illuminated with fluorescent lights.

Eggs and larvae were pipetted from these cultures, which were terminated on the sixth day after hatching. Larvae were immobilized in a refrigerator (ca. 10°C) before preservation in 2.5% buffered formaldehyde. This practice resulted in fewer distorted and curled larvae than did placing them directly in preservative.

All measurements and counts were made with a microscope equipped with an ocular micrometer. At the usual magnification (50×) the precision of measurement is ± 0.02 mm. Illustrations are camera lucida drawings, subsequently inked, by B. Sumida. Owing to rapid loss of certain pigments after preservation, a size series of larvae was microphotographed with color film for subsequent reference.

Illustrations of early larvae (day 6 and younger) show pigment patterns observed in live larvae. Pigment patterns retained after preservation are so noted in the text. Pigments stabilized in older larvae so that differences between live and dead larvae became much less pronounced with age. Illustrations of these larger larvae (day 8 and older) were made from preserved specimens.

**DEFINITIONS, MERISTICS AND MORPHOMETRICS**

*Body depth*  At insertion of pectoral fin. (Prior to pectoral bud formation, taken through shoulder.)

*Dorsum*  Region dorsal to medial horizontal line through body.

*Eye diameter*  Horizontal diameter of orbit.

*Head length*  Tip of snout to posterior margin of operculum.

*Larva*  Larva after yolk absorption completed and prior to metamorphosis when scales and lateral line develop. (All of our specimens were larvae based on this definition.)

*Lateral line streak*  Dashed line of pigment along the lateral midline of body.

*Snout to anus length*  Tip of snout to vertical from anus.

*Standard length (SL)*  Prior to notochord flexion and formation of hypural bones, SL taken from snout to tip of notochord. Thereafter, taken to posterior margin of hypural plate. **SL** = mean standard length. Deviations from means are standard deviations. All length measurements were made on preserved specimens, except where noted.

*Ventrum*  Region ventral to medial horizontal line through body exclusive of abdominal area; generally area inclusive of hypomeres.

*Yolk sac larva*  Larva from hatching to approximately the third day when yolk absorption was nearly complete.

**DEVELOPMENT OF THE EGG**

Because the development of the omaka egg proceeds rapidly in discrete stages, we have chosen to summarize it as follows:

**Early stage**

Blastodisc stage to blastopore closure (fertilization to blastopore closure) (Figure 1A).

**Egg size:**

(diameter) Live: 722 ± 19 µ.

Preserved: 722 ± 19 µ.

**Figure 1A.**—Ventral view of early stage egg of *Caranx mate*. BP = blastopore.
The omaka egg is pelagic, clear, and spherical with a single oil droplet at the vegetative pole. At the time of collection the eggs were in the early blastodisc stage.

**Oil globule:**
- Diameter in live egg: 190-200 μ.
- Diameter in preserved egg: 176-192 μ.
- Positioned at the vegetative pole, the oil globule was almost centered on the polar axis of the developing blastodisc (Figure 1A).

and later between the head and tail bud of the early embryo. At the time of blastopore closure, the oil globule was situated slightly off-center and closer to the tail end of the developing embryo. The blastopore closed between the oil globule and the tail end of the embryo.

**Perivitelline space:**
- Size range: 26 ± 4 μ.
The perivitelline space was not evident in the early blastoderm stages but developed as the egg advanced.

Yolk:
(diameter) $660 \pm 23 \mu$.
The segmentation of the yolk was apparent in the form of irregular polygons across the egg diameter in the early stage eggs (not illustrated). This pattern was lost with preservation of the eggs in 2.5% formaldehyde, whereupon the yolk took on a "bubbly" irregular appearance.

Embryo development:
The optic vesicles were evident on the young embryo before blastopore closure of the egg (not illustrated). Initiation of somite development in the anterior end of the embryo was also observed before closure of the blastopore. Kupffer's vesicle was conspicuous at the tip of the rudimentary tail bud.

Pigmentation:
No pigmentation was present in the egg or embryo during this stage.

Duration of early stage:
11-12 h subsequent to capture. Estimated total time—14 h.

Middle stage
Following blastopore closure to separation of the tail bud from the yolk (Figure 1B).

Noteworthy events:
Advanced development of the embryo and pigmentation patterns. Egg size, width of perivitelline space, etc., same as above.

Oil globule:
The oil globule remained nearly centered between the developing head and tail of the embryo. The underside of the oil globule (closest to the embryo) appeared heavily pigmented during the latter part of the middle stage owing to melanophores which had migrated from the surrounding yolk surface (Figure 1C).

Yolk pigmentation:
In the early middle stage, numerous small melanophores were observed overlying the anterior surface of the yolk surrounding the oil globule (Figure 1B). Most of these melanophores migrated during the middle stage and aggregated on the underside of the oil globule.

Embryo pigmentation:
Small, faintly pigmented melanophores first appeared along the lines separating the developing somites and spread laterally covering the dorso-lateral region of the body. A conspicuous patch of pigment was noticeable at the anterior and posterior margins of the optic vesicles, and a small cluster of melanophores in the area of the snout. Later in this stage, larger melanophores appeared in an irregular line along the medial dorsal surface of the body (Figure 1D).

Somite development:
By the end of the middle stage, 21 well-defined myomeres could be counted. Kupffer's vesicle was still evident in the middle stage.

