

MORPHOLOGY AND DISTRIBUTION OF LARVAL WAHOO  
*ACANTHOCYBIUM SOLANDRI* (CUVIER)  
IN THE CENTRAL PACIFIC OCEAN

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ABSTRACT

Descriptions are presented of the early developmental stages of the wahoo, *Acanthocybium solandri* (Cuvier), ranging from 2.8 to 23.7 mm. in standard length. Developmental changes in body pigmentation, body form, fin formation, and ossification of bones and other hard parts were studied for 38 larvae collected in the central Pacific Ocean. Drawings of larvae at various sizes are included. Certain adult characters are discussed, such as: the number of vertebrae and the vertebral formula; the number of

spines and rays in the first dorsal, second dorsal, and anal fins; and the number of dorsal and anal finlets.

Larval and adult wahoo live in the open ocean as well as near land. The adults spawn throughout the tropical and subtropical waters between lat. 30° N. and 25° S. The species spawns throughout the year in the equatorial waters between lat. 14° N. and 15° S., and during the northern and southern summer in areas farther from the Equator.

Although considerable knowledge has been gained in recent years about the early life history of the commercially important mackerels and tunas, the larval and juvenile stages of many scombroid fishes are poorly known. This is particularly true of the larvae of the wahoo, *Acanthocybium solandri* (Cuvier). The smallest wahoo previously recorded was a 23.7-mm. juvenile from the central Pacific Ocean (Strasburg, 1964). Prior to this record, the only mention of a young wahoo in the literature was a 28-cm. juvenile caught off Japan in 1917 (Kishinouye, 1923).

The wahoo, a member of the Scombridae, is usually taken in small quantities as incidental catches on the longline, and in larger quantities by surface trolling (Iversen and Yoshida, 1957). It is found in tropical and subtropical areas of the oceans.

While sampling for tuna larvae in the central Pacific Ocean from 1950 to 1962, the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, collected 38 young wahoo from 2.8 to 17.8 mm. SL (standard length) in plankton net hauls. The morphology and dis-

tribution of the larvae were studied to increase our knowledge of the early life history of the scombroid fishes.

This paper describes the developmental changes in body pigmentation, fin formation, and ossification of various bones. It also discusses certain adult characters that require definition, such as the number of vertebrae and the vertebral formula, the number of spines and rays in the dorsal and anal fins, and the number of finlets. The growth rates of various body parts are included, as well as new information on distribution of the species in the central Pacific Ocean, as determined from captures of the larvae and adults.

COLLECTION AND TREATMENT  
OF MATERIAL

Plankton hauls were made with a 1-m. plankton net on 32 cruises of the Bureau of Commercial Fisheries research vessels *Hugh M. Smith* and *Charles H. Gilbert* from May 1950 to July 1962. The types of hauls varied slightly over the years; generally, the net was hauled obliquely from a depth of 200 m. to the surface before 1956, but from 1956 to 1962, it was

hauled obliquely from 140 m. to the surface. On a few cruises the net was hauled obliquely from a depth of 60 m. and horizontally near the surface. Each haul lasted 30 minutes.

Of the 1,643 plankton samples obtained, 600 were taken near the Hawaiian Islands (lat. 15° to 30° N., long. 150° to 165° W.) and most of the others in the equatorial region (lat. 10° N. to 10° S., long. 110° to 170° W.). The 38 wahoo larvae were found in 34 plankton samples; 2 larvae were found in two samples and 3 larvae in one (fig. 1 and table 1). All

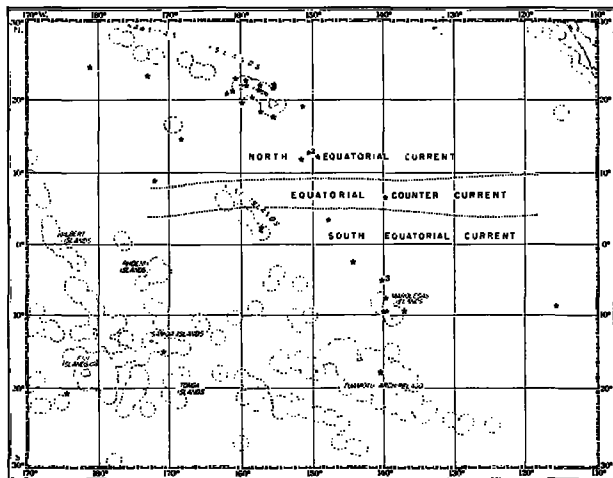


FIGURE 1.—Locations at which wahoo larvae were taken in plankton net hauls. Each star represents a single larva. A star and number show catches of two or more larvae. Broken lines indicate a distance of 110 kilometers from land. Major currents of the central Pacific Ocean are shown.

the larvae were preserved in a 10 percent solution of Formalin.<sup>1</sup> The wahoo larvae ranged from 2.8 to 17.8 mm. SL. The size range was extended to 23.7 mm. by the inclusion of a juvenile (collected in a midwater trawl) described by Strasburg (1964).

Of the 38 larvae, 21 were cleared in a weak (1-2 percent) solution of potassium hydroxide and stained with alizarin in the technique described by Lipman (1935). Standard length and various body parts were measured, and counts of fin rays and spines, myomeres, teeth, and branchiostegal rays were made before clearing and rechecked after staining. Verte-

<sup>1</sup> Trade names referred to in this publication do not imply endorsement of commercial products.

TABLE 1.—Record of larval and juvenile wahoo captured in plankton net hauls in the central Pacific Ocean, 1950-62

Limits of latitude and date	Cruise	Position		Local time	Surface temperature ° C.	Distance from land Km.	Standard length Mm.
		Lat.	Long.				
<b>Lat. 15°-30° N.</b>							
May 17, 1950.	HMS-4 <sup>1</sup>	21°08' N.	161°06' W.	0925	24.6	139	3.4
May 18, 1950.	HMS-4	19°25' N.	159°50' W.	1048	24.8	185	4.1
May 24, 1950.	HMS-4	21°53' N.	159°09' W.	0120	22.8	98	2.8; 4.2
June 17, 1954.	HMS-26	20°51' N.	161°59' W.	0512	25.9	222	3.1
July 1, 1950.	HMS-5	22°58' N.	173°00' W.	2312	26.1	333	7.4
July 12, 1962.	CHG-58 <sup>1</sup>	22°44' N.	160°47' W.	0100	25.5	139	5.8
July 22, 1951.	HMS-10	22°27' N.	159°15' W.	0715	25.6	37	4.8
July 30, 1951.	HMS-10	21°25' N.	155°30' W.	1343	25.5	110	4.3
Aug. 5, 1953.	HMS-21	21°10' N.	167°28' W.	0240	25.4	28	5.5
Aug. 7, 1953.	HMS-21	21°53' N.	155°21' W.	0315	24.8	157	3.8
Aug. 16, 1960.	CHG-48	24°15' N.	178°54' E.	1800	26.7	692	8.7
Aug. 19, 1950.	HMS-6	20°15' N.	158°24' W.	2340	26.7	130	8.4
Aug. 21, 1953.	HMS-21	17°40' N.	155°30' W.	0120	25.0	130	4.6
Aug. 21, 1953.	HMS-21	18°14' N.	157°09' W.	2058	25.8	148	4.3
Sept. 10, 1952.	HMS-17	21°48' N.	157°18' W.	1149	25.2	37	4.4
Oct. 4, 1951.	HMS-11	19°00' N.	151°19' W.	0750	25.4	389	5.7
<b>Lat. 14° N.-14° S.</b>							
Jan. 12, 1959.	HMS-50	12°42' N.	150°24' W.	2006	26.1	890	7.6; 7.9
Feb. 9, 1958.	HMS-43	7°35' S.	139°40' W.	2110	28.5	46	7.8
Mar. 13, 1954.	CHG-15	8°42' S.	115°39' W.	1954	26.4	2,057	5.8
Mar. 16, 1956.	HMS-33	5°03' S.	140°16' W.	1949	26.3	315	5.2; 6.2; 6.6
Apr. 16, 1954.	CHG-15	2°09' N.	157°05' W.	1932	27.7	28	4.3
Apr. 23, 1958.	CHG-38	2°34' S.	144°12' W.	2003	28.4	732	17.8
Apr. 25, 1958.	CHG-38	3°15' N.	147°40' W.	2003	28.6	1,047	9.0
May 20, 1952.	HMS-15	6°36' N.	139°44' W.	1035	27.7	1,556	6.6
June 10, 1954.	HMS-26	14°33' N.	168°25' W.	1739	26.6	232	10.7
June 19, 1958.	HMS-45	12°02' N.	149°03' W.	2012	27.0	1,055	5.9
July 6, 1950.	HMS-5	8°54' N.	172°00' W.	2012	26.9	912	4.5
Aug. 30, 1956.	CHG-30	9°22' S.	137°01' W.	2000	25.2	187	9.2
Oct. 6, 1957.	CHG-35	11°42' N.	151°30' W.	0000	27.6	908	5.2
Dec. 1, 1957.	CHG-35	9°33' S.	139°51' W.	0839	27.5	56	10.2
Dec. 1, 1957.	CHG-35	9°34' S.	139°50' W.	1406	28.6	56	3.9
<b>Lat. 15°-25° S.</b>							
Feb. 14, 1962.	CHG-55	20°34' S.	175°29' E.	2004	27.0	145	13.2
Mar. 5, 1957.	HMS-38	17°56' S.	140°28' W.	2030	28.1	28	2.8
Mar. 13, 1962.	CHG-55	15°05' S.	170°48' W.	2000	27.9	56	6.8

<sup>1</sup> Bureau of Commercial Fisheries research vessels, Hugh M. Smith (HMS) and Charles H. Gilbert (CHG).  
<sup>2</sup> Length of 7.9-mm. and 6.6-mm. specimens estimated.

brae were counted after the specimens had been stained. In a few instances where the body was slightly bent, a small piece of glass slide was placed over the specimen to straighten it before measuring. The following measurements were made on each specimen:

**Standard length:** The distance from anteriormost tip of snout to posterior end of notochord; after the notochord had flexed dorsad, the distance from tip of snout to posterior edge of hypural complex was measured.

**Head length:** The distance from anteriormost tip of snout to dorsal end of gill cover.

**Snout length:** The distance from anteriormost tip of premaxillary to anterior edge of orbit.

**Orbit diameter:** The greatest distance measured along the longitudinal axis of the body.

This measurement was chosen over eye diameter because the eyes tend to shrink in preservative, and some had been lost.

**Premaxillary length:** The distance from tip to anterior edge of the mesethmoid, measured along the dorsal profile of the snout.

**Upper and lower jaw lengths:** The distance from anteriormost tip to posterior edge of maxillary and mandible.

**Body depth:** Vertical distance immediately behind the anus.

**Snout to anus distance:** The straight-line distance from anteriormost tip of snout to posterior edge of anal opening.

**Snout to first and second dorsal fins:** the straight-line distance from anteriormost tip of snout to origins of the fins.

### DEFINITION OF CERTAIN ADULT CHARACTERS

In the identification of larval and juvenile fishes, it is important that the adult characters be defined accurately because they are often applicable to the young as well. One useful skeletal

character for the diagnosis of adult scombrids is the number of vertebrae. Previous literature on the wahoo contains a wide variation in vertebral number, which is unusual in the family Scombridae. The number of vertebrae among most scombrids is known to be nearly constant (Ford, 1937; Godsil and Byers, 1944; Clothier, 1950), but a number of reports with descriptions of wahoo (table 2) give the vertebral formula as 23 to 33 + 31 to 34 = 54 to 66 (precaudal vertebrae + caudal vertebrae = total vertebrae).

I found that all papers published after 1923 which contained the formula 23 to 33 + 31 to 34 = 54 to 66 included Kishinouye (1923) as a reference. Kishinouye (1908, 1915, 1923) did not, however, discuss the wide range in number of precaudal vertebrae, or refer to the seemingly low count of 23 precaudals. It seems likely that the 23 first reported by Kishinouye (1923) is a typographical error and that 32 is the correct number.

