

Abstract—This study describes the early life stages of the Japanese dory (*Zenion japonicum*) based on 5 larvae collected during a 2004 Hawaiian Islands biomass survey. The fish larvae were sampled with a 1-m² Multiple Opening/Closing Net and Environmental Sensing System equipped with 335- μ m mesh sized nets and an Intelligent Operative Net Sampling System. The larvae are between 3.08 mm notochord length and 4.89 mm standard length, and except for the largest specimen, they are the smallest series described thus far. We identified larvae to species level based on the similarity of the pigmentation pattern between specimens and the meristic counts of the dorsal (VI, 23) and anal (I–II, 23) fins, which appear to be unique among the *Zenion* species, in the most developed and largest larva examined.

Early life stages of the Japanese dory (*Zenion japonicum*) (Zeniontidae: Zeiformes) from the central North Pacific Ocean

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Like taxonomists in general, the cohort of larval-fish taxonomists are [sic] ageing rapidly... (Leis, 2015:24)

Introduction

The 4 species of the genus *Zenion* (Jordan and Evermann, 1896) are small to medium-sized fishes with deep bodies, long dorsal fins, long pelvic fins with large spines, and large eyes located near the dorsal profile. The species of the genus *Zenion* occur on continental shelves and island slopes in the photic and mesopelagic zones between 200 and 700 m. The Japanese dory (*Zenion japonicum*) (Kamohara, 1934) inhabits the western and southeast Pacific (Machida, 1984; Okamura et al., 1985; Pequeño, 1989). *Zenion hololepis* (Goode and Bean, 1896) is a widespread species, reportedly from the tropical and subtropical parts of the Atlantic, the Caribbean, the Gulf of Mexico, and the

western central Pacific, Indian Ocean, and the South China Sea (Goode and Bean, 1896; Smith and Heemstra, 1986; McEachran and Fehhelm, 1998; Ditty, 2006; Martins et al., 2012; Rufus et al., 2021). Historical records place the elongate dory (*Z. leptolepis*) (Gilchrist and von Bonde, 1924) in the west Indian Ocean to South Africa and the southwest Pacific (Smith and Heemstra, 1986; Paulin et al., 1989). *Zenion longipinnis* (Kotthaus, 1970) is known from the western Atlantic, the Gulf of Mexico, the Caribbean, the north coast of Brazil (Ditty, 2006; Fricke, 2015).

Myers (1960) established the family Zeniontidae exclusively for the fishes of the genus *Zenion*. However, Tyler et al. (2003) grouped *Zenion* with the monotypic genus *Capromimus*

Table 1

Early life history stages and lengths for the 10 zeiform fishes for which descriptions exist. SL=standard length; juv.=juvenile.

Species	Stage/length	Source
<i>Zeus faber</i>	Entire series	Schmidt (1908), Sanzo (1931)
<i>Alloctytus folletti</i>	31mm and 78mm SL	Okiyama (2014)
<i>A. guineensis</i>	1 early juv.	Ditty (2006)
<i>A. verrucosus</i>	1 l. and 1 late juv.	Ditty (2006)
<i>Oreosoma atlanticum</i>	?	Abe and Kaji (1972)
<i>Pseudocyttus maculatus</i>	1 late juv.	Ditty (2006)
<i>Xenolepidichthys dalgleishi</i>	10.7mm and 17.2mm SL	Ditty (2006)
<i>Cyttopsis rosea</i>	9.5mm SL	Ditty (2006)
<i>Zenion japonicum</i>	4.7 and 5.6mm SL	Okiyama (2014)
<i>Zenion hololepis</i> (caudal skeleton)	8.9 mm	Johnson and Patterson (1993)

(rough dory [*Capromimus abbreviatus*]) and the 2 species of *Cyttomimus* (*Cyttomimus stelgis* and *Cyttomimus affinis*) in the family Zeniontidae. A more recent comprehensive study by Grande et al. (2018), based on morphological characters mainly from Tyler and Santini (2005) and molecular data, suggested that the Zeniontidae are paraphyletic, with *Cyttomimus* and *Capromimus* closely related to Oreosomatidae, and returned *Parazen* to the monotypic Parazenidae. The enigmatic *Macrurocyttus acanthopodus* was occasionally included in the family Zeniontidae as well but is now placed in the family Grammicolepididae (Tyler et al., 2003).