Duration of the middle stage:
11-12 h at 24.5°C.

Late stage
Tail bud completion to hatching of larva (Figure 1E).

Oil globule:
When the advanced embryo had coiled around the yolk, the oil globule shifted in position and became situated closer to the head rather than maintaining a median position under the embryo. Pigmentation became more abundant, extending over the hemisphere of the underside in contrast to the small, dense cluster in the middle stage. Virtually no pigment remained on the surrounding yolk.

Embryo pigmentation:
Dense pigmentation remained on the dorso-lateral surfaces of the body. Melanophores appeared over the top of the head in addition to those on the snout and along the anterior and posterior margins of the eye. A band of small melanophores developed around the body near the tail region. There also appeared a ring of melanophores on the yolk surface posterior to the tip of the tail bud. This was subsequently lost in the final span of the late stage when fin fold formation was completed and tail flexure occurred. Kupffer's vesicle was observed in the early part of the late stage but was subsequently lost.

Somite development:
The adult complement of 24 somites was attained in the late stage embryo.

Duration of late stage:
0.5-1 h at 24.5°C.
**YOLK SAC LARVAE**

The newly hatched omaka larvae measured 1.32 mm to 1.70 mm SL live, with a mean of 1.46 ± 0.12 mm for 47 larvae. Following preservation in 2.5% formaldehyde, a different group of ten larvae ranged from 0.87 mm to 1.03 mm with a mean of 0.98 ± 0.05 mm. The difference between means (0.48 mm) indicates a shrinkage of 33%.

**Pigmentation**

**Live Larvae at Hatching**

Newly hatched omaka larvae resembled advanced embryos in pigmentation pattern. Melanophore pigment was heaviest on the dorso-lateral surfaces of the body with melanophores usually forming a loop posterior to the head. Additional small clusters of melanophores were observed on the top of the head and at the anterior and posterior margins of the eye vesicles. A broad band of small melanophores encircled the body about 6 myomeres posterior to the anal papilla. Ventral body pigment was not apparent in the newly hatched larvae but was found in older yolk sac larvae, perhaps due to the migration of some dorso-lateral melanophores and those in the band region (see Orton, 1953). Dendritic melanophores (Figure 2A) lined the posterior margin of the yolk sac. The oil globule displayed heavier pigmentation than in the late egg stage, with melanophores present on both its anterior and posterior surfaces.

**Preserved Larvae at Hatching**

The remaining pigmentation following preservation in 2.5% formaldehyde for at least 24 h were the melanophores on the head and dorso-lateral region of the body. The band of pigment around the body posterior to the anal papilla was lost except for a few scattered melanophores. The yolk sac and oil globule had contracted and obscured any pigment which may have remained.

**Live Larvae One to Three Days Old**

The pigmentation pattern of the yolk sac larvae changed markedly during the first few days after hatching. Owing to the rapid change, larvae (preserved) at any time exhibited various stages of pigment development. Therefore the descriptions presented are "average" patterns observed. Had the larvae come from simultaneously fertilized eggs, the differences would probably have been less pronounced. As the pigment pattern stabilized with age, variations among larvae were correspondingly reduced.

There was a loss of lateral pigmentation coinciding with a coalescence of the small dorsal melanophores to form fewer, large melanophores on the dorsal edge of the body, and also with the appearance of pigment on the ventral edge of the hypomeres. These changes were apparent in most of the day-old larvae.

By the end of the second day, the larvae possessed discrete melanophores on the dorsal and ventral edges of the body in a single discontinuous line. The dorsal body melanophores showed branches or "dendrites" which projected up into the fin fold. These were most pronounced in the region of the dorsal fin opposite the divergence of the posterior end of the gut from the body. A network of dendritic melanophores developed about midway along the dorsal and ventral fin folds (Figure 2B). These networks were gradually lost within the next five days of growth.

Also evident on the second day was the cluster of melanophores on the top of the head and over the snout region (present in the advanced embryo). The first indication of eye pigmentation appeared with faintly pigmented melanophores over the iris, but concentrated along its posterior margin. The caudal region usually possessed a single minute melanophore dorsal and two or three ventral to the end of the notochord (Figure 2A). The dorsal melanophore was lost in the older larvae, but the ventral melanophores persisted and were situated over the early caudal actinotrichia at about the sixth day. Three-day-old larvae were similar in pigmentation to the two-day-old larvae except in their heavier eye pigmentation and fewer melanophores on the dorsal body edge.

**Preserved Larvae One to Three Days Old**

Following preservation in 2.5% formaldehyde for 48 h, virtually all pigmentation, except for the dorsal and ventral body, eye, and head melanophores, were lost. In a few specimens,
Figure 2A.—Yolk sac larva, *Caranx mate*, just after hatching, 1.62 mm SL.

Figure 2B.—Three-day old larva, *Caranx mate*, 2.26 mm SL.

Figure 2C.—Six-day old larva, *Caranx mate*, 3.06 mm SL.

Figure 2D.—Twelve-day old larva, *Caranx mate*, 3.96 mm SL.
faint traces of the fin fold and oil globule pigment could be distinguished.