Other evidence supports my suspicion that the reported low count of 23 precaudal verte-

TABLE 2.—Counts of some meristic characters of wahoo

Source	Length <sup>1</sup>	First dorsal spines	Second dorsal fin			Anal fin			Vertebrae		
			Rays	Finlets	Total	Rays	Finlets	Total	Pre-caudal	Caudal	Total
<i>From literature</i>	<i>Mm.</i>	<i>Number</i>	<i>Number</i>	<i>Number</i>	<i>Number</i>	<i>Number</i>	<i>Number</i>	<i>Number</i>	<i>Number</i>	<i>Number</i>	<i>Number</i>
Cuvier and Valenciennes (1831)		26	11	9	20	12	10	22			
Lay and Bennett (1839)		25		9½			9½				
Poey (1860) <sup>2</sup>	1,300 (FL)	25									
Doderlein (1872) <sup>2</sup>		26									
Jordan (1885)		24	I, 12	9	22	I, 12	9	22			
Jenkins (1904)		27	13	9	22		8	20			
Jordan and Evermann (1905)		25									
Kishinouye (1908)		26	11	10	21	11	9	20			65
Starks (1910)									32	34	66
Kishinouye (1915)		26	11	9	20	11	9	20	32 or 33	31	63-64
Kishinouye (1923)		26	11	9	20	11	9	20	32-33	31	63-64
Kishinouye (1923)	1,092 (FL)	26	11	9	20	11	9	20	33	31	64
Meek and Hildebrand (1923)	1,200 (FL)	26	12	9	21	II, 10	9	21			
Conrad and La Monte (1937)	1,468 (FL)										
Conrad (1938)		26							31	31	62
Morice (1953)		26		4			4				64
Strasburg (1964)	23.7 (SL)	27			24			23	32	31	63
<i>Specimens examined by present author</i>											
Longline fishing	1,435 (FL)	27	12	9	21	13	9	22	32	33	65
Do.	1,554 (FL)	27	13	9	22	12	9	21	31	32	63
Do.	1,252 (FL)	27	12	9(10)	21	12	9(10)	21	32	31	63
Do.	1,066 (FL)	27	12	9(10)	21	13	9(10)	22	32	31	63
Do.	1,300 (FL)								32	30	62
Do.	1,245 (FL)								32	31	63
Marlin stomach	159 (SL)								32	31	63
Do.	152 (SL)								32	31	63
Skipjack stomach	117 (SL)								31	33	64
Plankton haul	17.8 (SL)	27			23			22	33	30	63
Do.	13.2 (SL)	27			23			22	32	31	63

<sup>1</sup> FL (fork length); SL (standard length).

<sup>2</sup> From Lütken, 1880.

<sup>3</sup> Number of precaudal and total vertebrae as corrected.

<sup>4</sup> From figure.

<sup>5</sup> Last 2 finlets fused.

brae is erroneous. First, no other report in the literature shows a wahoo having between 23 and 31 precaudal vertebrae, as one would expect if these counts encompassed the actual range of variation; instead, the number of precaudal vertebrae has always been cited as 31, 32, or 33 when it was referable to a particular specimen. Second, I found that six adult wahoo taken during a cruise of the *Charles H. Gilbert* to the southwestern Pacific in 1963 had either 31 or 32 precaudal vertebrae and 30 to 33 caudal vertebrae (table 2). Six juvenile specimens from other sources had 31 to 33 precaudal and 30 to 33 caudal vertebrae.

Although the number of vertebrae may vary slightly more in wahoo than in tunas, the variation is less than Kishinouye (1923) reported. The vertebral formula for wahoo can be restated as  $31 \text{ to } 33 + 30 \text{ to } 34 = 62 \text{ to } 66$ ; the most typical formula is  $32 + 31 = 63$ .

Other adult characters that are useful for identifying young wahoo are the number of spines and rays in the dorsal and anal fins. Varying counts have been given for these characters, also. Different authors have reported 24 to 26 first dorsal spines, except Jenkins (1904) who reported 27 (table 2). Each of four adult wahoo that I examined had 27 first dorsal spines, but the last 2 were greatly reduced and were buried beneath the skin and muscle tissue. Although it was relatively easy to locate the 26th spine by probing, it was extremely difficult to locate the 27th even with careful dissection of skin and musculature. This difficulty may account for the generally lower spine counts reported previously for the first dorsal fin. Three juvenile wahoo that I examined, including the specimen previously reported by Strasburg (1964) as having 26 spines, also had 27 first dorsal spines. The last spine was extremely small and appeared almost to be the first spine in the second dorsal fin. The number of spines in the first dorsal fin of the wahoo thus appears to be constant at 27.

The number of rays seems to vary slightly in the second dorsal (12 to 14) and anal fins (12 to 13). The counts of 11 rays for both fins in all of Kishinouye's reports and 11 rays for the second dorsal fin reported in Cuvier and Valen-

ciennes (1831: table 2) may be too low (by error), or may represent extreme variations.

In adult wahoo the dorsal and anal finlets appear to be constant at 9, although Robert H. Gibbs, Jr. (personal communication) found the number to vary between 7 and 9 in 16 specimens he examined. While preparing the skeletal material for the present study, I observed that the posteriormost dorsal finlet and the posteriormost anal finlet, which appeared to be perfectly formed single finlets, were actually composed of two separate finlets that had become fused. The extra finlet is clearly reflected in the total ray and finlet counts of the three smallest wahoo (table 2). In both dorsal and anal series the number of elements is generally larger than the combined ray and finlet number of the adults.

#### DESCRIPTION AND DEVELOPMENT OF LARVAL AND JUVENILE WAHOO

Identification of wahoo larvae is simplified because it is a single species (Lütken, 1880; Jordan and Evermann, 1905; Beaufort and Chapman, 1951; Collette and Gibbs, 1963) and therefore the problem of differentiating morphologically similar species is eliminated. The larval characteristics described and illustrated in this paper were obtained from specimens that had been preserved in 10 percent Formalin for many years and were sometimes based on single specimens. The description, therefore, may differ slightly from that of newly caught specimens.

Larval wahoo less than 3.4 mm. SL are readily recognized by several characteristics: (1) the large number of body segments in relation to body length; (2) the elongate viscera; and (3) the presence of one or two black pigment spots on the ventral surface of the caudal peduncle, similar to those on larvae of skipjack tuna (*Katsuwonus pelamis*). Larvae as small as 2.8 mm. have 63 to 65 body segments, including the urostyle (compared with 42 to 43 segments in skipjack), and the viscera extend well over one-half the body length. Larvae above 4.4 mm. can be recognized by the large number of body segments, the extent of the viscera (over two-thirds the body length), and

the length of the snout (more than twice the diameter of the orbit).

The development of the larval and early juvenile stages is discussed in the following sequence: (a) changes in pigmentation, (b) changes in body form, and (c) sequence of ossification. The term "larva" includes all specimens from the smallest to the juvenile stage, which starts at the time the full complement of spines and rays in all fins has ossified. In wahoo this point is reached before 23.7 mm. SL. The term "postlarva" is not used here. Standard length is the measure of body length, except when specified otherwise.

#### CHANGES IN PIGMENTATION

As is true for all fish larvae preserved in Formalin, the only pigment spots visible in wahoo larvae are the melanophores. Unlike larvae of *Trachurus* (Ahlgren and Ball, 1954), *Exocoetidae* (personal observation), *Istiophoridae* (Ueyanagi, 1963), *Coryphaena* (Mito, 1960), and others, the wahoo larvae have comparatively few melanophores. Large changes in pigmentation as the larvae increase in size are seen only in four areas: (1) snout, (2) base of second dorsal fin, (3) base of anal fin, and (4) digestive tract (figs. 2 and 3). The following descriptions of pigmentation are based on the left side of the body as seen in lateral view.

##### Head Pigmentation

The midbrain area remains unpigmented in larvae smaller than 4.4 mm. (fig. 2A and B). The only exception was a 3.1-mm. larva which possessed a melanophore in this location. A single melanophore is present on the anterior portion of the midbrain in about half the larvae between 4.4 and 5.5 mm. (fig. 2A). Pigmentation in the anterior portion of the midbrain increases gradually with body length; 6 melanophores are present in the 10.7-mm. larva (fig. 3C), and about 27 in larvae up to 13.2 mm. long (fig. 3D).

Pigmentation appears on the forebrain much later than on the midbrain and the number of melanophores is small. A single melanophore appears on the forebrain in larvae about 7.4 mm. long, and the number of melanophores increases to only four or five in larvae up to 17.8 mm. long (specimen similar in appearance

to that of figure 3D, except for heavier pigmentation).

Lateral pigmentation on the posterior portion of the head is completely lacking in larvae up to 13.2 mm. long, but about 50 small melanophores are present in the area posterior to the orbit and on the surface of the preopercle in larvae about 17.8 mm. long. In larvae of yellowfin tuna (*Thunnus albacares*) and skipjack tuna, some melanophores usually are present in the postorbital region in specimens shorter than 6.0 mm.

Pigmentation on the snout develops in two major areas: near the primordial nasal cavity and on the tip of the upper jaw. It is present on the snout in the smallest larva as a single small melanophore within the primordial nasal cavity and two or three melanophores on the tip of the upper jaw (fig. 2A). The pigmentation at the primordial nasal cavity develops slowly; additional melanophores are added within the cavity and on the surface of the snout anterior to it. As the nostrils form (when the larvae are between 10.7 and 13.2 mm. long), a few more melanophores appear on the surface of the snout between the anterior and posterior nostrils. The number of melanophores in this area is small, however, for no more than 13 to 15 are present in the 13.2-mm. larva (fig. 3D).

The number of melanophores increases slowly on the anterior portion of the upper jaw of larvae up to a length of about 4.3 mm.; however, above this size, as the upper and lower jaws begin to grow more rapidly in relation to body length, pigmentation on the anterior portion of the upper jaw increases noticeably. At a length of 6.8 mm. (fig. 3A), two or three rows of 18 to 25 melanophores are on the anterior part of the upper jaw. The number of melanophores increases with further growth of the fish, and the entire surface of the upper jaw anterior to the mesethmoid is covered in larvae larger than 13.2 mm. (fig. 3B-D). Additional melanophores develop posteriorly on the snout, and in the 17.8-mm. larva the pigmentation on the anterior portion of the upper jaw and around the nostrils has merged into a single, large pigmented area.

The tip of the lower jaw in larvae 2.8 mm. long has few melanophores, but the number

