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Metamorphosis of the Leptocephali of the Ten-pounder, *Elops hawaiensis*, from Ishigaki Island, Japan

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Abstract Several leptocephali of the genus *Elops*, collected from Ishigaki Island, Ryukyu Islands, were reared, and the process of metamorphosis was clarified. Consequently larval development can be divided into four phases, i.e., leptocephalus phase, 1st metamorphic phase, 2nd metamorphic phase and juvenile phase, mainly by the position of the dorsal and anal fins, gas bladder shape, body shape and size, pigmentation, dentition, ossification of the endoskeleton and growth rate.

The larvae have 66~68 myomeres and 67 vertebrae, and are identified as *Elops hawaiensis*. The present study suggests that the Japanese species of *Elops* is *E. hawaiensis*, not *E. machnata* as previously recorded.

The genus *Elops*, Elopidae, comprises six species, *E. affinis* Regan, *E. hawaiensis* Regan, *E. lacerta* Valenciennes, *E. machnata* (Forsskål), *E. saurus* (Linnaeus) and *E. senegalensis* Regan (Regan, 1909; Bertin, 1944; Whitehead, 1962). These fishes are known to occur in the temperate and tropical waters of the world, and to grow through metamorphosis, like apodes, from leptocephalus larvae to juvenile. But information concerning the metamorphosing process of these fishes is scarce, consisting of the studies of *E. saurus* by Alikunhi and Rao (1951) and Gehringer (1959), and, in addition, the developmental study of the kidney of *E. hawaiensis* by Holstvoogd (1936).

Recently the authors collected many leptocephali of *Elops* from Ishigaki Island, Ryukyu Islands, and reared several individuals to juveniles. As a result, the larvae were identified as *E. hawaiensis*, and the process of the metamorphosis of this species was clarified.

Materials and methods

The Nagura River is a small stream of about 5.2 km in length, on Ishigaki Island (24°20′N, 125°15′E), Ryukyu Islands. Two small set-nets, one with an opening directed upstream and the other with an opening directed downstream, were placed in the lowermost portion of the river about 800 m above its mouth to the East China Sea. A total of 392 leptocephalus specimens of *Elops* were obtained from the operation of the set-nets during the periods of May 1~14, August 1~25, October 28~November 21, 1977, January 25~February 18, and May 22~27, 1978.

Eight leptocephali (27~37 mm in TL) collected from May 22 to 26, 1978, were transported back to the Yaeyama Branch of the Okinawa Prefecture Fisheries Experiment Station and placed in three 30 *l* plastic aquaria (Tanks A, B and C), each containing 15 *l* of water at 22.6~29.2°C. The chlorinity of the tank water was maintained at the same level as the river water at the time of collection: Tank A, containing three leptocephali (fish No. I, II, III), 6,700 ppm; Tank B, two leptocephali (fish No. IV, V), 3,900 ppm; Tank C, three leptocephali (fish No. VI, VII, VIII), 6,300 ppm. Each day they were fed *Brachionus plicatilis* and *Daphnia* sp., and uneaten food and waste were removed and one third of the water was replaced.

All specimens other than those reared in aquaria were fixed in 10% formalin immediately after their capture.

Measuring and counting methods followed Gehringer (1959). Measurements of live individuals were made with section paper placed on the back wall of the aquaria. The number of measured specimens is as follows: leptocephalus phase, seven; 1st metamorphic phase, 331; 2nd metamorphic phase, 50 and juvenile phase, four.

For the identification of the Japanese form of *Elops*, the following three specimens, which

were used in the study of Jordan and Hubbs (1925), were examined: UMMZ (Division of Fishes, Museum of Zoology, the University of Michigan) 142870, 252.0 mm SL, Kobe Market, Japan, November 11, 1922; SU (Department of Ichthyology, California Academy of Science) 23825, 251.1 mm SL, Misaki, Japan, 1922; No. 13061 in the Department of Ichthyology, American Museum of Natural History, 239.5 mm SL, Japan, 1922.

Osteological observations were made on cleared and stained specimens. The nomenclature of larval teeth followed Takai (1959), and counts were taken from the left side of the jaws.