**Morphological Development of Yolk Sac Larvae**

Omaka larvae hatch in a relatively undifferentiated state, the only conspicuous structures being the large yolk sac, the unpigmented eyes, otic vesicles, and heart. The oil globule, positioned forward of the head at the extreme anterior margin of the yolk sac, is characteristic of carangids (Ahlstrom and Ball, 1954). Ten hours after hatching (1.80 mm SL), the larvae had developed a narrow, straight gut tube (it became convoluted on the fifth day) terminating at the anal papilla and urinary bladder (Figure 2B). The gradual yolk resorption resulted in the oil globule’s shifting its position posteriad while remaining at the anterior margin of the sac. The oil globule lay just ventral to the head at 10 h.

Pectoral buds appeared in the larvae by the end of the second day and the jaw buds by the third day. After three days most of the yolk had been absorbed, and the oil globule had diminished in size to a small, barely noticeable spherical body. The end of the third day was thus selected as the termination of the yolk sac stage of the larvae.

By the fourth day, the eyes were completely pigmented, the mouth was open and the broad, membranous pectoral fins were functional. The small collapsed yolk sac containing the now minute oil globule was still evident ventral to the anterior portion of the abdominal cavity.

**LARVAE**

**Pigmentation**

**Head Pigmentation**

Following yolk absorption (in three–to four–day–old larvae), head pigmentation was present in the following areas: (1) the median dorsal surface of the midbrain (optic lobes) consisting of one or two small melanophores; (2) the floor of the otic vesicle with two or three expanded melanophores which remained visible until obscured by the overgrowth of tissue in older larvae at about day 10 (Figure 2C); (3) along the dorsal margin of the opercle which exhibited a few faintly pigmented melanophores; (4) on the lower jaw with a melanophore situated at the tip of the lower jaw and another at the angular bone, with most of the larvae having a melanophore midway between these two.

As the larvae grew, the density of head pigmentation increased—particularly over the mid- and forebrain region and on the jaws. The number of melanophores increased on the postero-lateral half of the midbrain lobe while a ring of melanophores concurrently outlined the margin of the midbrain capsule. Larvae of approximately 3.5 mm (day 8–not illustrated) exhibited a cluster of expanded melanophores over the midbrain which gradually extended antero-ventrally to the forebrain and snout region. Pigmentation on the surface of the head had intensified in the older larvae, with the cap over the midbrain being especially conspicuous.

By the tenth day (4.0 mm SL), most larvae possessed a melanophore at the tip of the upper jaw in addition to those on the lower jaw; pigmentation subsequently increased over the premaxillary, maxillary, and dentary region as the larvae advanced. Melanophores located on the jaws were smaller and more punctate than those on the top of the head and along the operculum.

Pigmentation on the membrane overlying the branchiostegal rays and along the gular region developed in eight– to ten–day–old larvae (3.5-4.0 mm SL) (Figure 2D). The most anterior branchiostegal rays were initially pigmented with pigmentation proceeding distad until the full complement of seven rays was pigmented. Pigmentation of each ray also proceeded distad resulting in larvae of 20 to 22 days (8.3–9.5 mm SL) possessing as many as two or three melanophores over the basal end of each branchiostegal ray (Figure 3A). This pigmentation was barely discernible in larvae of 26 days (10.9 mm SL) and eventually lost altogether in larvae of 28 days (11.4 mm SL). Melanophores along the median gular region similarly increased in density, forming an almost continuous dotted line of contracted melanophores posterior to the isthmus in larvae of 14 days (5.2 mm SL). Additional melanophores formed along this line but pigmentation in this region gradually disappeared, like the branchiostegal pigmentation, in the advanced larvae.
The operculum was never heavily pigmented, although melanophores formed along the region between the preopercular spines of larvae from day 8 to 16 (3.5-6.2 mm SL), as the spines were being resorbed. In addition there were several melanophores scattered over the upper region of the operculum posterior to the eye.

**Body Pigmentation**

**ABDOMINAL REGION.**—The abdominal region of the omaka larvae following yolk absorption as used here refers to the peritoneal cavity with its overlying tissue. At six days (3.0 mm SL) the one or two faintly pigmented melanophores could be seen immediately ventral to the base of the pectoral fin. These melanophores persisted until the larvae were 14 days old (5.2 mm SL) (Figure 2C, D). A few melanophores were scattered over the abdominal wall in the early larvae with increasing numbers being formed in older larvae.

The spherical gas bladder was apparent by the sixth day (3.0 mm SL) with its dorsal cap of embedded pigmentation. The gas bladder was gradually depressed into an elliptical shape by day 10 (4.0 mm SL) and its pigment largely obscured with the increasing growth of musculature dorsally.

A line of melanophores developed by day 6 (3.0 mm SL) (Figure 2C) extending along the dorsal wall of the abdominal cavity from the gas bladder to the terminus of the gut where it converged with the ventral line of melanophores along the edge of the hypomeres (see section on ventrum pigmentation). This pigmentation increased in density through day 8 (not illustrated) until it was obscured by the growth of overlying tissue by day 12 (Figure 2D). This pigmentation had a diffused appearance owing to its internal, dorsal position, but consisted of discrete melanophores.

Also evident in six-day-old larvae was peritoneal pigmentation along the ventral edge of the abdominal cavity, including a small precleithral cluster of melanophores, a larger cluster just ventral to the liver (where the pelvic bud subsequently appeared), and a row of melanophores extending from the ventral surface of the stomach to the anus. These pigments gradually diminished.
and were obscured or lost in larvae of about 26 days (10.9 mm SL).