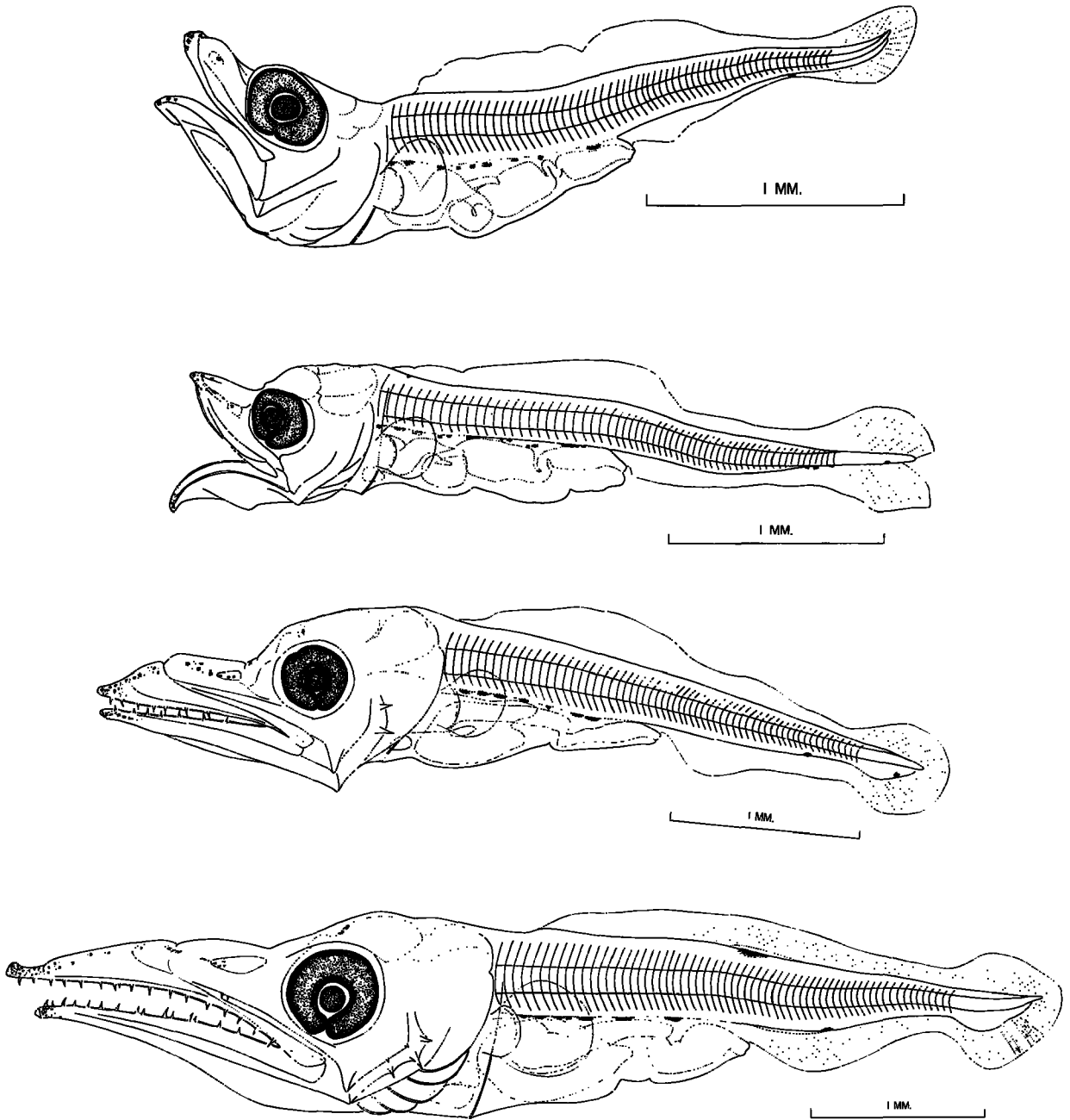


FIGURE 2.—Development of the larva of wahoo: A. larva, 2.8 mm. long; B. larva, 3.4 mm. long; C. larva, 4.4 mm. long; D. larva, 5.8 mm. long.

increases gradually to about seven or eight in the 8.4-mm. larva (fig. 3B). No melanophores appear on the conical cartilaginous projection at the tip of the jaw in larvae shorter than 5.8

mm., but some are present at lengths above 6.8 mm. In larvae over 10.7 mm., melanophores on the lower jaw are found only on the cartilaginous projection (fig. 3A-D).

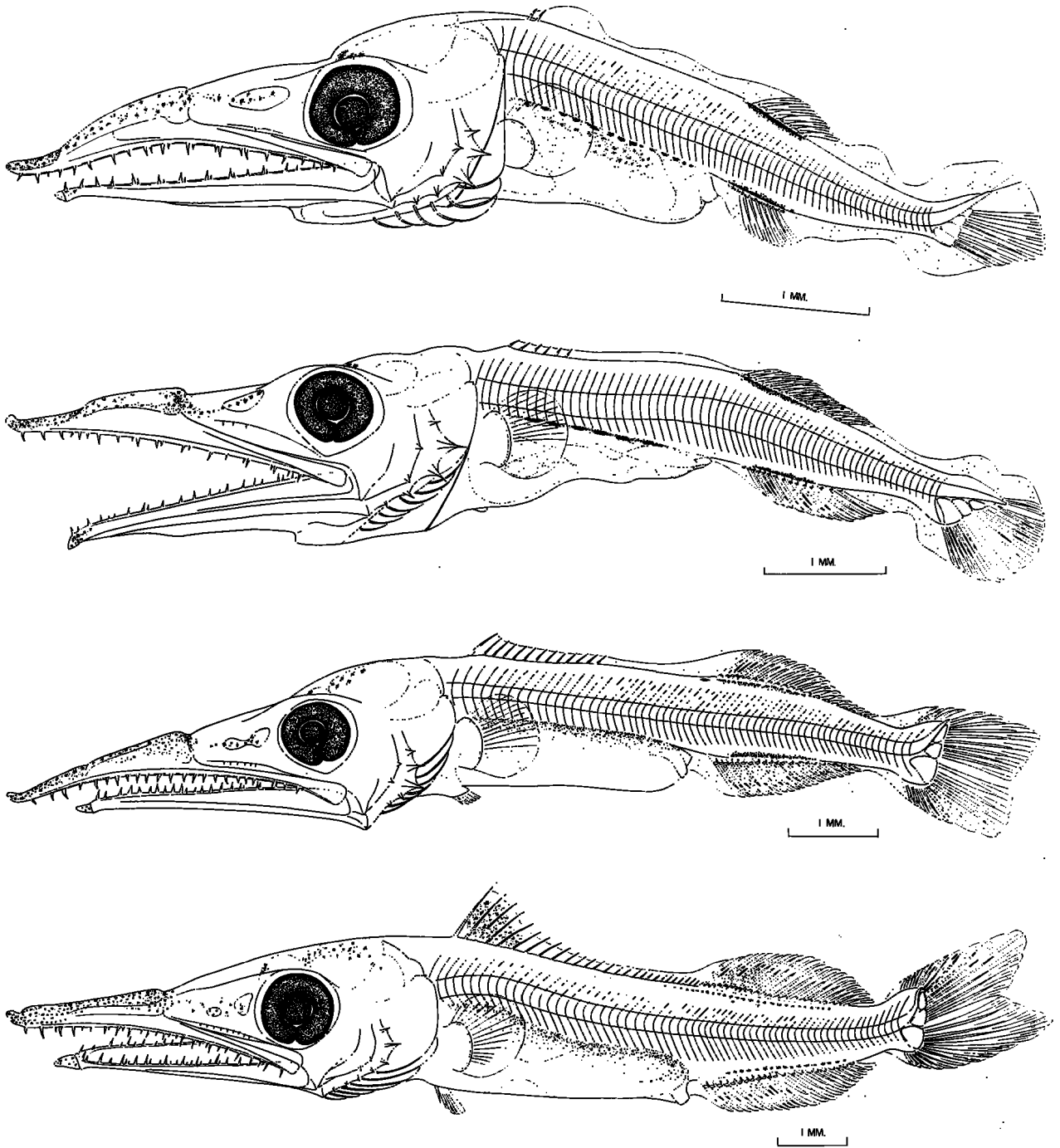


FIGURE 3.—Development of the larva of wahoo: A. larva, 6.8 mm. long; B. larva, 8.4 mm. long; C. larva, 10.7 mm. long; D. larva, 13.2 mm. long.

#### Preanal Trunk Pigmentation

The preanal trunk region is free of dermal pigmentation in larvae smaller than 10.7 mm.; the only pigmentation present is internal, along the dorsal part of the abdominal cavity. The pigmentation here consists of 7 to 10 large pigment spots, each composed of either a single melanophore or several small melanophores which are contiguous. These melanophores can be seen through the thin abdominal musculature in larvae smaller than 8.4 mm. (fig. 2A-D). The number of abdominal melanophores increases and they spread out ventrally over the peritoneum when the larvae are about 6.8 mm. long, but not in all larvae—see, for example, the 8.4-mm. larva of figure 3B. Evidently this spreading of melanophores varies among individuals. The abdominal melanophores of the 10.7-mm. larva have spread ventrally over the dorsal one-third of the digestive tract, and a few dermal melanophores have developed on the surface of the body over the dorsal part of the abdominal region (fig. 3C). Subsequently, only these dermal melanophores are noticeable, owing to a thickening of the abdominal musculature. Dermal pigmentation is lacking along the ventral surface of the body in the abdominal region. The 17.8-mm. larva has about 14 small dermal melanophores on the dorsal part of the first few myomeres, and a wide band of dermal melanophores over the lower half of the body posterior to the pectoral fin. This band extends to the level of the posterior end of the base of the anal fin.

Orton (1953) has shown that in certain teleost larvae, including two scombroids, *Pneumatophorus diego* and *Sarda lineolatus*, the pigment cells along the dorsal region of the body migrate ventrally and that in all pelagic species that she examined the first "wave" of pigment migration is typically completed in 2 days after hatching. In all except one wahoo larvae that I examined, the pigment spots were in a ventral position. One larva had a pigment spot at the nape (fig. 2B); possibly this was a melanophore that had not yet migrated ventrally.

#### Postanal Trunk Pigmentation

Two stages of pigment formation are evident

in the postanal trunk area. The first is seen in larvae less than 4.4 mm. long, which usually have one but sometimes two or three melanophores on the ventral midline of the body near the caudal peduncle, and, in most specimens, a very small melanophore is near and ventral to the posterior end of the notochord (fig. 2A-D). These pigment spots resemble those in larvae of skipjack tuna. The second stage is seen in larvae 5.8 to 6.2 mm. long (fig. 2D); the melanophore at the caudal peduncle region has migrated anteriorly to the base of the anal fin and has increased in size. The 6.8-mm. larva has a group of fine granules of pigment that extend along the base of the anal fin (fig. 3A) in place of the enlarged melanophore; this pattern prevails until the larvae are more than 10.7 mm. long. In the 13.2-mm. larva, the granules of pigment are replaced by a series of evenly spaced melanophores that extend from about the middle of the anal fin to the base of about the eighth anal finlet (fig. 3D).

#### Fin Pigmentation

Fin pigmentation is not extensive, except on the first dorsal fin. Some fins, the pectoral, pelvic, and caudal, are unpigmented throughout the larval and early juvenile stages. Pigmentation on the first dorsal fin develops when the larvae are 10.7 to 13.2 mm. long. At 13.2 mm., at least the first five interspinous membranes of the first dorsal fin are pigmented with scattered melanophores of various sizes (fig. 3D), and at 17.8 mm., the first eight interspinous membranes are pigmented. In the 17.8-mm. larva, melanophores are also developed on the basal portion of nearly all dorsal and ventral finlets. When the juveniles are about 23.7 mm. long (see Strasburg, 1964: fig. 2), the basal half of the entire first dorsal fin and of all dorsal and ventral finlets is darkly pigmented.

#### CHANGES IN BODY PARTS

To study the growth of body parts, measurements (table 3) were made as described previously. Measurements of the larger body dimensions, such as standard length, head length, and distance from snout to anus and snout to second dorsal fin, were made to the



TABLE 3.—Measurements of body parts of larval and juvenile wahoo

Standard length <sup>1</sup>	Head length	Snout length	Orbit diameter	Premaxillary length <sup>2</sup>	Jaw length		Body depth	Distance snout to:			Pectoral fin length <sup>3</sup>	Pelvic fin length
					Upper	Lower		Anus	First dorsal fin	Second dorsal fin		
Mm.	Mm.	Mm.	Mm.	Mm.	Mm.	Mm.	Mm.	Mm.	Mm.	Mm.	Mm.	Mm.
2.8	0.8	0.24	0.26	0.05		0.45	0.20	1.8			(0.29)	
2.8	.8	.25	.26	.05		.45	.20	1.8			(.31)	
3.1	.9					.49	.20	1.9			(.29)	
3.4	1.0	.33	.33	.05		.53	.20	2.0			(.33)	
3.8	1.2	.47	.37	.08		.61	.20	2.4			(.41)	
3.9	1.2	.49	.37	.10		.66	.23	2.5			(.41)	
4.1	1.2	.49	.39	.10		.69	.24	2.5			(.45)	
4.2	1.3	.52	.39	.15		.76	.25	2.5			(.37)	
4.3	1.4	.53	.41	.17		.84	.27	2.7			(.41)	
4.3	1.6	.74	.41	.27		.94	.29	3.0			(.41)	
4.3	1.7	.78	.42	.27		.98	.27	2.9			(.41)	
4.4	1.8	.87	.43	.33	1.09	1.03	.27	3.1			(.41)	
4.5	1.9	.90	.44	.38	1.15	1.07	.33	3.1			(.47)	
4.6	1.9	1.00	.47	.36	1.25	1.16	.38	3.1			(.49)	
4.8	2.1	1.00	.49	.49	1.41	1.28	.38	3.3			(.53)	
5.2	2.2	1.09	.51	.53	1.39	1.31	.43	3.4			(.49)	
5.2	2.3	1.25	.51	.68	1.52	1.39	.44	3.6			(.49)	
5.5	2.4	1.25	.54	.61	1.58	1.47	.41	3.8			(.49)	
5.7	2.6	1.31	.57	.74	1.63	1.50	.47	3.9			(.61)	
5.7	2.4	1.33	.57	.78	1.64		.46	4.1			(.53)	
5.8	2.9	1.55	.57	.80	1.83	1.63	.49	4.3			(.50)	
5.9	2.7	1.52	.57	.86	1.84	1.64	.49	4.1			(.57)	
6.2	2.7	1.64	.57	.94	1.91	1.66	.49	4.3			(.53)	
6.6	3.3	1.93	.68	1.15	2.30	1.97	.55	4.9	3.4	4.3		
6.8	3.3	1.89	.68	1.15	2.35	2.00	.56	4.9	3.7	5.1		Bud
7.4	3.4	1.97	.74	1.23	2.30	1.95	.60	5.2	3.6	5.3		Bud
7.6	3.4	2.01	.78	1.23	2.42	2.11	.64	5.3	3.8	5.4		
7.8	3.6	2.13	.78	1.31	2.62	2.17	.64	5.5	3.9	5.5		
8.4	3.8	2.46	.82	1.56	2.87	2.34	.70	6.0	4.2	6.3		Bud
8.7	3.9	2.34	.82	1.56	2.85	2.30	.68	6.4	4.4	6.5		Bud
9.0	4.0	2.38	.84	1.60	2.87	2.30	.70	6.4	4.4	6.5		Bud
9.2	4.3	2.54	.90	1.68	3.07	2.46	.94	6.4	4.6	6.6		0.16
10.2	4.9	3.03	1.03	1.97	3.65	2.95	1.07	7.6	5.4	7.8		.10
10.7	4.9	3.07	1.09	2.01	3.77	3.07	1.12	7.7	5.5	8.1		.29
13.2	6.4	3.57	1.40	2.25	4.43	3.69	1.48	9.9	6.7	10.0		.82
17.8	7.4	4.06	1.72	2.46	5.12	4.18	2.05	12.9	8.0	13.3		1.50
23.7	9.8	4.61	2.40	2.64	5.66	5.31	2.87	16.0	8.8	16.2		1.83