Metamorphosis of larvae

The process of the development of these larvae was divided into the following four phases on the basis of the position of the dorsal and anal fins, gas bladder shape, body shape and size, pigmentation, larval teeth, ossification of the endoskeleton, growth rate, etc. The division and naming of larval phases by Alikunhi and Rao (1951) and by Gehringer (1959) were not followed because of the ambiguity in their delimitation of stages. The characters of each larval phase are as follows.

Leptocephalus phase (A in Figs. 1, 2, 3): Initial length increases up to the size at which metamorphosis commences. Dorsal fin situated between 52nd～60th myomeres, occupying six to eight myomeres, and has 20～21 fin rays (not ossified). Dorsal finfold connected with caudal fin. Anal fin situated between 57th～65th myomeres, occupying four or five myomeres, and has 12～13 fin rays (not ossified). Anal finfold connected with caudal fin. No rays in pectoral fins. Pelvics not appearing. Caudal fin rays fixed in number, 19 (10+9). Gas bladder appears between 29th～31st myomeres, in small coeca shape. Body, translucent and ribbon-shaped, rather high in depth, highest at kidney. A few melanophores on caudal peduncle and a longitudinal series from thorax to anus. The difference between anterior and posterior teeth is not so clear as in apodes Takai (1959). No slender tooth, one grasping tooth, two to four anterior teeth and five to seven posterior teeth located in upper jaw, one grasping tooth, five anterior teeth and eight to ten posterior teeth in lower jaw. Maxillary and mandible (not differentiated into pieces) already ossified, unlike other bones in head. Vertebral column in the state of notochord. Hypurals fixed, seven in number, but not ossified. First uroneural visible, but only its base ossified. TL ranged from 18.1 to 39 mm (17.1～36 mm in SL). Growth rate, +1.0 mm in TL/day (only one reared individual).

First metamorphic phase (B and C in Figs. 1, 2, 3): The body shrinks rapidly to the size of about 29 mm in TL and few changes occur in characters during metamorphosis. Dorsal fin situated between 51st～60th myomeres, occupying seven or eight myomeres, and has 19～23 ossified fin rays. Dorsal finfold separated from caudal fin. Anal fin situated between 57th～64th myomeres, occupying four or five myomeres, having 12～13 ossified fin rays. Anal finfold separated from caudal fin. No rays in pectoral fins. Buds of pelvics appearing between 30th～32nd myomeres, first seen in a specimen of 34.4 mm in TL (30.8 mm in SL), but has no rays. Gas bladder situated between 30th～32nd myomeres, increasing cylindrically in length in dorsal direction. Body still translucent and thin, relatively lower in depth than in the former phase. Melanophores appear at mid-lateral portion of trunk and on caudal fin membrane, increasing in number. Larval teeth decreasing in number, zero to one grasping tooth, zero to two anterior teeth and five to six posterior teeth in upper jaw, and zero to one grasping tooth, one to five anterior teeth and seven to eight posterior teeth in lower jaw. Rudiment of operculum ossified, increasing in size. Vertebral column still in the state of notochord. Hypurals partially ossified. Upper part of 1st uroneural and 2nd uroneural ossified, both increasing in size. TL ranged from 40.0 to 29.0 mm (37.2～26.1 mm in SL). Growth rate averaged −1.347 mm in TL/day (ranging from −1.124 to −1.772).

Second metamorphic phase (D and E in Figs. 1, 2, 3): During metamorphosis, the body shrinks slowly to the smallest recorded size, and remarkable changes occur in characters. Dorsal fin situated between 36th～60th myomeres, occupying eight to 14 myomeres, and