Heemstra (1999) synonymized *Z. japonicum* and *Z. longipinnis* with *Z. hololepis* without providing evidence for his decision. In a more recent study, however, Heemstra (2016) provided evidence for his decision to synonymize *Z. longipinnis* and *Z. hololepis*. According to Heemstra (2016), the shape of the lateral line does not differ between the 2 species, as previously described by Kotthaus (1970). Further, Kotthaus (1970) believed that the lack of scales on the isthmus, as defined by Goode and Bean (1896) for *Z. hololepis*, is due to damage to the specimen rather than a character to differentiate the 2 species. Martins et al. (2012) found a 10.1% average divergence in the cytochrome *c* oxidase subunit I sequence between *Z. japonicum* and *Z. hololepis*, confirming the validity of both.

Descriptions of early life history stages of zeiform fishes are rare, and of the 33 putative species within the group, only 10 larval descriptions exist (Table 1). The John dory (*Zeus faber*) is the only species for which the entire early life history is well documented (Schmidt, 1908; Sanzo, 1931). While the larvae of the genus *Zenion* are relatively easy to recognize, the ambiguous number of valid species often prevents further identification of the larvae to species. At present, the only description of larvae of *Z. japonicum* is that of 5.6 mm and 4.7

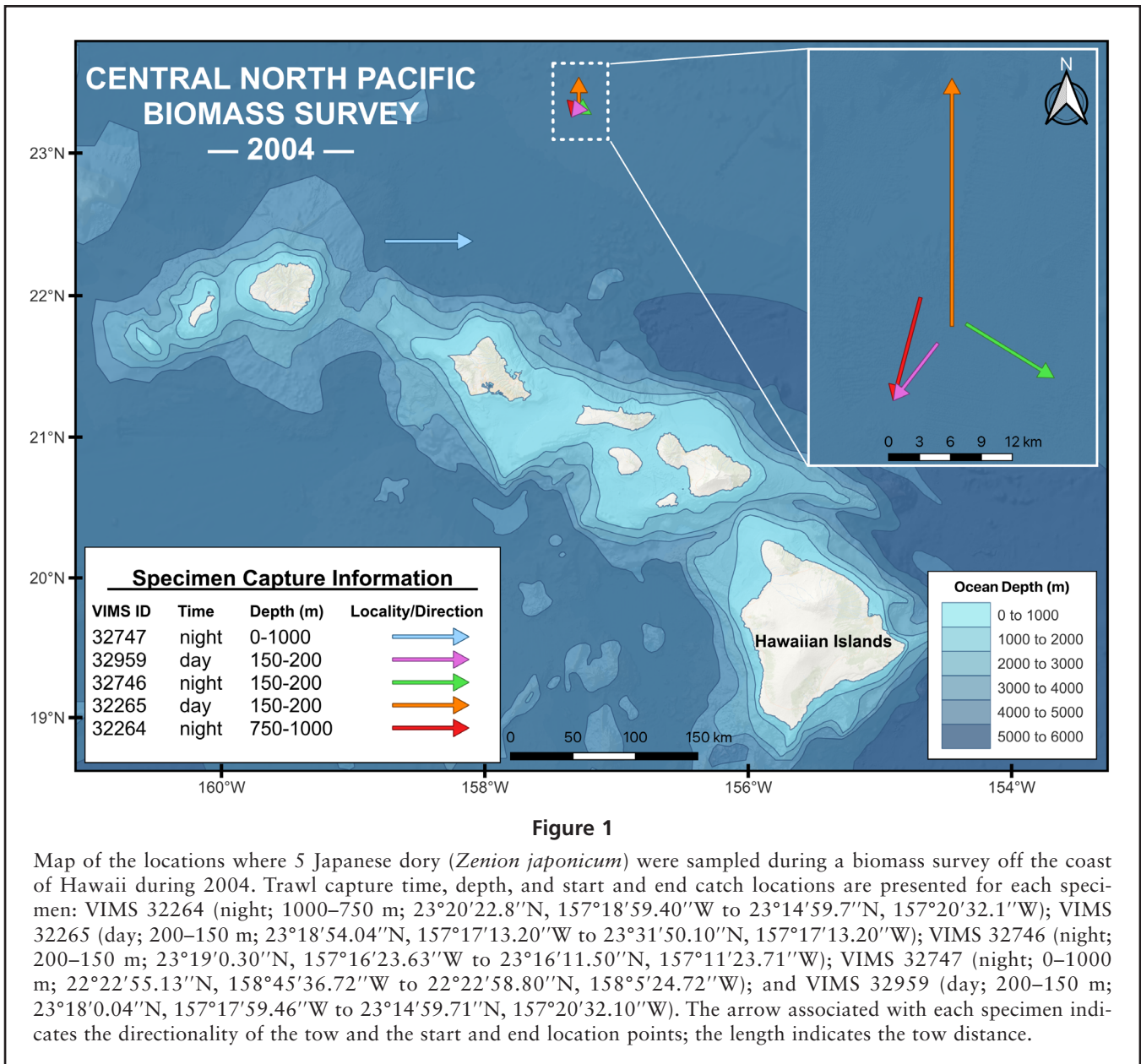
mm standard length (SL) specimens by Okiyama (2014), which included an illustration of the larger larva.