<sup>1</sup> Two badly damaged larvae (estimated lengths, 6.6 and 7.9 mm.) were not included in the series.

<sup>2</sup> The distance from tip to anterior edge of mesethmoid, measured along the dorsal profile of the snout.

<sup>3</sup> Length of larval pectoral fin in parentheses.

nearest 0.1 mm. at low magnification (7X objective lens) of a dissecting microscope, but that of the smaller dimensions, such as snout length, orbit diameter, premaxillary length, body depth, etc., were made to the nearest 0.01 mm. at high magnification (30X objective lens). At the higher magnification each division on the disc micrometer represented 0.02 mm.

Plots of body part length against standard length indicated varying degrees of nonlinear growth in premaxillary length, snout length, head length, and in body depth. Because snout and head length were found to be affected greatly by a rapid growth of the premaxillary, snout-less-premaxillary length and head-less-snout length were plotted (fig. 4) and compared against standard length.

The relation of these body parts to standard length is best described by the allometric growth equation,

$$Y = bX^\alpha$$

where  $Y$  is the body part,  $X$  is the standard

length,  $\alpha$  is the ratio of the instantaneous growth rates of  $Y$  and  $X$ , and  $b$ , is a constant of proportionality, sometimes referred to as the "initial growth constant" (Simpson, Roe, and Lewontin, 1960). This equation when transformed to logarithms

$$\text{Log } Y = \text{Log } b + \alpha \text{ Log } X$$

is linear.

Because not all the points for each body part could be fitted by a single curve, they were separated into several groups, and regression lines were fitted to each group separately. The original data are plotted in figure 4, and the constants for the allometric growth equations are given in table 4. The subdivision of the data was made after they had been tested for deviations from simple allometry as suggested by Richards and Kavanaugh (1945). Such subdivision of data seems justified on the basis of the tests and on the premise that in nature relative growth may deviate considerably from simple allometry, often revealing the existence

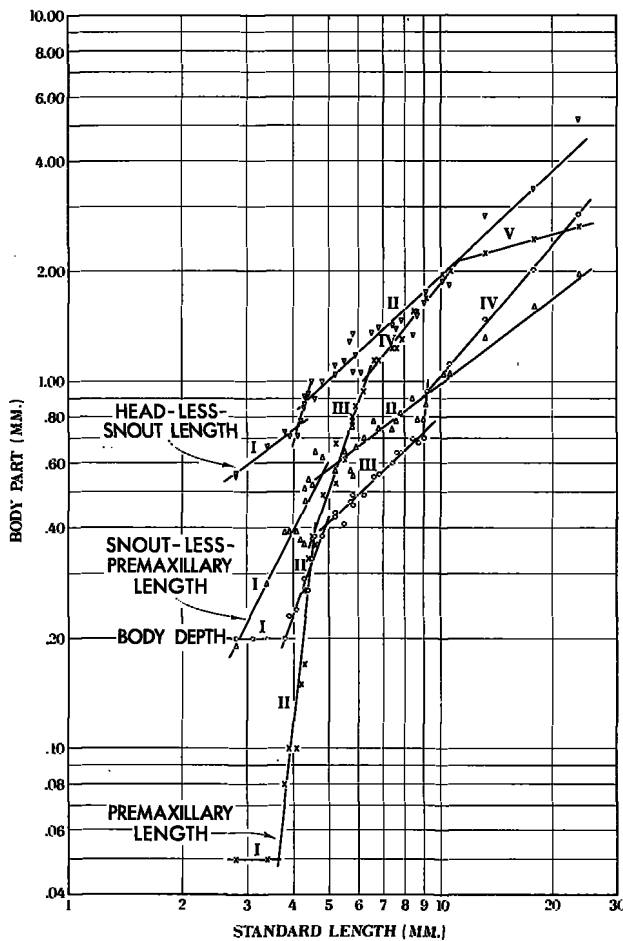


FIGURE 4.—Scatter diagram of body-part measurements plotted against standard length of larval and juvenile wahoo. Straight-line segments are regression lines fitted by the least squares method to respective groups of points. Roman numerals indicate curve segments.

of distinct growth patterns or gradients (Simpson et al., 1960). The subdivision of the wahoo data provides a satisfactory description of the growth relation.

Certain points should be kept in mind when interpreting the curves fitted to the wahoo data. The curves are based on a small number of observations, and some curves are based on a narrow range of standard lengths. Since there is little variability in the wahoo data, the small number of observations appear adequate. The narrow range in standard lengths for some curves appears to be a phenomenon of the growth of many fishes. In addition, it is known that shrinkage of fish larvae occurs in pre-

TABLE 4.—Constants for the allometric equation  $Y=bX^a$  for larvae and juvenile wahoo collected in the central Pacific Ocean, 1950-62

Body part	Curve segment	b	$\alpha$
Premaxillary length	I	0.050	0.000
	II	$.307 \times 10^{-2}$	9.250
	III	$.445 \times 10^{-2}$	2.944
	IV	.099	1.273
	V	1.104	.276
Snout-less-premaxillary length	I	.026	1.969
	II	.167	.771
Head-less-snout length	I	.266	.727
	II	$.523 \times 10^{-2}$	3.500
	III	.216	.951
	IV	.200	.000
Depth	I	$.423 \times 10^{-2}$	2.865
	II	.085	.976
	III	.069	1.180
	IV	.069	1.180

served specimens. It is known also that maximum shrinkage occurs within the first few months of preservation and that shrinkage is small after 1 or 2 years, provided there is no drastic change in the amount and concentration of the preservative. As all wahoo specimens had been preserved more than 4 years and were treated in the same manner, the effects of shrinkage are thought to be negligible.

A difficulty in dealing with changes in body form in wahoo larvae is that the snout grows much more rapidly than do other parts of the body; this differential growth influences comparisons based on standard length. To determine how snout length influences standard length, I computed regressions of body parts on standard length and on standard length-less-snout length for the four body parts shown in figure 4. Both regression lines showed allometric growth in all four body parts. Since the regressions based on standard length fit the data better than do those based on standard length-less-snout length, standard length was used as the basis of comparison.

#### Head and Its Components

The most striking change in body form occurs in larvae longer than 3.8 mm., in which head length increases very rapidly. In larvae of this size, head length is nearly one-third of the standard length, but, in larvae 6.6 mm. long, it represents one half the standard length. This large increase in head length is due mostly to rapid growth of the premaxillary.

Five separate curves are required to describe premaxillary growth in wahoo 2.8 to 23.7 mm. long (fig. 4 and table 4). The first curve

(larvae 2.8 to 3.4 mm. long) shows no increase in premaxillary length ( $\alpha = 0.000$ ), but the second (larvae 3.8 to 4.4 mm. long) and third curves (larvae 4.5 to 6.2 mm. long) indicate positive allometry ( $\alpha = 9.250$  and  $2.944$ , respectively), i.e., the premaxillary grows at a higher rate than standard length or  $\alpha$  is greater than 1.0. The fourth curve (larvae 6.6 to 10.7 mm. long) shows only slight positive allometry ( $\alpha = 1.273$ ) and the fifth curve (larvae 13.2 to 23.7 mm. long) represents negative allometry ( $\alpha = 0.276$ ), i.e., the premaxillary grows at a lower rate than standard length or  $\alpha$  is less than 1.0.

Growth of the snout less premaxillary can be described by two curves. The first curve (larvae 2.8 to 4.5 mm. long) shows positive allometry ( $\alpha = 1.969$ ), but the second curve (larvae 4.6 to 23.7 mm. long) shows negative allometry ( $\alpha = 0.771$ ).

Because the very rapid growth of the snout (premaxillary included) would mask the growth of the remainder of the head and unduly influence head-length measurements, the head-less-snout length was examined. Regression lines for head-less-snout length are markedly different from those for snout-less-premaxillary and for premaxillary length (fig. 4). In larvae smaller than 4.1 mm., the head-less-snout length increases relatively slower than standard length ( $\alpha = 0.727$ ), but, in larvae between 4.2 and 4.4 mm. long, it increases much faster ( $\alpha = 3.500$ ). Above 4.5 mm. the growth rates of head less snout and standard length are nearly alike ( $\alpha = 0.951$ ).

The sharp increase in the premaxillary and snout affects the appearance of the jaws considerably. In larvae shorter than 4.3 mm., the lengths of the upper and lower jaws are equal (table 5); this condition is typical of larvae of yellowfin tuna, skipjack tuna, and frigate mackerel. At a length of 4.4 mm., however, the upper jaw becomes longer than the lower and remains longer throughout the rest of the larval stages (the difference in length is still apparent in the 23.7-mm. juvenile). The greatest difference in jaw lengths is in larvae between 9.0 and 9.2 mm. long, whose ratios of upper to lower jaw are 1.25:1. This inequality diminishes progressively in larger individuals; in the 23.7-mm.

juvenile, the upper jaw is only slightly longer than the lower (ratio, 1.07:1). In the adults the lower jaw is slightly longer than the upper.

TABLE 5.—Ratios of upper jaw length to lower jaw length, upper jaw length to head length, and lower jaw length to head length by standard length for larval wahoo collected in the central Pacific Ocean, 1950-62

Standard length	Upper jaw length/lower jaw length	Upper jaw length/head length	Lower jaw length/head length	Standard length	Upper jaw length/lower jaw length	Upper jaw length/head length	Lower jaw length/head length
<i>Mm.</i>				<i>Mm.</i>			
2.8	1.00	0.562	0.562	5.8	1.08	0.683	0.562
3.1	1.00	0.530	0.545	5.8	1.12	0.631	0.562
3.4	1.00	0.508	0.530	5.9	1.12	0.681	0.607
3.8	1.00	0.508	0.508	6.2	1.15	0.707	0.615
3.9	1.00	0.550	0.550	6.6	1.17	0.697	0.597
4.1	1.00	0.575	0.575	6.8	1.17	0.712	0.606
4.2	1.00	0.585	0.585	7.4	1.18	0.676	0.574
4.3	1.00	0.600	0.600	7.6	1.15	0.712	0.620
4.3	1.00	0.588	0.588	7.8	1.21	0.728	0.603
4.3	1.00	0.576	0.576	8.4	1.23	0.755	0.616
4.4	1.08	0.606	0.572	8.7	1.24	0.731	0.590
4.5	1.07	0.605	0.563	9.0	1.25	0.718	0.575
4.6	1.08	0.658	0.610	9.2	1.25	0.714	0.572
4.8	1.10	0.671	0.610	10.2	1.24	0.745	0.602
5.2	1.06	0.632	0.595	10.7	1.23	0.769	0.626
5.2	1.09	0.661	0.604	13.2	1.20	0.692	0.576
5.5	1.07	0.658	0.612	17.8	1.22	0.692	0.565
5.7	1.08	0.627	0.577	23.7	1.07	0.578	0.542

The length of each jaw relative to head length also changes significantly. In larvae smaller than 4.3 mm., the ratios of upper and lower jaws to head length are between 0.508:1 and 0.600:1 (table 5). In larvae larger than 4.4 mm., however, the length of the upper jaw increases sharply to a maximum ratio of 0.769:1 in the 10.7-mm. larva, and the lower jaw attains a maximum ratio of 0.626:1. In larvae above 10.7 mm., the ratio of jaw to head length decreases for each jaw; at a length of 23.7 mm. the ratios of the upper and lower jaws to head length are only 0.578:1 and 0.542:1, respectively.