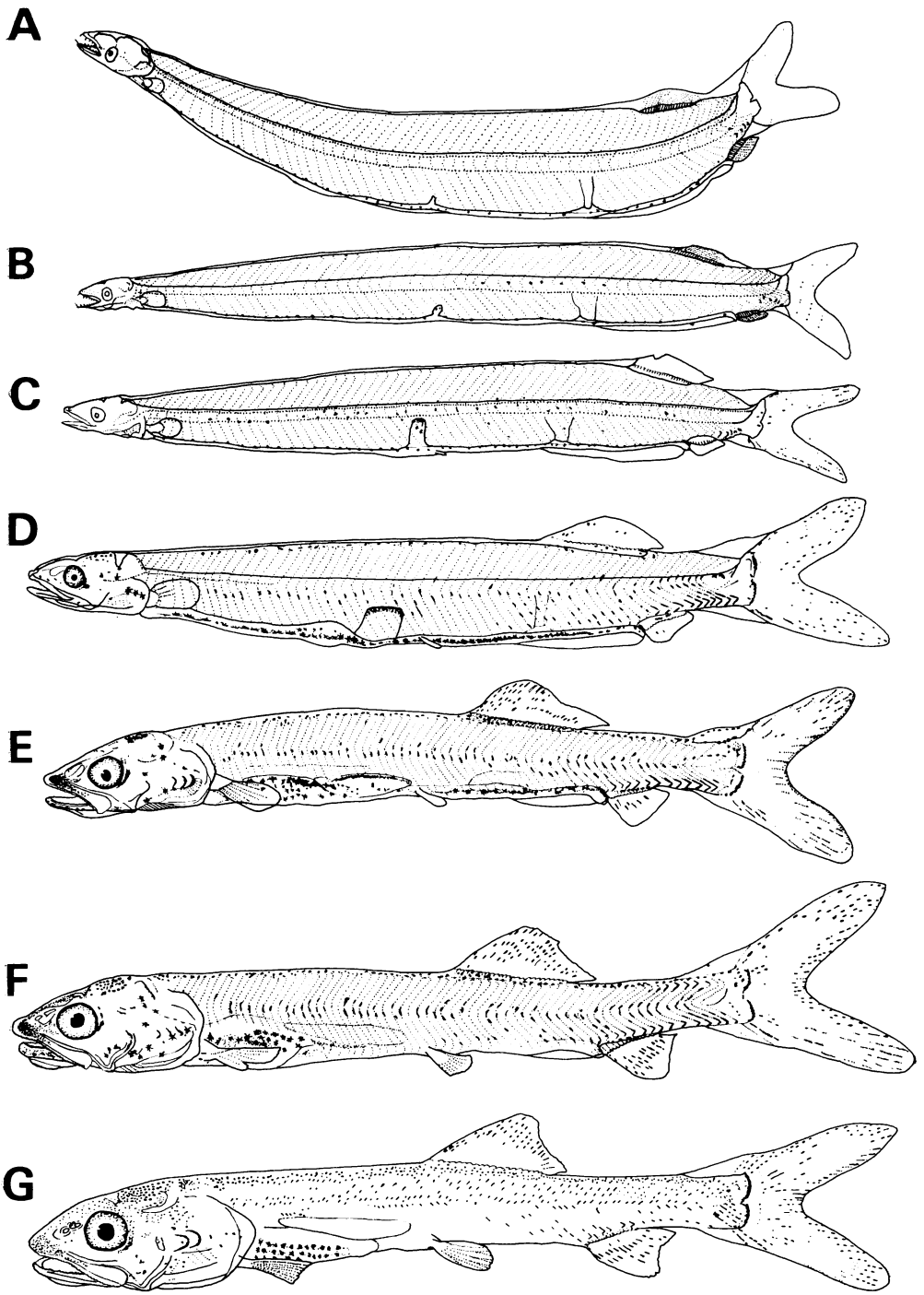

Fig. 1. Metamorphosis of *Elops hawaiensis*. A: leptocephalus phase, 31.5 mm TL (28.5 mm SL). B: 1st metamorphic phase, 40.0 mm TL (37.2 mm SL). C: 1st metamorphic phase, 30.0 mm TL (27.0 mm SL). D: 2nd metamorphic phase, 25.4 mm TL (21.9 mm SL: fish No. VI). E: 2nd metamorphic phase, 23.5 mm TL (19.6 mm SL: fish No. IV). F: juvenile phase, 26.4 mm TL (22.3 mm SL: fish No. V). G: juvenile phase, 35.6 mm TL (28.0 mm SL: fish No. VIII). Vertical fin rays are not drawn in order to show the chromatophores.