**DORSUM.**—Dorsum pigmentation of the post yolk sac larvae of four days of age (2.6 mm SL) consisted of a single line of 9 to 13 large, stellate melanophores extending posteriorly from the base of the hindbrain to the 17th to 19th myomere along the dorsal edge of the body (Figure 2C). At ten days (4.0 mm SL), numerous small melanophores had formed ventro-laterally, interspersed along the prominent line of melanophores of the dorsal edge. The appearance of these lateral melanophores coincided with the appearance of dorsal and anal fin anlagen (which were visible as opaque thickenings in the fin fold).

By day 12 (Figure 2D) (4.5 mm SL) the dorsal melanophores had become smaller and more numerous, bordering each side of the ventral margin of the dorsal fin anlage. The formerly conspicuous single row of large melanophores on the edge of the dorsum was now lost, having been replaced by these smaller dorsal melanophores in a double row along the base of the fin anlage and continuing in a single row posteriorly.

Larvae of 15 to 16 days of age (5.2-6.2 mm SL) showed increased lateral spreading of pigmentation. By 18 days (7.4 mm SL) (Figure 3A), melanophores had formed along the more posterior two-thirds epaxial myoseptal lines, which became more pronounced in 20-day-old larvae (8.3 mm SL). This epaxial myoseptal pigment pattern was gradually obscured by the increasing density of pigmentation over the entire area of the dorsum beginning in 22-day-old larvae (9.5 mm SL).

The caudal peduncle remained sparsely pigmented both dorsally and ventrally throughout development. (The pigment along the base of the caudal fin is described in the section on fin pigmentation.)

**VENTRUM.**—The pigmentation changes of the ventrum from the four-day-old larvae followed a similar pattern to that of the dorsum with a few exceptions. The larvae of four to eight days of age exhibited a single line of 12 to 26 small melanophores along the ventral edge of the body from the anus to the 23rd or 24th myomere. These ventral melanophores were smaller and extended more posteriorly than those aligned along the dorsal edge of the body until fin formation was well initiated. In addition, two to four minute punctate melanophores appeared on the ventral tip of the notochord (which subsequently migrated ventrally to become situated along the proximal edges of the caudal actinotrichia discussed in the section on fin pigmentation).

With the first appearance of the anal fin anlage in ten-day-old specimens, faint melanophores formed dorsolaterally over the ventrum, followed by the appearance of a double line of melanophores along the base of the anal fin anlage in 12-day-old larvae (4.5 mm SL) from the previously single line as it occurred along the base of the dorsal anlage. From day 14 to 16 (5.2-6.2 mm SL), melanophores formed a conspicuous pattern along the hypaxial myoseptal lines, with others scattered in the surrounding region (Figure 3A, B). These latter were most concentrated over the ventral one-third of the hypomeres. The hypaxial myoseptal pigment pattern remained visible in the largest larvae (18.0 mm) in contrast to that on the dorsum and remained as a major distinguishing characteristic.

"LATERAL LINE streak".—The "lateral line streak" refers to the dashed line of pigmentation along the lateral midline of the body as described for several other carangid larvae (see Ahlstrom and Ball, 1954; and Kramer, 1960). It appeared in the six-day (Figure 2C) omaka larvae (3.0 mm SL) with two or three elongate melanophores arising near the vertical of the anterior portion of the hindgut, with as many as 13 melanophores having formed in eight-day-old (3.5 mm SL) larvae. Indeed, body pigmentation of the larvae at this age was characterized by three lines: along the dorsal and ventral edges of the body, and the lateral line streak.

Although it was largely obscured by the overgrowth of tissue and heavier lateral pigmentation, the streak was still noticeable in the 36-day-old larvae (16.6 mm SL). It provided a sharp line of demarcation between the heavily pigmented dorsum and the more sparsely pigmented ventrum in the older larvae (Figure 3B).

**Fin Pigmentation**

**CAUDAL.**—Prior to notochord flexion, a few small melanophores were present along the distal margin of the early hypural plate (Figure 2D). In addition, a line of minute melanophores had formed along the ventral margin of the caudal.
fin fold, but was lost in older larvae (ca. 7.5 mm SL).

Following flexion of the notochord (ca. 6.0 mm SL), melanophores were still evident along the posterior margin of the hypural bones and along the dorsal and ventral margins of the fin membrane in the caudal peduncle region, with additional caudal fin pigment developing distally between the rays. The density of melanophores increased in the older larvae, generally forming in one or two rows between the rays.

PECTORAL.—Larvae of ca. 6.0 mm SL had minute melanophores scattered along the distal margin of the pectoral fin, but pigmentation remained sparse compared to that of the caudal, dorsal, and anal fins. By 8.5 mm, the pigmentation had increased to rows of three to five melanophores interspersed between the more dorsal rays, with this pigmentation spreading ventrad as the larvae grew.

DORSAL AND ANAL.—Pigmentation of the dorsal fin fold was described earlier. In the early larvae up to ca. 3.0 mm, there were dendritic melanophores lining the edge of the preanal fin fold which were lost in larvae by 4.5 mm.