Jaw development is also unequal in larval and juvenile *Scomberomorus* (Hildebrand and Cable, 1938; Eckles, 1949). As in larval wahoo, the longer upper jaw of *Scomberomorus* can be attributed to increased growth of the premaxillary. The premaxillary and head lengths of the wahoo were compared with the same measurements of sierra mackerel (*S. sierra*) and skipjack tuna from the eastern Pacific Ocean (Carlsberg Foundation's "Dana" Expedition 1928-30 and Inter-American Tropical Tuna Commission) and central Pacific Ocean (Bureau of Commercial Fisheries Biological Lab-

oratory, Honolulu) (table 6).

All available data are included in table 7, although the comparison is restricted to individuals between 7.0 and 17.0 mm. because the full range of sizes for the three species was not identical. The ranges of ratios of premaxillary length to head length and the ratios of premaxillary length to standard length are distinctive for each species, and without overlap among the three. The ratio of premaxillary length to head length is largest in wahoo and smallest in skipjack. The lower and upper limits of the range for sierra mackerel (0.221:1.250:1) are about 1.71 and 1.54 times greater, respectively, than those for skipjack (0.129:1.0163:1), and the lower and upper limits of the range for wahoo (0.332:1-0.413:1) are 2.57 and 2.53 times greater, respectively, than those for skipjack. Logarithmic plots of the pre-

TABLE 6.—Measurements of standard length, head length, and premaxillary length, and ratios of premaxillary length to standard length and premaxillary length to head length of larval and juvenile wahoo, sierra mackerel, and skipjack tuna

Size	Specimens	Average measurements			Premaxillary length/standard length	Premaxillary length/head length
		Standard length	Head length	Premaxillary length		
Mm.	Number	Mm.	Mm.	Mm.		
<b>Wahoo</b>						
2.0-2.9...	2	2.8	0.8	0.05	0.018	0.062
3.0-3.9...	3	3.7	1.1	0.08	.022	.073
4.0-4.9...	9	4.4	1.7	.28	.064	.165
5.0-5.9...	7	5.6	2.5	.71	.127	.284
6.0-6.9...	3	6.5	3.1	1.08	.166	.348
7.0-7.9...	3	7.6	3.5	1.26	.186	.360
8.0-8.9...	2	8.6	3.8	1.57	.183	.433
9.0-9.9...	2	9.1	4.2	1.68	.185	.400
10.0-10.9...	2	10.4	4.9	1.99	.191	.406
13.0-13.9...	1	13.2	6.4	2.25	.170	.352
17.0-17.9...	1	17.8	7.4	2.40	.138	.332
23.0-23.9...	1	23.7	9.8	2.64	.111	.270
<b>Sierra mackerel</b>						
7.0-7.9...	2	7.4	3.2	.75	.101	.234
11.0-11.9...	2	11.6	5.0	1.25	.108	.250
12.0-12.9...	3	12.6	5.4	1.33	.106	.248
13.0-13.9...	1	13.1	5.9	1.33	.097	.227
14.0-14.9...	1	14.0	6.4	1.58	.113	.247
15.0-15.9...	2	15.1	6.6	1.54	.102	.234
16.0-16.9...	1	16.2	6.8	1.50	.093	.221
17.0-17.9...	1	17.3	7.0	1.75	.101	.250
18.0-18.9...	2	18.7	7.2	1.62	.087	.225
<b>Skipjack tuna</b>						
5.0-5.9...	3	5.6	2.3	.30	.054	.130
6.0-6.9...	4	6.7	2.8	.46	.069	.164
7.0-7.9...	1	7.8	3.6	.50	.064	.139
8.0-8.9...	2	8.5	3.8	.62	.073	.163
10.0-10.9...	1	10.2	4.6	.67	.066	.146
11.0-11.9...	1	11.8	5.6	.83	.070	.148
12.0-12.9...	2	12.6	5.4	.83	.067	.154
13.0-13.9...	4	13.4	5.5	.77	.057	.140
14.0-14.9...	4	14.2	5.7	.77	.054	.135
15.0-15.9...	3	15.4	5.8	.75	.049	.129
16.0-16.9...	2	16.4	6.8	.96	.058	.141
17.0-17.9...	1	17.6	6.4	.91	.052	.142
18.0-18.9...	1	18.1	6.4	.91	.050	.142
23.0-23.9...	2	23.9	8.3	.96	.040	.116

maxillary length against standard length (fig. 5) show this more clearly.

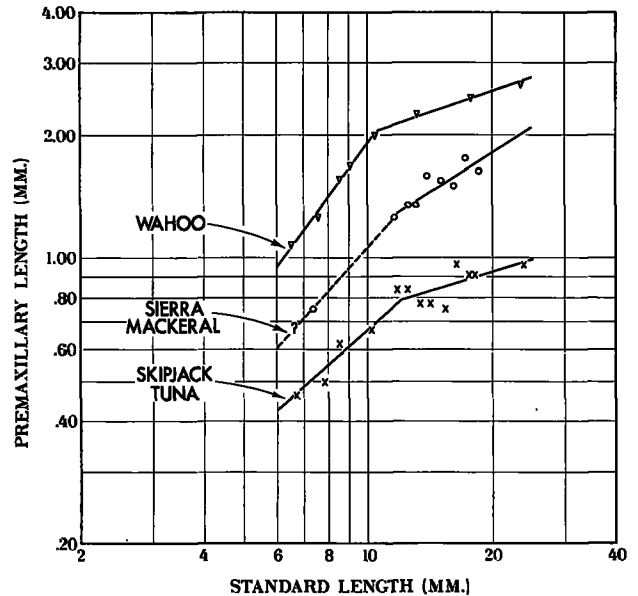


FIGURE 5.—Scatter diagram of premaxillary lengths plotted against standard length of larval and juvenile wahoo, sierra mackerel, and skipjack tuna. Line segments are regression lines fitted by the least-squares method.

These large differences in the ratios of premaxillary length to head length suggest that the size of the premaxillary may be of generic significance. This view is contrary to Conrad's (1938) opinion that the long, pointed premaxillary, thought to be so characteristic of the genus *Acanthocybium*, "is an unfortunate illusion." Conrad based his opinion upon the closeness of the ratios of premaxillary length to skull length of *Scomber* and *Acanthocybium*, 0.23:1 and 0.24:1, respectively; however, a careful check of his ratio for *Scomber* indicates a possible error.

Conrad defined premaxillary length as "the length of premaxillae anterior to the dermethmoid" and length of skull as the length "from anterior tip of premaxillae to posterior tip of supra-occipital crest." He did not give the species name or the source of his *Scomber* measurements, but judging from his numerous citations of Allis (1903) concerning this genus, it is very likely that the measurements were obtained from the figure of *S. scomber* by Allis. Using the reference points defined by Conrad,

TABLE 7.—Meristic counts of larvae and juvenile wahoo <sup>1</sup>

Standard length	Myomeres			Branchiostegal rays	Teeth <sup>2</sup>				Fin spines and rays					Caudal fin rays	
	Pre-anal	Post-anal	Total		Upper jaw	Lower jaw	Palatine	Vomerine	First dorsal	Second dorsal plus finlets	Anal plus finlets	Pectoral	Pelvic	Dorsal (principal and secondary)	Ventral (principal and secondary)
Mm.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.
2.8	26	39	65	0	0	0	0	0	0	0	0	0	0	0	0
2.8	29	35	64	0	0	0	0	0	0	0	0	0	0	0	0
3.1	28	37	65	0	0	0	0	0	0	0	0	0	0	0	0
3.4	28	37	65	0	0	0	0	0	0	0	0	0	0	0	0
3.8	30	35	65	0	0	0	0	0	0	0	0	0	0	0	0
3.9	27	37	64	0	0	0	0	0	0	0	0	0	0	0	0
4.1	27	37	64	0	1	1	0	0	0	0	0	0	0	0	0
4.2	29	35	64	0	2	1	0	0	0	0	0	0	0	0	0
4.3	29	36	65	0	3	4	0	0	0	0	0	0	0	0	0
4.3	29	35	64	0	D	D	0	0	0	0	0	0	0	0	0
4.3	30	35	65	0	8	9	0	0	0	0	0	0	0	0	0
4.4	29	35	64	0	7	7	0	0	0	0	0	0	0	0	0
4.5	27	37	64	0	7	8	0	0	0	0	0	0	0	0	0
4.6	27	38	65	0	9	7	1	0	0	0	0	0	0	0	0
4.8	27	37	64	0	10	10	2	0	0	0	0	0	0	0	0
5.2	27	37	64	0	13	13	2	0	0	0	0	0	0	0	0
5.2	27	38	65	1	16	14	2	0	0	0	0	0	0	0	0
5.5	26	38	64	2	15	12	2	0	0	0	0	0	0	0	0
5.7	27	38	65	4	14	14	2	0	0	0	0	0	0	0	0
5.8	28	36	64	3	16	14	2	0	0	0	0	0	0	3+0	3+0
5.8	30	35	65	5	17	15	2	0	0	0	0	0	0	3+0	2+0
5.9	27	36	63	4	17	16	2	0	0	0	0	0	0	3+0	2+0
6.2	26	39	65	5	17	15	3	0	0	0	0	0	0	4+0	3+0
6.6	32	32	64	6	18	16	3	0	0	3	4	4	0	5+0	4+0
6.6 (est.)	27	36	63	5	D	D	D	D	0	5	4	5	0	5+0	4+0
6.8	31	34	65	6	23	20	1	0	2	7	7	4	Bud	7+0	4+0
7.4	26	38	64	6	20	17	3	0	3	9	8	5	Bud	7+0	5+0
7.6	27	37	64	7	21	18	3	0	4	11	10	6	0	7+0	6+0
7.8	29	35	64	6	20	18	3	1?	5	12	11	6	0	6+0	5+0
7.9 (est.)	26	38	64	6	20	20	3	0	5	12	11	7	0	7+0	5+0
8.4	28	37	65	7	22	21	3	1	6	15	14	10	Bud	9+2	8+0
8.7	26	37	64	7	24	20	3	1	6	16	16	11	Bud	9+4	8+2
9.0	26	39	65	7	23	21	3	1	8	20	18	11	Bud	9+3	8+1
9.2	30	35	65	7	24	20	4	1	8	20	19	11	Bud	9+4	8+3
10.2	27	37	64	7	23	20	5	1	10	21	20	12	I, 2	9+4	8+3
10.7	28	36	64	7	23	21	6	2	13	21	20	11	I, 4	9+4	8+3
13.2	29	36	65	7	30	25	9	2	27	23	22	14	I, 5	9+7	8+6
17.8	26	38	64	7	28	24	8	2	27	23	22	19	I, 5	9+9	8+9
23.7				7	28	25	7	2	27	24	22	23	I, 5	9+15	8+15

<sup>1</sup> Standard length (mm.) and numbers of precaudal vertebrae and caudal vertebrae for each of three specimens in which vertebrae were counted were as follows: 13.2 mm.—33, 31; 17.8 mm.—32, 31; 23.7 mm.—32, 31.

<sup>2</sup> D = damaged.

I obtained a premaxillary length to skull length ratio of 0.11:1 for the *S. scomber* illustrated by Allis (1903), and ratios of 0.12:1, 0.12:1, 0.11:1, and 0.10:1 for four *S. japonicus* that were 220, 271, 284, and 386 mm. fork length, respectively. These ratios vary considerably from the 0.23:1 which Conrad reported for *Scomber*.