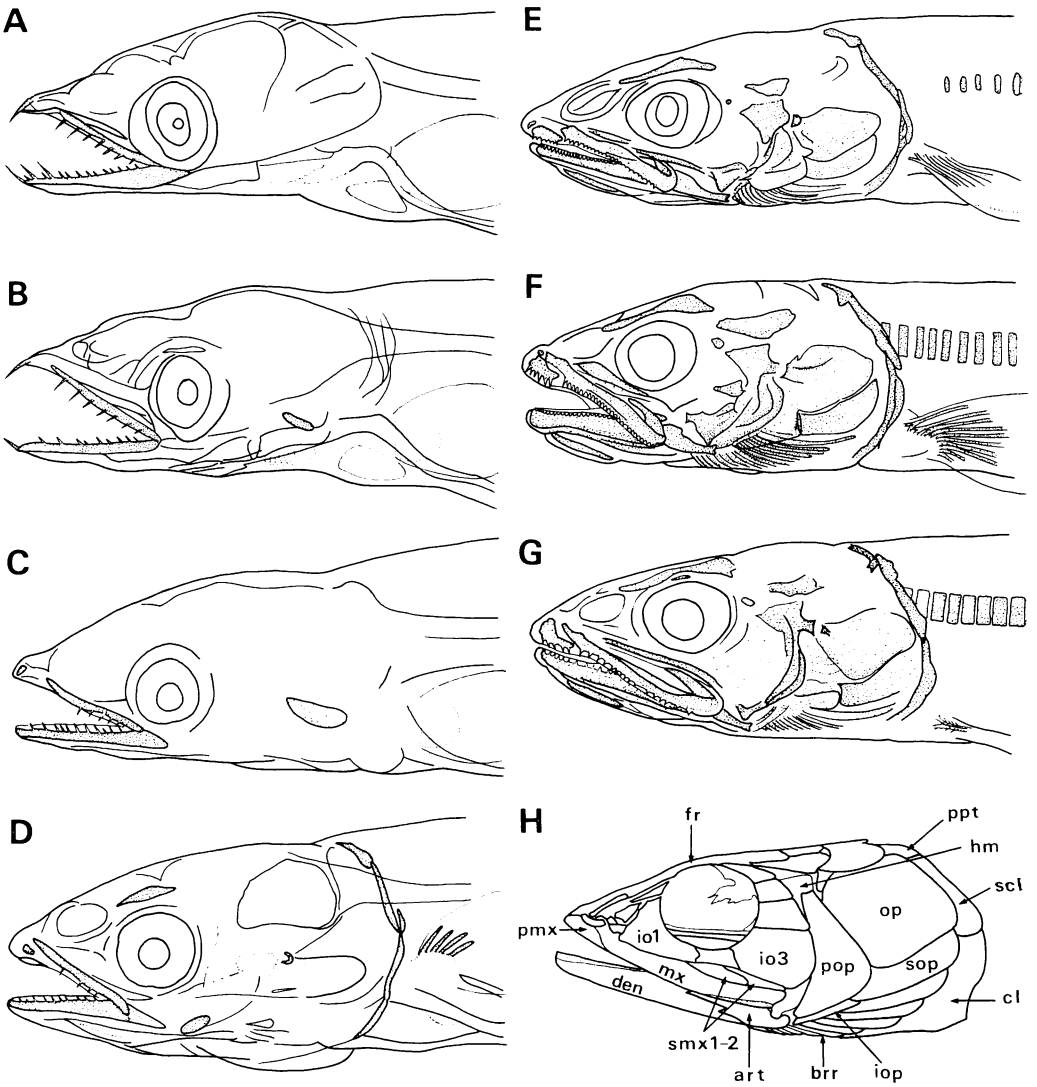

Fig. 2. Ossification in the heads of the specimens drawn in Fig. 1. Degree of darkness of shaded figures shows the degree of ossification. H: Adult redrawn from Forey (1973). art, articular; brr, branchiostegal ray; cl, cleithrum; den, dentary; fr, frontal; hm, hyomandibular; io 1～5, infraorbital 1～5; iop, interoperculum; mx, maxillary; op, operculum; pmx, premaxillary; pop, preoperculum; ppt, posttemporal; scl, supracleithrum; smx 1～2, supramaxillary 1～2; sop, suboperculum.