The pattern of pigment development was similar for both fins, although that on the anal was formed earlier. This was consistent with the apparent earlier formation of the anal fin. By 6.0 mm, larvae displayed the beginning of a row of melanophores along the distal margin of the anal pterygiophores (Figure 3A). Initially each of these melanophores was situated between adjacent pterygiophores in the anterior portion of the fin; more developed posteriad in older larvae. The entire length of the proximal margin of the anal fin had this pigment by 8.0 mm, but the dorsal fin margin showed no evidence of it until ca. 7.0 mm. Approximately three-fourths of the anterior portion of the dorsal fin margin was pigmented at 10.0 mm.

Rows of two to four melanophores were evident along the distal region of the fin membrane between the anteriormost anal fin rays at ca. 6.0 mm. The fin pigmentation process proceeded posteriad, with the melanophore number increasing to as many as 14 in double rows between rays in larvae of ca. 10.5 mm.

Larvae of ca. 8.5 mm showed melanophores forming distally on the fin membrane surrounding the dorsal spines and between the first few dorsal rays. Subsequently, the fin pigment developed posteriad as in the anal fin; and the density of melanophores on the dorsal fin membrane was similar to that of the anal fin by 11.3 mm.

PELVIC (VENTRAL).—Like the pectoral fin, each pelvic fin was sparsely pigmented. Two or three melanophores were observed on the small, rayless fin on larvae of ca. 6.0 mm. By ca. 7.6 mm, two or three rows of a few small, inconspicuous melanophores had formed between the rudimentary fin rays (Figure 3A).

Fin Development

The omaka larvae hatched with no developed fins but a broad, flat fin fold. The subsequent formation of fins (first development of lepidotrichia) followed a sequential pattern much like that described for Trachurus symmetricus (Ahlstrom and Ball, 1954), viz. caudal, pectoral, anal and soft dorsal, spiny dorsal, and pelvic (ventral) in that order.

The stage of omaka fin development particularly, appeared to us to be more dependent on size attained than age. Smaller, older larvae were found to have not yet completed certain stages, while some precocious (larger) larvae had. Owing to rapid development of larvae, larger samples at more frequent time intervals would be required to test a hypothesis of size versus age dependence of developmental events.

Caudal

Caudal actinotrichia could be observed in larvae as small as 2.2 mm in the form of faint lines projecting distally from the area around the tip of the notochord. True rays (lepidotrichia) were first evident in larvae ca. 3.4 mm (day 7) and became more prominent in 4.0 mm larvae as ventrally projecting incipient rays from the presumptive hypural plate below the tip of the notochord. These rays were well-defined in larvae of ca. 4.5 mm (day 12), when notochord flexion was initiated. At this time as many as 15 rays of the total 17 principal caudal rays could be observed still projecting obliquely from the developing unossified hypural bones lying ventral to the notochordal tip. Notochord flexion and the formation of the 17 principal caudal rays (nine
above the midline of the hypural plate, eight below) were completed in larvae by 6.0 mm (day 16). (Secondary rays were added anteriad along the dorsal and ventral margins of the caudal peduncle with as many as nine formed on each edge in the largest larvae.)

The rounded caudal fin fold was confluent with the dorsal and anal fin folds in the young larvae, but an indentation of the fin fold occurred in the region of the future caudal peduncle in the older larvae. The caudal fin was separated from the dorsal and anal fin membranes in larvae between 5.3 mm and 6.0 mm (day 14-16). At this stage of development the caudal fin possessed a straight margin, rather than rounded, along its posterior edge and subsequently attained a bilobate shape in larvae of ca. 10.5 mm (day 24).

**Pectoral**

The pectoral fin developed early during the yolk sac stage (see earlier sections). However, rays did not form until the larvae were ca. 5.4 mm (day 14) when six or more rays could be counted in the upper region of the fin. Addition of rays proceeded ventrally with the rays decreasing in length ventrally to give the pectoral fin an obovate shape in the older larvae compared to the earlier, more rounded, membranous larval fin.

The adult complement of 21 to 22 rays was attained in larvae of 9.3 mm. A short, inconspicuous spine at the extreme dorsal margin of the pectoral was evident upon close examination of our cleared and stained specimens of minimal length 8.4 mm and larger cleared and stained juveniles from our field-collected samples.

**Anal**

Formation of the anal fin was first evidenced by the appearance of the anal anlage in larvae as small as 3.75 mm. (See section on ventrum pigmentation.) Following the formation of the dorsal and anal anlagen, it appeared that the separation of the fin fold into dorsal, anal, and caudal sections coincided with the development of incipient rays and first few spines of the dorsal and anal fins in larvae from 5.4 mm to 5.5 mm (day 14).

One anal spine formed concurrently with six or more incipient rays in larvae of 5.4 mm or larger; the two remaining spines developed anteriad to the first formed spine in larvae between 7.0 and 9.0 mm which had at least 15 rays formed posteriorly.

Generally by 9.0 mm, the two most anterior anal spines had separated from the third which remained associated with the soft rays. However, a well-defined separation of the fin membrane did not occur until the larvae were 16.0-17.0 mm in length. The adult complement of II-I, 17-19 for the anal fin was completed in larvae by 9.0 mm, although three smaller specimens (8.13, 8.63 and 8.88 mm SL) had complete anal fins.