Strasburg (1964) has mentioned the presence of a small, cartilaginous pad at the tip of the lower jaw in juvenile wahoo. The pad is barely noticeable in the 4.2-mm. larva but is clearly developed in the 4.3-mm. larva. The pad assumes its characteristic conical shape in larvae more than 5.8 mm. long.

**Body Depth**

In many fish larvae, body depth at the pectoral fin is greatly influenced by the amount of food in the digestive tract. Furthermore, the distention of the gill cover and the bending of

the body at the junction of the head and trunk also distort the body depth of fish larvae at the pectoral fin. The variability produced by this distortion can be eliminated by discarding all distorted specimens, but this measure was not possible because few wahoo larvae were available. Consequently, body depth of wahoo larvae was measured at the posterior edge of the anus, where distortions caused by bending are minimal.

Body depth follows a different course of growth from that of premaxillary length. Differences between the two growth curves are seen mainly in larger larvae (fig. 4 and table 4); where the premaxillary grows at a uniform rate in larvae 6.6 to 10.7 mm. long, the body depth increases abruptly when the larvae are about 9 mm. long, and where the premaxillary grows relatively slower than standard length in larvae larger than 10 mm. ( $\alpha = 0.276$ ), the

depth increases slightly faster ( $\alpha = 1.180$ ) than the body.

#### Distance from Snout to Anus

Snout-to-anus distance shows positive allometry, but this phenomenon results from the sharp increase in snout length relative to standard length. If the snout length is subtracted from both snout-to-anus distance and standard length, a linear relation,  $Y = -0.09 + 0.623X$ , is evident (fig. 6). Thus the snout-to-anus dis-

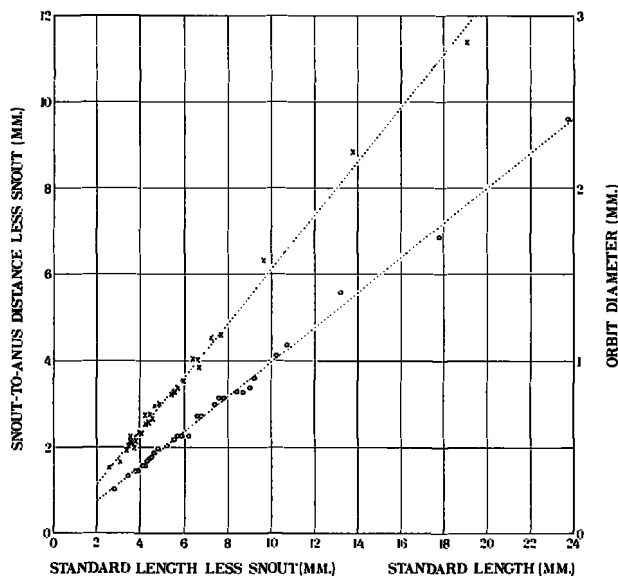


FIGURE 6.—Regressions of snout-to-anus distance less snout on standard length less snout (upper line), and orbit diameter on standard length (lower line). Lines fitted by the method of least squares.

tance, less snout length, increases 0.623 mm. for each 1.0-mm. increase in standard length, less snout length. A linear relation between snout-to-anus distance and standard length also exists in the Pacific mackerel, *Pneumatophorus diego* (Kramer, 1960).

The low rate of increase in the snout-to-anus distance of wahoo larvae is probably related to the shape of the digestive tract and the position of the anus. The digestive tract in wahoo larvae, unlike that in larvae of yellowfin tuna and skipjack tuna, is elongate, and the anus is situated near the origin of the anal fin, i.e., between the 26th and 29th myomeres, in larvae as small as 2.8 mm. (table 7). The anus maintains this relative position throughout the larval and

juvenile stages. In yellowfin tuna and skipjack tuna less than 7.0 mm. long, however, the digestive tract is compact and the anus is located at a point midway between the posterior edge of the head and the origin of the anal fin, i.e., between the 9th and 11th myomeres; furthermore, the anus shifts posteriorly as the larvae increase in size, until it is situated near the origin of the anal fin in larvae 11.0 to 13.0 mm. long.

In one respect the digestive tract resembles that of larvae of yellowfin tuna and skipjack tuna: it forms a complete loop, which is clearly visible in larvae 2.8 to 5.8 mm. long (fig. 2A-D). The loop is difficult to see in larvae larger than 6.8 mm. because of the heavier abdominal musculature and the increased pigmentation over the digestive tract (fig. 3A-D). The 4.0-mm. and 5.0-mm. Pacific mackerel larvae illustrated by Kramer (1960) have a similar loop in the digestive tract.

#### Orbit Diameter

Throughout the size range examined, the relation of orbit diameter to standard length is linear,  $Y = -0.019 + 0.0101X$ , the orbit increasing 0.101 mm. in diameter for 1.0-mm. increase in standard length (fig. 6). The eye is cleft ventrally.

### OSSIFICATION OF SKELETON

Myomeres, vertebrae, teeth, branchiostegal rays, fin rays, and spines were counted (table 7), and the ossification of bones was studied after the larvae had been stained with alizarin. A bone is considered as ossified if it absorbs the stain. Ossification proceeds more slowly in wahoo than it does in some other scombrids. The sequence of ossification is summarized in table 8.

#### Pectoral Girdle

The cleithrum is one of the first bones to ossify. The process begins in larvae about 2.8 mm. or smaller and is complete at 3.1 mm. or larger.

#### Upper and Lower Jaws

In the upper jaw, the development of the maxillary and premaxillary is similar to that described for *Trachurus* (Berry, 1964). The

TABLE 8.—Sequence of ossification of bones of wahoo larvae

Body part	Fish length at start	Fish length at finish
	Mm.	Mm.
Cleithrum.....	2.8	3.1
Parasphenoid.....	2.8	3.1
Maxillary.....	3.1	3.1
Dentary.....	3.1	3.8
Gill arch.....	3.4	6.8
Premaxillary.....	3.8	4.5
Teeth—upper jaw.....	4.1	
Preopercular spines.....	4.1	
Teeth—lower jaw.....	4.2	
Preopercle.....	4.3	
Articular.....	4.3	4.5
Palatine.....	4.3	8.4
Vomer.....	4.5	8.4
Palatine teeth.....	4.6	13.2
Branchiostegal rays.....	5.2	8.4
Parietal.....	5.7	10.7
Frontal.....	5.7	17.8
Caudal fin (principal rays).....	5.8	8.4
Pectoral fin.....	6.6	23.7
Second dorsal fin and finlets.....	6.6	10.2
Anal fin and finlets.....	6.6	13.2
Vertebrae.....	6.8	17.8
First dorsal fin.....	6.8	13.2
Vomerine teeth.....	8.4	
Caudal fin (secondary rays).....	8.4	<23.7
Palvic fin.....	10.2	13.2
Opercle.....	<13.2	
Supraoccipital crest.....	13.2	>23.7

maxillary ossifies first in larvae about 3.1 mm. long. The premaxillary begins to ossify at about 3.8 mm., but the development is restricted to the anterior half of the jaw. Ossification proceeds posteriad until the full length is developed in larvae about 4.5 mm. long. The premaxillary essentially excludes the maxillary from the gape (i.e., from the functional biting surface of the jaw) by its position ventral to the maxillary.

The lower jaw also has two bones, the dentary and articular. The dentary first develops in larvae about 3.1 mm. long and is completely ossified in larvae over 3.8 mm. Ossification of the articular begins in larvae about 4.2 mm. long and is complete at about 4.5 mm.

#### Gill Arches

The gill arches do not absorb stain until the larvae are about 3.4 mm. long. After the first arch has ossified, however, subsequent arches develop in quick succession and all are completely ossified in larvae about 6.8 mm. long. As in the adults, the larvae and juveniles have no gill rakers.

#### Teeth

The teeth in both jaws develop at a smaller size in wahoo larvae than in yellowfin tuna larvae, but slightly later than in skipjack tuna

larvae. Teeth in the upper jaw are formed only on the premaxillary, when the larvae are about 4.1 mm. long. The first few teeth appear almost simultaneously as small protuberances. In the lower jaw, teeth develop on the dentary when the larvae are about 4.2 mm. long. About seven widely spaced teeth of uniform size are present in each jaw when the larvae are about 4.4 mm. long. In larvae above 5.8 mm., smaller teeth are added near the bases of the larger ones; at 13.2 mm., one or two small teeth are usually present between two adjacent long teeth (fig. 3D). Initially, when the jaws are of equal length, the number of teeth in each is about equal. As the upper jaw protrudes beyond the tip of the lower jaw, three to four additional teeth appear on the protruded section of the upper jaw (figs. 2D and 3A-D). The three or four anteriormost teeth in the upper jaw become slightly recurved; the teeth posterior to these appear straight and more nearly vertical to the longitudinal axis of the jaw. When the juveniles attain a length of 13.2 mm., about half the number of teeth found in the adults are already ossified; however, the conical shape of the teeth of the larvae differs from the compressed and triangular teeth of the adults.

The palatine bone begins to ossify in larvae about 4.3 mm. long, and ossification is complete at about 8.4 mm. The first palatine tooth develops when the larvae are about 4.6 mm. long. The number of teeth increases slowly and reaches a maximum of nine in the 13.2-mm. larva.

The vomer begins to ossify later than the palatine, when the larvae are about 4.5 mm. long, but completes ossification at the same time as the palatine. The first vomerine tooth is developed in larvae about 8.4 mm. long; two are present at about 10.7 mm., and this number remains constant through the 23.7-mm. stage.

#### Preopercular Spines, Preopercle, and Opercle

Unlike the preopercular spines of skipjack tuna, which appear when the larvae are about 3.7 to 3.9 mm. total length (Matsumoto, 1958), the preopercular spines of the wahoo appear when the larvae are longer than 4.1 mm., SL. At this stage only a single spine is ossified at

the angle of the preopercle. Additional spines develop slowly; at 4.3 mm., only two spines are ossified (fig. 2C). The third spine is first seen on the 4.7-mm. larva, and the fourth and fifth spines appear in larvae longer than 6.8 mm. The number of spines remains constant until the larvae attain a length of 13.2 mm., when two spines are added on the horizontal edge. The 23.7-mm. juvenile possesses the greatest number of spines: five on the horizontal and three on the vertical edge of the preopercle. The preopercular spines of the wahoo are relatively shorter than those in larvae of yellowfin or skipjack tuna, and the preopercle has already overgrown most of the spines in the 13.2-mm. juvenile.

As in larvae of yellowfin and skipjack tuna, but to a lesser degree, additional spine development occurs on a ridge on the preopercular surface anterior to the base of the preopercular spines. In larvae between 4.5 and 5.8 mm., a single short spine is present on this ridge, and two spines are developed in larvae between 6.8 and 10.7 mm. In yellowfin tuna, skipjack tuna, and black skipjack (*Euthynnus* spp.), three or more spines are already present in larvae less than 5.5 mm. total length (cf. Matsu-moto, 1958, 1959).

The preopercular surface begins to ossify when the larvae are about 4.3 mm., soon after the first preopercular spine has developed. Ossification starts at the base of the preopercular spine and, as more spines are added, increases correspondingly. When the larvae are 7.4 mm. long, a small portion of the dorsal and ventral terminals of the preopercle also becomes ossified. The surface of the preopercle is almost completely ossified in the 23.7-mm. juvenile.

In larvae of yellowfin tuna, skipjack tuna, and black skipjack, between 5.0 and 6.0 mm. total length, a conspicuous spine develops in the posttemporal region of the head. This spine is absent in wahoo; instead it is represented by a bony ridge which is present throughout the larval and juvenile stages. This ridge is first apparent in the 8.4-mm. larva. A second ridge is seen dorsal to the first, and a groove appears between the two ridges in the 23.7-mm. juvenile. I presume that with continued growth of the juvenile, these two ridges unite to form a canal

that becomes part of the lateral line system.

The opercle begins to ossify when the larvae are about 13.2 mm. long. Ossification progresses slowly, and the opercle is still not completely developed at 23.7 mm.