has 20～24 rays. Dorsal finfold disappears. Anal fin situated between 52nd～62nd myomeres, occupying four or five myomeres, and has 12～15 rays. Anal finfold remains just in front of the anal fin, continuing to decrease in size. Fin rays appearing in pectral and pelvic fins, four in upper part of the former and four in outer part of the latter, first seen in a specimen of 25.4 mm in TL (Figs. 1D, 2D). Gas bladder stretched longitudinally and situated between 24th～31st myomeres. Body gradually becomes opaque and round in shape, losing ribbon-like form. Melanophores appear on head, dorsal side of trunk along each myocommata, gas bladder, intestine, dorsal and anal fin membranes, and base of caudal fin, increasing in number. Guanophores observed in body cavity of reared

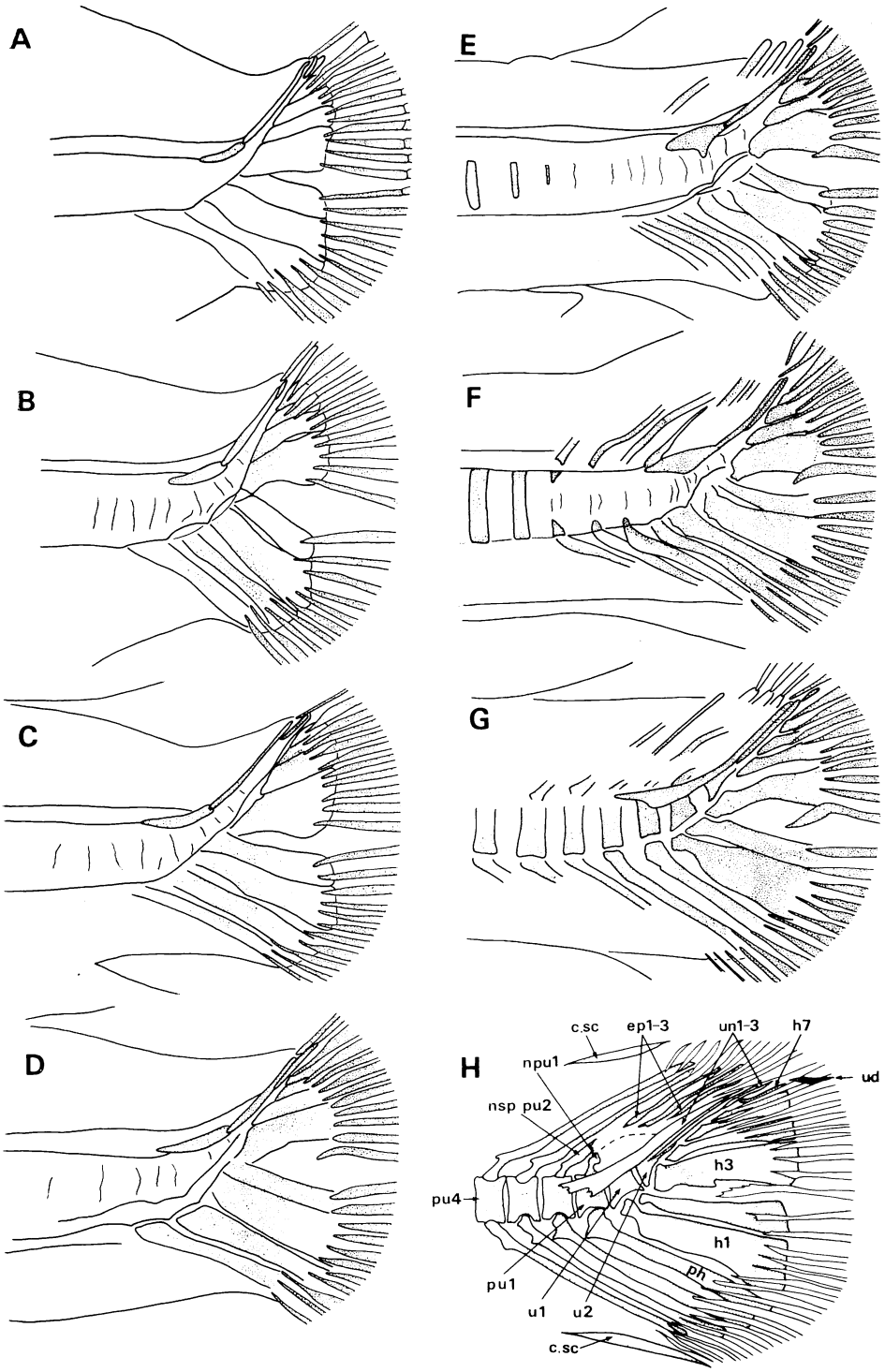

Fig. 3. Ossifications in the caudal skeleton of the specimens drawn in Fig. 1. Degree of darkness of shaded figures shows the degree of ossification. H: Adult redrawn from Forey (1973). c.sc, caudal scute; ep 1~3, epural 1~3; h 1~7, hypural 1~7; npu 1, neural arch associated with 1st preural centrum; nsp pu 2, neural spine associated with preural centrum 2; ph, parhypural; pu 1~4, preural centrum 1~4; u 1~2, ural centrum 1~2; ud, urodermal; un 1~3, uroneural 1~3.

individuals. Grasping tooth completely disappears on both jaws. Differentiation between anterior and posterior teeth not possible. They never disappear, unlike apodes. Minimum number of small teeth, four on upper jaw and seven on lower jaw, gradually increasing in number, and also appearing on premaxillary. Premaxillary, supramaxillary, gill arches, some suspensoria, frontal, posttemporal, supracleithrum and cleithrum ossified. Gular plate appears in rudiment, and ossified at the smallest size (Figs. 1E, 2E), gradually increasing in size. Branchiostegals begin to ossify, four to 14 on left side and three to 13 on right, always larger by one in number on the former. Vertebrae begin to ossify; 23 ossified vertebrae observed in a specimen, 24.5 mm TL (20.7 mm in SL), from 37th to 59th myomeres, and, 54 vertebrae in the smallest specimen (E in Figs. 1, 2, 3) from eighth to 61st myomeres. TL ranged from 29.0 to 23.1 mm (25.2～19.6 mm in SL). Growth rate averaged −0.761 mm in TL/day (range −0.558～−0.917).