An inconspicuous flap of tissue could be observed developing over the bases of the spines and first few rays of the anal fin in most of the larvae by 11 mm. The flap was not completely formed along the basal margin of the anal fin in our largest larva (18 mm) but had covered only about three-fourths of the length of the fin base. This was the precursor to the flap of tissue which overlies the entire length of the dorsal and anal fin bases in adult omaka.

**Dorsal**

The dorsal anlage appeared at approximately the same size as the anal anlage. Development of the soft dorsal occurred prior to formation of the spiny dorsal. There was no clear difference in the rate of development of the soft dorsal fin and anal fin in contrast to the jack mackerel (Ahlstrom and Ball, 1954).

Distal pterygiophores of the soft rays were evident in larvae of 5.0 to 5.4 mm, with incipient rays becoming differentiated in 5.55 mm (and larger) larvae. Subsequent fin development was rapid. Four to six spines had developed with as many as 16 rays in larvae of 5.8-6.0 mm. Spines were added anteriad and rays posteriad. Most of the larvae of 7.3 to 8.0 mm length had attained a dorsal fin complement of IX-20 to IX-22. In larvae larger than 9.0 mm, the ninth spine had separated from the preceding eight to separate the two dorsal fins. The fourth dorsal spine remained the longest in the larger larvae, with the others progressively decreasing in length. Larvae from 9.0 to 18.0 mm possessed the adult fin complement of VIII-I, 20-23.

By 9.25 mm, only cleared and stained specimens showed a small, embedded, forwardly projecting spine arising from the pterygiophore of the first external spine. We did not count this spine.
separately in the fin complement, although some investigators have apparently done so in presenting spiny dorsal meristics for *C. mate* as I+VIII+I (e.g., Smith, 1965; Munro, 1967). The spine is apparent only upon dissection of juveniles and adults of the omaka.

A narrow flap of tissue had begun to form over the basal edge margin of the anterior three to four dorsal spines in larvae of 10 mm. It appeared slightly earlier than that for the anal fin. Like the flap over the anal fin base, the dorsal flap had only developed along three-fourths of the length of the dorsal fin base in our largest reared larva (18 mm).

**Pelvic (Ventral)**

The inconspicuous pelvic fin bud appeared in larvae of 4.4 to 5.7 mm, except for two specimens of 3.64 and 3.96 mm which had already formed the fin buds. These appeared as small protuberances just ventral to the liver and gradually differentiated into a larval fin in 6.0 mm larvae. Two or three rays had formed in larvae by 6.2 mm, and the adult complement of I, 5 was completed in larvae of 7.7 mm.

**OSSIFICATION**

Eighteen larvae, one of each age group sampled and representative of the size range in the sample, were cleared and stained with alizarin following the technique described by Hollister (1934). (Three 7-day-old larvae were cleared and stained to further define the sequence of tooth formation on the upper jaw.) The specimens were cleared and stained primarily to confirm the meristics taken and developmental descriptions presented earlier on unstained material.

In order to determine the limits of precision for our statements derived from these cleared and stained larvae about size of first structural development, length differences among our relatively few specimens were measured. They ranged from 0.1 to 0.2 mm for 2.9-3.5-mm specimens, 0.5 mm for specimens 3.5-4.6 mm, and about 1 mm for larger specimens.

Ahlstrom and Ball (1954) present a thorough discussion of the ossification sequence for the carangid, *T. symmetricus* (jack mackerel). Our cleared and stained specimens showed exactly the same sequence, but ossification (defined as taking up alizarin) of each bone began in smaller omaka larvae than jack mackerel (Ahlstrom and Ball, 1954). Likewise, most of these bones had completed ossification at a smaller size in omaka.

The cleithrum, upper and lower jaw bones, and preopercular spines were already ossified in our 2.94 mm larva. Minute teeth (ca. 4 on the upper jaw) had begun staining in the larva of 3.35 mm with numerous small teeth filling in the single row in larger larvae. Teeth on the lower jaw first appeared in the 9.25 mm larve. Five branchiostegal rays were stained in the larva of 3.50 mm, with all seven branchiostegal rays on each side of the base of the operculum being stained in the 4.58 mm larva. Gill arches were ossified or stained in the 4.09 mm specimen, and gill rakers began staining in the 5.42 mm larva. Meristics for ossification of fin elements are presented in Table 2.

All neural and haemal spines and centra of the 24 vertebrae (10 abdominal vertebrae, 14 caudal vertebrae) had completed ossification in the 6.25 mm larva. The initial vertebral ossification, indicated by the stain in the neural spines of the first few abdominal vertebrae and in the haemal spines of the caudal vertebrae, was present in the 4.09 mm larva.

Preopercular spines of the omaka larvae were formed along two rows as in the jack mackerel (Ahlstrom and Ball, 1954), viz. the posterior edge of the preoperculum and the "preopercular crest" just anterior to the preopercular edge (as defined by Ahlstrom and Ball, 1954). Those spines situated along the preopercular crest were fewer and smaller than those along the edge of the preoperculum. During the larval development of omaka, the number of spines along the

<table>
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<th>SL (mm)</th>
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<th>Pectoral</th>
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<th>Dorsal (second)</th>
<th>Dorsal (first)</th>
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ascending arm of the preoperculum increased from two (2.9-3.5 mm larvae) to as many as six (7.0-9.0 mm larvae) and from two to seven along the anteriorly projecting descending arm. The apical spine of the preoperculum remained slightly larger and broader-based than the others as in the jack mackerel (Ahlstrom and Ball, 1954), but was still smaller and less prominent than in our other common carangid larva, Gnathanodon speciosus (unpublished data), and provides one characteristic for separating the two species.