#### Branchiostegal Rays

The first branchiostegal ray is seen in the 5.2-mm. larva. The number of rays increases to four in the 5.7-mm. larva and to six in larvae 6.6 to 6.8 mm. long. The full complement of seven rays is generally ossified in larvae about 8.4 mm. (fig. 3B), although a 7.6-mm. larva already had seven rays. The posteriormost ray ossifies first, and subsequent ossification proceeds anteriorly.

#### Other Head Bones

The parasphenoid first begins to ossify in larvae 2.8 mm. or smaller, and its entire length is ossified in about 3.1 mm.

It is difficult to determine the initial development of the frontal and parietal bones because these bones did not stain sufficiently in some of the specimens. The first sign of ossification appears in the 5.7-mm. larva. The parietal bone develops faster than the frontal bone and is completely ossified in larvae 10.7 mm. long. The frontal bone, on the other hand, is completely ossified only in the 17.8-mm. larva and the 23.7-mm. juvenile.

In contrast to these three bones, ossification of the supraoccipital crest, which develops only after nearly all the fin rays and vertebrae have completely ossified, starts in larvae about 13.2 mm. long. Ossification is completed only after the individuals exceed 23.7 mm.

#### Fins

The sequence of fin formation in wahoo larvae is similar to that of jack mackerel and Pacific mackerel (Ahlstrom and Ball, 1954; Kramer, 1960); the only difference is in the length of body at which fin development commences. In all fins, the actinotrichia first develop in the larval fin fold. These are replaced by definitive rays, lepidotrichia, which are branched, jointed rays composed of bone. Fin spines arise by alteration and fusion of the joints of the lepidotrichia. The fins will be discussed in the order of their formation: (1)



larval pectoral (without rays), (2) caudal, (3) pectoral, (4) second dorsal and anal, (5) first dorsal, and (6) pelvic.

*Larval pectoral fins.*—The larval pectoral fins are formed on the smallest larva, 2.8 mm. long. The fin membrane is large and fanshaped, and fin rays do not develop until the larvae are well past 6 mm. (table 8).

*Caudal fin.*—The caudal fin of wahoo develops first as a thickening ventral to the posterior portion of the notochord in larvae about 4.4 mm. long (fig. 2C). As the size of this thickening increases, the posterior portion of the notochord turns upward; at this stage the larvae are shorter than 6.8 mm. (fig. 3A). This thickening eventually develops into the hypural bones.

The principal caudal rays, those that are ultimately supported by the hypural bones, develop before any of the secondary caudal rays are formed. When the larvae are about 5.8 mm. long, the first two to four rays near the middle of the posterior edge of the hypural thickening develop almost simultaneously. The midline separating the ultimate dorsal and ventral lobes of the tail is clearly discernible, owing to the wide spacing between the two medial rays. The initial group of rays lies at an oblique angle to the notochord, but as the posterior part of the notochord turns upward, it pulls the rays up to a horizontal position. Subsequent ray development proceeds dorsally and ventrally from the medial rays. As in most percomorph fishes, there are 17 principal caudal rays in the wahoo: 9 are dorsal and 8 ventral to the midline of the fin. All the principal rays are completely developed in larvae over 8.4 mm. long (fig. 3B).

The secondary caudal rays first appear on larvae about 8.4 mm. long with the development of two dorsal rays anterior to the tip of the notochord. The sequence of ossification is from posterior to anterior for both the dorsal and ventral secondary rays. At a length of 23.7 mm., the caudal fin has 15 dorsal and 15 ventral secondary rays, which is within the range for adults.

The shape of the caudal fin changes as the rays are being developed. At first the larval caudal fin, represented by the median fin fold,

is roundly lobed. As the principal rays develop, the initial medial rays are longer than the rest of the fin fold. With the flexion of the notochord and the subsequent shift in position of the rays to a horizontal plane, the fin outline becomes angular (fig. 3A). After all the principal rays have developed, the dorsal and ventral rays begin to outgrow the medial rays, so that the posterior margin of the fin gradually assumes a square and finally a forked shape. The fork in the caudal fin is evident in the 10.7-mm. larva (fig. 3C) and is pronounced in larvae above 13.2 mm. long (fig. 3D).

*Pectoral fins.*—The larval pectorals already are present in the smallest wahoo (fig. 2A). The initial pectoral rays begin to develop near the dorsal part of the fin when the larvae are about 6.6 mm. long, and are much shorter than the pectoral membrane. At a length of 8.4 mm., these rays extend to the margin of the larval pectoral fin. As is usual in pectoral-fin development, the dorsal rays appear first. Twenty-three pectoral rays are developed in the 23.7-mm. juvenile. This total is within the range for adults.

*Second dorsal fin and finlets.*—The base of the second dorsal fin first appears as a thickening on larvae as small as 5.8 mm., and the first rays are developed in larvae 6.6 mm. long. The first two or three rays develop simultaneously near the middle of the fin; subsequent rays develop anteriorly and posteriorly to these. The first few finlets develop before the formation of the anteriormost ray of the second dorsal fin. The last finlet, however, develops only after the formation of all the second dorsal fin rays.

In the early stages of development, it is extremely difficult to differentiate rays from finlets. Consequently, the number of ray and finlet elements for the larvae were combined. A similar grouping for the adults shows that the full complement of rays and finlets for the second dorsal fin ranges from 20 to 22 (table 2). As discussed earlier, two elements, which are separated in the larvae, form the last adult finlet. Consequently, the total number of larval fin ray and finlet elements comparable with those of the adult must be more than 21. The full complement of rays and finlets in the second dorsal is already present in the 13.2-mm.

larva (table 7). The last two finlets in the 23.7-mm. juvenile (Strasburg, 1964: fig. 2) are situated very close together but are not yet fused.

*Anal fin and finlets.*—Ossification of anal fin rays occurs simultaneously with that of the second dorsal fin. Although subsequent development of rays and finlets is nearly identical with that of the second dorsal fin and finlets, the adult complement is not attained until the juvenile has exceeded 10.7 mm. long. All the rays and finlets are completely formed in the 13.2-mm. larva. As in the dorsal finlets, the last two anal finlets on the 23.7-mm. juvenile (Strasburg, 1964: fig. 2) are very close together; their bases nearly touching each other.

*First dorsal fin.*—As in the anal and second dorsal fins, the base of the first dorsal fin thickens when the larvae are about 6.2 mm. long. The first two or three spines develop almost simultaneously and are first seen in the 6.8-mm. larva (fig. 3A). The first spines are short (0.10 mm.), and, unlike the sequence of ray development in the anal and second dorsal fins, subsequent spines are added only posteriorly. Additional spines develop slowly; the number increases from 2 in the 6.8-mm. larva to 10 in the 10.2-mm. larva. In larvae over 10.2 mm. long, however, the spines are added more rapidly, so that 27 spines are already evident in the 13.2-mm. larva (table 7).

The height and shape of the fin also change with growth of the larvae. Larvae between 8.4 and 8.7 mm. long have all six spines of equal height. Shortly thereafter, the anteriormost spine becomes the longest and each succeeding spine is shorter than the one preceding it. A concavity in the fin outline becomes noticeable after the eighth or ninth spine has ossified (i.e., when the larvae are about 9.0 or 10.0 mm. long). All spines after the ninth are about equal in height (fig. 3D).

*Pelvic fins.*—The pelvic fins are the last to develop. They appear first, as a protuberance on the ventral contour of the body below the pectoral fin base, in larvae between 6.8 and 9.0 mm. Unlike the interradial membranes of other fins, which develop from the larval fin fold, those of the pelvic fins grow out from the fin base. Initially, the spine and one or two rays

ossify almost simultaneously and are first noticed in the 9.2-mm. larva. Both spine and rays are short (0.29 mm.), but their length increases rapidly, so that in the 17.8-mm. larva (table 3), the longest pelvic fin ray (1.44 mm.) is almost as long as the longest pectoral ray (1.50 mm.). The full complement of one spine and five rays is completely formed in juveniles longer than 13.2 mm.

#### Vertebral Column

In the wahoo, as in many other fishes, the vertebral spines ossify before the centra. A vertebra is considered to be developing as soon as any part begins to ossify, as indicated by stain absorption. Because the anterior abdominal vertebrae, which develop first, lack haemal spines, the ossification of the neural spines is the first stage of vertebral development. Neural spines first appear in wahoo at 6.7 mm. The number of neural spines increases rapidly from 1 in the 6.8-mm. larva to 10 in the 8.4-mm. larva. All the neural and haemal spines are partially or completely ossified in the 13.2-mm. larva, and all the centra in the 17.8-mm. juvenile.

The sequence of development of the centra is from anterior to posterior, in the order of their position. As in the Pacific mackerel, ossification of the centrum starts at the dorsal and ventral portions and progresses laterally until the two ossified portions meet at the midline. The dorsal portion of the first six centra and the ventral portion of the first four are ossified in the 8.4-mm. larva. In the 13.2-mm. larva, the first 10 centra are completely ossified, the 11th to 22d centra are partially ossified, and the dorsal and ventral portions of the 23d to 34th centra are beginning to ossify. The ventral portions of the two centra anterior to the last one, which give rise to the urostyle, also begin to ossify in the 13.2-mm. larva. The remaining 26 centra become ossified between lengths of 13.2 and 23.7 mm.

The urostyle first develops in larvae about 8 mm. long and is completely ossified in larvae larger than 13 mm. In the 13.2-mm. larva, only about half the area of the largest hypural element is ossified. The early development of the urostyle and the last two centra is similar

to the ossification in Pacific mackerel (Kramer, 1960). All the bones in the hypural complex are completely ossified in the 17.8-mm. larva.

The neural spines are initially based on the anterior end of their centra. As each centrum grows progressively longer, the base of the corresponding neural spine seems to shift posteriorward, until it is near the middle of the centrum. This change in position of the base of the neural spine is evident in the last six vertebrae (excluding the terminal vertebra) of the 23.7-mm. juvenile. In the adult the bases of the 50th to 59th neural spines have shifted further caudad, to the posterior edge of their corresponding centrum.

The haemal spines, which first appear near the anterior part of the centra, generally remain in their original position throughout the larval stage. In the juvenile stage the bases of the last six or seven haemal spines have shifted posteriorward to the middle of the centrum. This condition is evident in the 23.7-mm. juvenile and is similar to that found in the adult, in which the bases of the 53d to 58th haemal spines have shifted further caudad to the posterior edge of their corresponding centra. This posterior shifting of the neural and haemal spines and the simultaneous decrease in the angle formed by the spines and longitudinal axis of the vertebral column produce the narrow caudal peduncle so characteristic of the scombrids.

Unlike the Pacific mackerel, which develops zygapophyses at about 8.7-mm. body length (Kramer, 1960), the wahoo develops zygapophyses when the larvae are 17.8 to 23.7 mm. long. No zygapophysis is ossified in the 17.8-mm. larva, but in the 23.7-mm. juvenile, the neural prezygapophyses of the 2d to 61st vertebrae and the neural postzygapophyses of the 1st to the 60th vertebrae are ossified. Some differences exist between juvenile and adult neural postzygapophyses of vertebrae near the caudal end. Neural postzygapophyses are widely separated from the bases of the neural spines in juveniles, but in adults those of the 54th to 62d vertebrae have become partially or entirely fused to the neural spines, as each succeeding spine gradually inclines toward the horizontal axis of the vertebral column.

The haemal zygapophyses also ossify when the larvae are between 17.8 and 23.7 mm. long. No haemal zygapophysis is developed in the 17.8-mm. larva, but most of the adult complement are ossified in the 23.7-mm. juvenile. In the latter specimen, the first haemal prezygapophysis is seen on the 27th vertebra; the first two or three appear as small projections near the anterior edge of the centrum and anterior to the base of the haemal arch. All succeeding vertebrae possess haemal prezygapophyses. These structures are presumed to develop anteriorly from the 27th vertebra as the juveniles increase in length, since in the adults the anteriormost haemal prezygapophysis is on the 19th to 21st vertebra.

The haemal postzygapophyses follow a sequence of ossification slightly different from that of the prezygapophyses. In the 23.7-mm. juvenile, haemal postzygapophyses are ossified on the 11th to the 60th vertebra. In the adults, haemal postzygapophyses are present on about the 6th to 57th or 58th vertebra. Consequently, I presume that, as the fish matures, ossification of haemal postzygapophyses continues anteriorly, and the postzygapophyses of the last five or six caudal vertebrae fuse with the haemal spines.