Juvenile phase (F and G in Figs. 1, 2, 3): The larvae again increase in length from the smallest size to juvenile. Dorsal fin situated between 31st～50th myomeres, occupying 13～15 myomeres, and has 23～24 rays (fixed in number). Anal fin situated between 49th～59th myomeres, occupying six or seven myomeres, and has 14～15 rays (fixed in number). Anal finfold just before anal fin has disappeared. Pectoral fin rays eight to 13, and pelvics five to ten, but neither fixed in number. Gas bladder in upper part of body cavity, but cannot be easily observed because of opaque body. Body shape adult-like. Melanophores especially dense on dorsal area. Xanthophores observed at the middle of both lobes of the caudal fin of reared individuals. Small teeth on maxillary and premaxillary increase further in number and begin to form narrow bands. Branchiostegals

Table 1. Growth process of larvae in TL during rearing experiments. Numbers in parentheses show total numbers of rearing days.

Tank	Measurements at the beginning			Intermediate measurements						Measurements at the end		
	Fish No.	Phase	TL (mm)	Days	Phase	TL (mm)	Days	Phase	TL (mm)	Days	Phase	TL (mm)
A	I	1st metamorphic phase	34	8	2nd metamorphic phase	25	—	—	—	2(10)	2nd metamorphic phase	24.5
	II	1st metamorphic phase	33	6	2nd metamorphic phase	26	—	—	—	6(12)	2nd metamorphic phase	24.2
	III	1st metamorphic phase	36	7	2nd metamorphic phase	26	4(11)	2nd metamorphic phase	24	11(22)	juvenile phase	29.0
B	IV	leptocephalus phase	37	2	1st metamorphic phase	39	7(9)	2nd metamorphic phase	29	6(15)	2nd metamorphic phase	23.5
	V	1st metamorphic phase	34	6	2nd metamorphic phase	27	5(11)	2nd metamorphic phase	24	4(15)	juvenile phase	26.4
C	VI	1st metamorphic phase	36	—	—	—	—	—	—	6	2nd metamorphic phase	25.4
	VII	1st metamorphic phase	33	6	2nd metamorphic phase	25	4(10)	2nd metamorphic phase	24	8(18)	juvenile phase	27.1
	VIII	2nd metamorphic phase	27	4	2nd metamorphic phase	25	—	—	—	14(18)	juvenile phase	35.6