The omaka larvae showed no serrated dorsal crest at the back of the head which was evident in the jack mackerel (Ahlstrom and Ball, 1954). It is considered to be a rather common feature of carangid larvae (Berry 1959, McKenney, Alexander, and Voss 1958, Okiyama 1970, Shojima 1962) and is present in several of our unidentified species of carangid larvae.

**GROWTH**

The growth rate and description of changes in body form are based mainly on specimens reared from eggs taken in surface tows from Kaneohe Bay on 22 February 1971 (Table 1). At that time the bay surface temperature was 24.4°C. Rearing tank temperatures ranged from 22.1° to 25.9°C, with a mean of 24.5°C, so the thermal environments were similar. As stated in the methods section, the salinity and oxygen level in the tank remained similar to those in the bay throughout the experiment. Without data on the quantity and quality of food for any given time of the rearing period, however, it is impossible to assess the reality of the growth rate. The general shape of the curve (a nearly straight line) and the absence of any mass mortality suggests that the rearing environment was at least adequate throughout the experiment. The absence of prolonged lags in growth suggest the absence of periods of major stress.

The growth curve (Figure 4) is composed of at least three segments of differing slope: from hatching through day 2; day 3 through day 5; and from day 6 onward. The inflection in the curve at day 2-3 coincides with the near final absorption of yolk, and perhaps more important, the development of a functional mouth. No major structural change occurs at day 6 which might be linked to that inflection. Among four rearing trials, the change in length from hatching to day 6 (ca. 2.5 mm) was extremely variable. In two of the trials, larvae increased in length through day 3, then shrank. It appears that the variability in early omaka growth rate might be linked to the success of larvae in obtaining their first exogenous energy (Thomas Cooney, pers. comm.—M.A. thesis research). Owing to this variability, the statistical description of the growth rate of larvae through day 5 is of little value. Interpolation between mean (preserved) size at hatching (1.03 mm) and mean size of day 6 (3.05 mm) yields an estimate growth of 0.35 mm/day.

The relationship chosen to express larval growth beyond day 6 was the linear regression: 

\[
SL (\text{in mm}) = -0.3016 + 0.4362 \times \text{(age in days)}
\]

(Figure 4), as determined from 153 preserved specimens. A slightly better fit would have been obtained with a more complex function, but the improvement in the curve would be slight.

The greatest departures from linear growth occurred at day 14 and day 28 (SL = 5.2 mm and 11.4 mm, respectively). No major morphological developments occurred at these sizes, so the causes (if the departures are real) are not known. The generally poorer fit of the data to the curve at the largest sizes is probably attributable to sampling. As the vagility of larvae increases with size, the probability increases that the smaller
larvae in a tank are selected for preservation. This effect is apparent from the larger (than predicted from the curve) mean size of the five fish on day 36, which were the last specimens in the tank when it was emptied.

One source of error in relating early growth rates of larvae to those of larger larvae is their shrinkage upon preservation. Five groups of ten live larvae (one to five days old), ranging in mean standard length from 2.46 to 2.85 mm, ranged in length from 2.13 to 2.55 mm 24 h after preservation. Shrinkage was also observed to begin within seconds after death when larvae died while being observed microscopically. This latter observation suggests that shrinkage was not entirely due to the effects of formaldehyde on body proteins. The percent shrinkage was not correlated in a simple way with size. Although, presumably, this percentage decreases with increased size of larvae, the shrinkage values, which ranged from 8 to 22% in the five groups, can introduce significant error into estimates of early larval growth. Newly hatched larvae shrank as much as 30% when they died.

Farris (1959) described two growth stanzas of the jack mackerel, viz. (A) from hatch to day 3 and (B) from day 3 to 7. If these correspond to our first two segments, then the second segment (day 3-7) of growth in omaka is twice that of jack mackerel (0.195 mm/day compared to 0.10 mm/day). Alternatively, comparing growth from hatching to yolk absorption—day 3 in omaka, day 6 in jack mackerel—yields a similar difference, 0.48 and 0.26 mm/day, respectively. The comparisons suggest that effects of starvation may occur prior to complete yolk absorption. Farris’ growth rates for segment B (on starved fish) may be underestimates. Lasker, Feder, Theilacker, and May (1970) found that larvae may begin to feed before complete yolk absorption. Comparisons need to be made between starved and fed yolk-sac larvae of the same species reared in the same physical environment before a definitive answer can be reached.

**BODY PROPORTIONS**

As Marr (1955) pointed out, expression of relationships between body dimensions as ratios contributes nothing more than plots of the original measurements, so the latter were used. Relationships between standard length and 1) head length, 2) eye diameter, 3) snout to anus length, and 4) body depth at pectoral fin were all adequately described by an equation of the form: \( Y = a + b(SL) \). All of the data used in the regressions are from one series of reared omaka larvae (Table 1). The ratios all adequately describe specimens captured in the field.