Clothier (1950) called the processes of the haemal arches the haemapophyses and named as parapophyses "the bony projections on each side of the anterior ends of the centra in the abdominal region to which the ribs are attached." I shall use these two terms as defined by Clothier. Perhaps some of the parapophyses and haemapophyses are already ossified in the 10.7-mm. larva, but this cannot be determined because the vertebral column of this specimen did not stain adequately. The anteriormost parapophysis on the side of the centrum is developed on the 13th vertebra in the 13.2-mm. larva, and the anteriormost haemapophysis is developed on the 18th. In the 17.8-mm. larva and the 23.7-mm. juvenile, the anteriormost parapophysis is seen clearly on the third vertebra in the dorsal third of the centrum, which is the adult condition. The parapophyses on succeeding vertebrae are situated progressively lower on the side of the centrum, and the first pair of haemapophyses at the ventral surface

of the centrum is ossified on the 17th vertebra.

To trace the development of the haemapophyses on larger wahoo, two juveniles, 152- and 159-mm. SL taken from stomachs, and two adults, 1,066- and 1,252-mm. fork length, were examined. Additional information from an adult 1,468 mm. long (type of length measurement not clearly defined) was obtained from Conrad (1938). The vertebra on which the anteriormost haemapophysis is located, listed in the order of fish size (length in millimeters shown in parentheses), is as follows: 17th (23.7), 12th (152), 13th (159), 14th (1,066), 15th (1,252), and 16th (1,468). This sequence suggests first, that after the initial ossification of the anteriormost haemapophysis on the 17th vertebra in the smallest juvenile, other haemapophyses develop anteriorly until the maximum number has been attained at a length of about 152 mm.; second, that as the fish increase in size, the position of the anteriormost haemapophysis apparently moves posteriorly, probably because of a gradual upward shift in the position of the haemapophysis on the centra as the vertebrae increase in size.

The development of the anteriormost haemal arch also suggests a shift in position. The position of the initial haemal arch shifts from the 23d or 24th vertebra in the juveniles to the 26th or 27th vertebra in the adults.

#### OCCURRENCE AND DISTRIBUTION OF WAHOO

The adult wahoo are generally found in tropical and subtropical waters and are taken as incidental catches by surface trolling and longlining. In both types of fishing, however, the catches are small: in the central Pacific Ocean only 236 wahoo were caught in 8,937 line-hours of trolling (Murphy and Ikehara, 1955) and 58 wahoo were taken on 14 POFI (now BCF Biological Laboratory, Honolulu) longline fishing cruises, during which 94,128 hooks had been fished at 450 fishing stations (Murphy and Shomura, 1953a, 1953b, 1955; Shomura and Murphy, 1955). Results of surface trolling within a few kilometers of land in the Line Islands in 1955 have led Iversen and Yoshida (1957) to infer that wahoo prefer shallow depths and are more abundant close to shore.

To determine whether the wahoo are taken on the longline more commonly in inshore than in offshore areas (areas less than or greater than 110 km. from land), I plotted the locations where wahoo were taken on the longline (fig. 7)

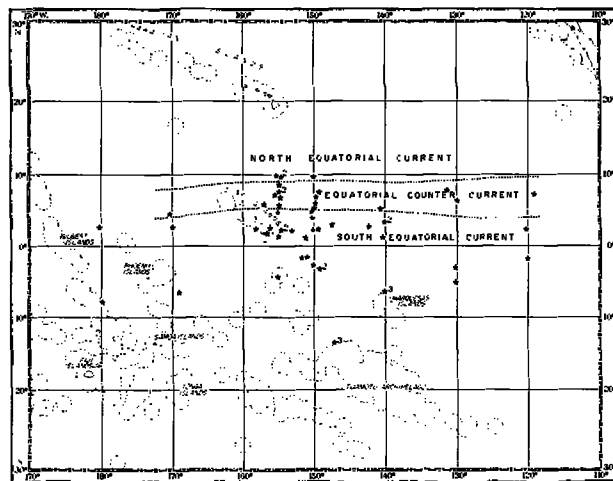


FIGURE 7.—Location and number of adult wahoo taken during 14 POFI (now Biological Laboratory, Honolulu) longline cruises. Each star represents a single wahoo taken at a fishing station. A star and number show catches of two or more wahoo per station. Broken lines around islands indicate a distance of 110 km. from land. Major currents in the central Pacific Ocean are shown.

and tested the catch data. The catches in the two areas were not statistically significant.

Larval wahoo were found also in tropical and subtropical waters of the Pacific Ocean between lat. 30° N. and 25° S., and between long. 175° E. and 115° W., the east-west extent of sampling along the Equator. Interestingly, differences between the catches of wahoo larvae in inshore and offshore areas (areas less than or greater than 110 km. from land) were not significant; 12 larvae were caught in 11 of 566 plankton net hauls in inshore areas and 26 larvae were caught in 23 of 1,077 net hauls in offshore areas. The distribution of catches of larvae (fig. 1), moreover, resembled that of the adults taken on the longline.

Of particular interest to this study are (1) the captures of larvae and adults far from land and (2) the scarcity of larvae in the Equatorial Countercurrent (fig. 1), although adults have been taken there on a number of longline

stations (fig. 7). One site of larval capture, lat. 8°42' S. and long. 115°39' W., was 2,057 km. from the nearest land mass, Ducie Island. This distance is only 181 km. less than the greatest distance from land where an adult wahoo has been taken. Six other capture sites were farther than 900 km. from land. Although adults frequent the Equatorial Countercurrent, they may not spawn there in appreciable numbers. Only one wahoo larva was taken there, representing a catch rate of 0.14 larva per tow.

More adult wahoo are taken around the Hawaiian Islands in summer (April through August) than in other seasons (Welsh, 1949). Seasonal trends are absent, however, near the Equator and around the Line Islands (Iversen and Yoshida, 1957), as they also were in the longline catches made on the 14 POFI cruises

TABLE 9.—Adult wahoo caught on 14 POFI longline cruises in the central Pacific Ocean between lat. 14° N. and 14° S.

Month	Wahoo caught	Catch of wahoo/1,000 hooks
	Number	Number
January.....	1	0.29
February.....	8	.96
March.....	6	1.33
April.....	0	.00
May.....	2	.29
June.....	4	.72
July.....	6	2.70
August.....	14	.69
September.....	6	.40
October.....	3	.30
November.....	4	.37
December.....	4	.56

TABLE 10.—Catch rate of wahoo larvae and number of plankton samples collected by months in three areas<sup>1</sup> of the central Pacific Ocean, 1950-62

Month	Area I		Area II		Area III		All areas
	Larvae per 100 samples	Plankton samples	Larvae per 100 samples	Plankton samples	Larvae per 100 samples	Plankton samples	Plankton samples
January.....	0.0	34	1.8	109	-----	-----	143
February.....	.0	23	1.0	96	3.4	29	148
March.....	.0	83	2.1	195	4.2	48	326
April.....	.0	32	6.1	49	-----	-----	81
May.....	4.2	96	2.9	34	-----	-----	130
June.....	4.8	21	1.8	111	-----	-----	132
July.....	6.1	66	2.4	42	-----	-----	108
August.....	3.3	180	1.2	81	-----	-----	261
September.....	3.2	31	0.0	45	-----	-----	76
October.....	2.6	39	1.3	75	-----	-----	114
November.....	0.0	53	0.0	46	0.0	2	101
December.....	-----	-----	8.7	23	-----	-----	23
All months.....	2.6	658	2.0	906	3.8	79	1,643

<sup>1</sup> Area I from lat. 30° to 15° N.; Area II from lat. 14° N. to 14° S.; Area III from lat. 15° to 25° S.

(table 9) between lat. 14° N. and 14° S. Most of the fishing on these cruises was done between lat. 9° N. and 8° S.

Monthly catches of larval wahoo show similar trends (table 10). In the area near the Hawaiian Islands (Area I) larvae were taken only in the summer and early fall (May through September), but in the equatorial region (Area II) they were taken in nearly all months of the year.

## SUMMARY

Thirty-eight wahoo larvae were taken in a 1-m. plankton net during 32 cruises of the Bureau of Commercial Fisheries research vessels, *Hugh M. Smith* and *Charles H. Gilbert*, in the central Pacific from May 1950 to July 1962. The standard lengths of these specimens ranged from 2.8 to 17.8 mm. In addition, six adults and four juveniles from other sources were examined.

Published accounts of adult wahoo give a vertebral formula, 23 to 33 precaudal + 31 to 34 caudal = 54 to 66 total vertebrae, which is an extremely wide range of variation for a fish belonging to the Scombridae. All studies based on examination of specimens indicate only minor variation (31 to 33) in the number of precaudals. Consequently, I conclude that the wide range of precaudal vertebrae first credited to Kishinouye (1923) is incorrect and that the lower figure of 23 precaudals must be a typographical error—a transposition of digits from 32 to 23.

The number of first dorsal spines is constant at 27 in both juveniles and adults. The number of finlets in juveniles is greater than that in adults by one, owing to the fusion of the last two finlets in adults.

Body pigmentation is relatively sparse in larvae smaller than 3.4 mm.; a few melanophores occur on the tip of each jaw, one in each primordial nasal cavity, one on the ventral margin of the caudal peduncle, and a series of about nine evenly spaced along the dorsal surface of the digestive tract. The most noticeable change in pigmentation occurs in larvae above 5.8 mm., when the melanophore at the caudal peduncle migrates to the base of the anal fin

and there the number increases until a series of melanophores forms over the entire base of the anal fin. A similar series of melanophores develops at the base of the second dorsal fin. The only other significant increase in pigmentation is in the first dorsal fin just before the larva reaches a length of about 13.0 mm.

Premaxillary length, snout length less premaxillary length, head length less snout, body depth at anus, and snout-to-anus distance less snout show allometric growth that can be described by the equation,  $Y = bX^a$ .

The most striking change in body form occurs in larvae longer than 3.8 mm., in which head length increases very rapidly. Most of this increase is due to the rapid growth in the premaxillary and snout. The shape and size of the mouth also are affected by the rapid growth in premaxillary and snout. Prior to attainment of 4.3 mm., both jaws have the same length; subsequently, the upper jaw protrudes beyond the lower, and at about 9.0 mm., the ratio of upper to lower jaw is 1.25:1. This ratio decreases to 1.07:1 in the 23.7-mm. juvenile, and in adults the upper jaw is equal to or slightly shorter than the lower. Before unequal jaw development begins, the ratios of upper and lower jaws to head length is between 0.508:1 and 0.601:1. After their lengths become unequal, the ratios of upper and lower jaws to head length increase to 0.769:1 and 0.626:1, respectively.

Body depth increases unevenly throughout the size range. The most rapid growth occurs in larvae between 9.0 and 9.2 mm. long.

Snout-to-anus distance less snout length is linearly related to standard length less snout length. It increases 0.623 mm. for each millimeter increase in standard length less snout length.

Unlike the digestive tract of larvae of yellowfin tuna or skipjack tuna, which is compact (anus located well ahead of the origin of the anal fin), the digestive tract of wahoo larvae is fully extended (anus located close to the origin of the anal fin). The digestive tract of wahoo resembles that of yellowfin tuna and skipjack larvae in that it forms a complete loop.

Orbit diameter is linearly related to stand-

ard length. It increases 0.101 mm. for each millimeter increase in standard length.

Ossification of bones and hard parts differs only slightly from the sequence found in jack mackerel and Pacific mackerel. The sequence in wahoo is as follows: Cleithrum and parasphenoid, maxillary and dentary, gill arches, premaxillary, teeth of upper jaw, preopercular spines, teeth of lower jaw, preopercle, articular, palatine, vomer, palatine teeth, branchiostegal rays, parietal, frontal, principal rays of caudal fin, pectoral fin, second dorsal and anal fins simultaneously, vertebrae, first dorsal fin, vomerine teeth, secondary caudal rays, pelvic fins, opercle, and supraoccipital crest.

Wahoo larvae were found in tropical and subtropical waters between lat. 30° N. and 25° S., and between long. 175° E. and 115° W., the east-west extent of sampling along the Equator. The numbers of larvae and adults caught inshore (less than 110 km. from land) and offshore were not significantly different. Wahoo larvae were taken mostly during the summer in the area north of lat. 15° N., and throughout the year along the Equator between lat. 14° N., and 15° S.

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