increase in number, 23 on left side and 22 on right in the case of a 35.6 mm in TL (28.0 mm in SL) specimen (Figs. 1G, 2G), but not fixed in number. 61 vertebrae ossified in a specimen of 26.4 mm TL (F in Figs. 1, 2, 3), and all 67 vertebrae ossified in a specimen of 35.6 mm TL (G in Figs. 1, 2, 3). 3rd uroneural ossified. Scales not yet present. TL ranged from 24.2 to 35.6 mm (20.6～28.0 mm in SL). Growth rate averaged +0.568 mm in TL/day (range +0.455～+0.829).

Notes. The larvae needed 13～15 days to undergo metamorphosis during the rearing experiment, i.e., seven days for the 1st metamorphic phase, and six to eight for the 2nd metamorphic phase. The process of the growth in TL is shown in Table 1.

Throughout the experiment, the larvae of the 1st metamorphic phase at first swam between the surface and middle layers of the aquaria, while the larvae of the 2nd metamorphic phase descended and occasionally moved on the bottom.

It seems that the metamorphosing process of the leptocephali in this study is not essentially different with that of *E. saurus* in Alikunhi and Rao (1951) and Gehringer (1959). Many morphological characters along with metamorphosis, with the exception of the body length and the number of myomeres, are similar in the two species. In addition, both studies about *E. saurus* also indicate that the process of metamorphosis of that species consists of two phases, i.e., a rapid shrinking phase (stage II of Alikunhi and Rao; early metamorphic stage of Gehringer) and a slow shrinking phase (stage III and IV of the former; a part of the mid-metamorphic stage of the latter).

Ecological aspects

Except when the river was flooded, the water depth of the surveyed area was about 40 cm at low tide, and about 140 cm at high tide (spring tide), and the mean drift of the flow was 4 m/sec at low tide. The chlorinity was remarkably different between the surface and the bottom water layer because a salt wedge was always observed at high tide. The chlorinity of the surface layer was 1,140～4,690 ppm at high tide and 65～431 ppm at low tide, and that of the bottom layer was 7,990～16,680 ppm at high tide and 100～880 ppm at low tide. The atmospheric and water temperatures are shown in Table 2.

Throughout the survey, the larvae were most numerous during May in 1977 and 1978 (Tables 2, 3). From the tidal point of view, they were mainly collected in a net opening downstream at high tide. However, even at low tide, they also occurred in this net (Table 3). This fact suggests that they move in the brackish region not only under the influence of tide but according to such factors

Table 2. Occurrence of larvae by larval phase during the operation of set-nets. Juveniles were not caught. Figures in parentheses show mean values. A.T., atmospheric temperature; W.T., water temperature.

Phase	Date	'77.5.1～5.14	'77.8.1～8.25	'77.10.28～11.21	'78.1.25～2.18	'78.5.22～5.27	Total number of individuals
	A.T.(°C)	21.9～33.3(26.7)	24.6～33.8(29.0)	19.8～28.2(23.6)	10.3～26.4(17.9)	21.9～30.9(24.9)	
	W.T.(°C)	25.3～32.0(28.0)	25.8～32.8(28.4)	18.7～27.2(22.6)	12.6～24.2(18.0)	21.5～25.5(23.1)	
Leptocephalus phase		6	—	—	—	2	8
1st metamorphic phase		228	23	12	10	64	337
2nd metamorphic phase		42	2	1	—	2	47
Total		276	25	13	10	68	392

as physiological requirements.

The 392 captured specimens were classified as follows: leptocephalus phase, eight; 1st metamorphic phase, 337; and 2nd metamorphic phase, 47. Specimens of juvenile phase did not occur. This composition of the collected specimens may suggest that the larvae change their habitat with growth.