In the following discussions of these relationships, comparisons are made between the omaka and jack mackerel (\( T. \ symmetricus \)), described by Ahlstrom and Ball (1954). The latter is the only carangid larva for which these kinds of data are published. With similar data for other carangid species, these may prove useful in a key to carangid larvae.

**Head Length**

Head length was related to standard length according to the equation: \( HL = -0.2796 + 0.3477(SL \text{ in mm}) \) (Figure 5). Unlike \( T. \ symmetricus \) (Ahlstrom and Ball, 1954), there was no inflection in the curve at ca. 4 mm. The slope of the regression line for omaka (0.3477) is not very different than that for the jack mackerel (0.378), so this ratio would not be very useful by itself in distinguishing the two species. Ahlstrom and Ball (1954) did find a different slope (0.556) in the jack mackerel larvae smaller than 4.2 mm, but several of our smaller larvae would fit either regression.

**Eye Diameter**

The relationship between eye diameter and
standard length was described by a straight line of the equation: ED = -0.1089 + 0.1266 (SL in mm) (Figure 6). Omaka larvae have almost the same (proportional) eye size as T. symmetricus (0.127), reported by Ahlstrom and Ball (1954). Therefore, this ratio is not useful as a distinguishing characteristic.

The omaka eye was somewhat ovoid with the blunt end anterior. The posterior, more acute, end of the eye became more angled up to day 4, then the trend was reversed so the juvenile round eye shape was reached by day 20 (SL = 8.27). The "squarish distortion" reported for T. symmetricus (Ahlstrom and Ball, 1954) did not occur in omaka.

Snout-to-Anus Length

The snout-to-anus length increased 0.5347 mm for each millimeter increment in standard length throughout larval development (Figure 7). As might be expected from the body depth differences between omaka and jack mackerel, the ratio between snout-to-anus length and standard length of omaka is slightly smaller than that for the jack mackerel (0.581), the latter being a more elongate larva. Again, however, the difference is probably too small to be useful in separating the species.

Body Depth at Pectoral Insertion

The relationship between the body depth and standard length remained constant throughout larval development (Figure 8). No inflection was evident in the omaka, as was reported for T. symmetricus by Ahlstrom and Ball, 1954 (larvae smaller than 4.2 mm). The slopes of the regression lines (0.425 for omaka and 0.278 for jack mackerel larvae) are different enough to be used to distinguish these species over 4 mm; omaka larvae are considerably deeper-bodied. The other common carangid in Kaneohe Bay, G. speciosus, has a still deeper-bodied larva (our unpublished data); so this ratio appears the most useful of the four discussed to distinguish at least these three species.
SUMMARY

1. Omaka eggs were pelagic and spherical with a single oil droplet and segmented yolk. The diameter was about 700-740 \( \mu \).

2. Egg development occurred in three distinguishable stages: early—fertilization to blastopore closure; middle—to tail flexure; and late—to hatching. Respective duration times at 24.5°C were 11-12 hours, 11-12 hours, and 0.5-1 hour.

3. Yolk sac larvae hatched at a length of 1.3-1.7 mm with the oil globule positioned forward in the yolk sac.

4. By the fourth day (SL = 2.6 mm), the eyes were pigmented, the yolk and oil globule absorbed, and the mouth functional.

5. Fin development (first appearance of lepidotrichia) occurred in the order: caudal (3.4 mm); pectoral (5.4 mm); anal and soft dorsal (5.4-5.5 mm); spiny dorsal (5.8 mm); and pelvic (6.2 mm).

6. Unlike many carangid larvae, omaka did not develop a serrated crest behind the head.

7. Values for ratios of body proportions to standard length were: head length, 0.3477; eye diameter, 0.1266; snout-to-anus length, 0.5347; body depth, 0.4246. Only the body depth/SL ratio was useful in separating omaka from jack mackerel and certain other Hawaiian carangid larvae.

8. The growth of our cultured omaka after day 6 was adequately described by a straight line with slope 0.44. Before day 6, growth was extremely variable, averaging about 0.35 mm/day.

9. Of primary use in separating omaka from jack mackerel larvae (the only other similarly described carangid larva) were pigment pattern, the absence of a serrated dorsal ridge behind the head, and the difference in the ratios of body depth to standard length.

10. Significant decreases in size (up to 33%) and pigmentation of larvae occurred upon preservation. Both of these effects decreased with age of larvae.

11. Although based on larvae reared in the laboratory, our data relating growth and development to time would be expected to simulate those from natural tropical habitats, especially the data for fish eggs and early larva.

ACKNOWLEDGMENTS

Throughout the paper reference is made to the excellent paper by Ahlstrom and Ball (1954), describing the eggs and larvae of the jack mackerel (\textit{T. symmetricus}). The authors acknowledge a debt to Ahlstrom and Ball for their example. Many of their descriptive techniques were used by us, and, in our opinion, should be considered a standard for all larval fish descriptions. Larval fish taxonomy suffers greatly from dissimilarities among descriptive techniques. Thanks are also extended to David Hashimoto, Senior Technician at the Hawaii Institute of Marine Biology, for rearing the larvae. This research was, in part, supported by University of Hawaii Sea Grant No. GH-93. (UNIHI-SEAGRANT-.IC-74-02.)

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