Identification

According to the revisions of *Elops* by Regan (1909), Bertin (1944) and Whitehead (1962), two species occur in the Indo-West Pacific region, i.e., *E. machnata* and *E. hawaiensis*. These two species are distinguished, according to the above revisions, as follows:

A. 63～64 vertebrae (63～66, personal communication from Whitehead); lower jaw projects and covers the anterior part of premaxillary tooth band when mouth is closed ..... *E. machnata*

B. 68～70 vertebrae (66～70, personal communication from Whitehead); lower jaw included and whole premaxillary tooth band exposed when mouth is closed ..... *E. hawaiensis*

Myomere counts were examined on 392 specimens, most of which have 67 myomeres (others have 66 and 68 myomeres). The number of vertebrae of two juveniles reared in aquaria is 67, being the same as the myomere counts in the majority of the larvae.

On the basis of these characters, the specimens of *Elops* studied here are identified as *E. hawaiensis*.

Notes. Three species of *Elops* have been reported from Japan: *E. machnata* (Temminck and Schlegel, 1842～1850; Jordan and Hubbs, 1925; Tanaka, 1931; Matsubara, 1955; almost all Japanese records after Matsubara (1955) followed his identification); *E. saurus* (Jordan and Herre, 1906; Tanaka, 1933; Okada, Uchida and Matsubara, 1935; Okada and Matsubara, 1938; Oshima, 1940; Okada, 1959～1960; Lindberg and Legeza, 1965); *E. hawaiensis* (Snyder, 1912; Jordan, Tanaka and Snyder, 1913; Tanaka, 1916).

None of these records, except those of Snyder (1912) and Jordan and Hubbs (1925), are based on detailed examination of morphological characters. Snyder (1912) counted 68 vertebrae in the Japanese species and identified it as *E. hawaiensis*. Jordan and Hubbs (1925) examined three Japanese specimens, one of which (UMMZ 142870) had 64 vertebrae, and identified them as *E. machnata*. But when the authors re-examined the three specimens (SU 23825; UMMZ 142870; and No. 13061 in Department of Ichthyology, American Museum of Natural History) used in the study of Jordan and Hubbs (1925), they proved to be *E. hawaiensis* due to the presence of 68 vertebrae (not 64 as mentioned by Jordan and Hubbs), the lack of lower jaw projection, and the exposure of the entire premaxillary tooth band when the mouth is closed.

According to the three revisions of *Elops* (Regan, 1909; Bertin, 1944; Whitehead, 1962), *E. saurus* is an Atlantic species and would not occur in Japan. Most of the reports on *E. machnata* are nominal, and some have proved to be misidentifications of *E. hawaiensis*, e.g., Temminck and Schlegel (1842～1850) after Snyder (1912), Jordan and Hubbs (1925) and Matsubara (1955) who considered the Japanese species as *E. machnata* only from the description of Bertin (1944), who cited

Table 3. Occurrence of larvae in relation to tidal conditions and the directions of net opening. D, net opening directed downstream; U, net opening directed upstream.

Tide	Net	Date					Total number of individuals
		'77.5.1～5.14	'77.8.1～8.25	'77.10.28～11.21	'78.1.25～2.18	'78.5.22～5.27	
High	U	16	2	—	—	11	29
	D	206	14	11	10	18	259
Low	U	33	8	2	—	20	63
	D	21	1	—	—	19	41
Total		276	25	13	10	68	392

the above incorrect report of Jordan and Hubbs (1925). These facts may indicate that *E. machnata* does not occur in Japan, but this question needs further investigation.

The authors recommend to use the Japanese name Karaiwashi for *E. hawaiensis*.

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石垣島から得られたカライワシ *Elops hawaiensis* の葉形幼生の変態

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琉球列島石垣島から得たカライワシ属 *Elops* の葉形幼生を数個体飼育し，その変態過程を明らかにした．その結果幼生の発生は背・臀鰭の位置，鰾の形，体形・体長，色素胞の配列，幼歯の形状，内部骨格の骨化，成長率などから葉形幼生期，第1変態期，第2変態期，稚魚期の4期に分けることができた．

本幼生は 66～68 筋節，67 個の脊椎骨を有し，*E. hawaiensis* と同定された．なお日本産カライワシは従来 *E. machnata* とされてきたが，*E. hawaiensis* の誤りと思われる．

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