The larvae included in this paper were identified and described as a project in an ichthyoplankton course at Oregon State University. Early life history stages of fishes are essential for many fields, such as phylogenetic systematics, ecology, fisheries science, etc. (Konstantinidis et al., 2015; Auth et al., 2020; McDowell et al., 2022). However, taxonomists who can identify larval fishes, such as Geoffrey Moser, are dwindling in number, and the field suffers from the lack of upcoming ichthyoplankton taxonomists. The ichthyoplankton course at Oregon State University, of which this description of the larval *Zenion* was a part, is one of only 2 regularly taught worldwide (the other is a course at the Marine Science Station in Concarneau, France).

The goals of this study are to present the description of early larval development of *Z. japonicum* to aid in the identification of zeiform larvae and to present illustrations of smaller larvae of the species to add to the information in Okiyama (2014).

Materials and methods

Steinberg et al. (2008) collected the 5 *Z. japonicum* larvae during a 2004 biomass survey off the coast of Hawaii (Fig. 1), with a 1-m² Multiple Opening/Closing net and Environmental Sensing System equipped with a 335- μ m mesh and an Intelligent Operative Net Sampling System. From the surface to 200 m, the discrete depth increments were 50 m; from 200 m to 500 m, the increments increased to 100 m; and between 500 m to 1000 m, the increments increased to 250 m. However, the larvae were all collected below 200 m. They are housed at the Nunnally Ichthyology Collection, Virginia Institute of Marine Science (VIMS). All survey samples, including



the specimens described in this paper, were fixed in 10% formalin–seawater prior to long-term storage in 70% ethanol. Body length (BL) was measured from the tip of the ethmoid region to the posterior tip of the notochord for preflexion (notochord length [NL]) and to the posterior tip of the hypurals for the postflexion specimens (standard length [SL]).

Specimens

Zenion sp.: VIMS 32265, 4.24 mm NL; VIMS 32264, 4.10 mm NL (not illustrated); VIMS 32746, 4.89 mm SL; VIMS 32747, 4.32 mm SL; VIMS 32959, 3.08 mm NL.

Imaging

We used a Zeiss SteREO Discovery.V20 stereomicroscope (Carl Zeiss AG, Oberkochen, Germany) with an attached AxioCam high-resolution digital camera (Carl Zeiss AG) to photograph all specimens and the ZEISS software (AxioVision 4.0) to obtain measurements. We adjusted for contrast and color balance and removed background debris with Adobe Photoshop CC 2015 (Adobe Systems Inc., San Jose, CA). The schematic drawings were created in Adobe Illustrator 2021 (Adobe Systems Inc.), and the figure plates were assembled in Adobe InDesign 2021 (Adobe Systems Inc.).

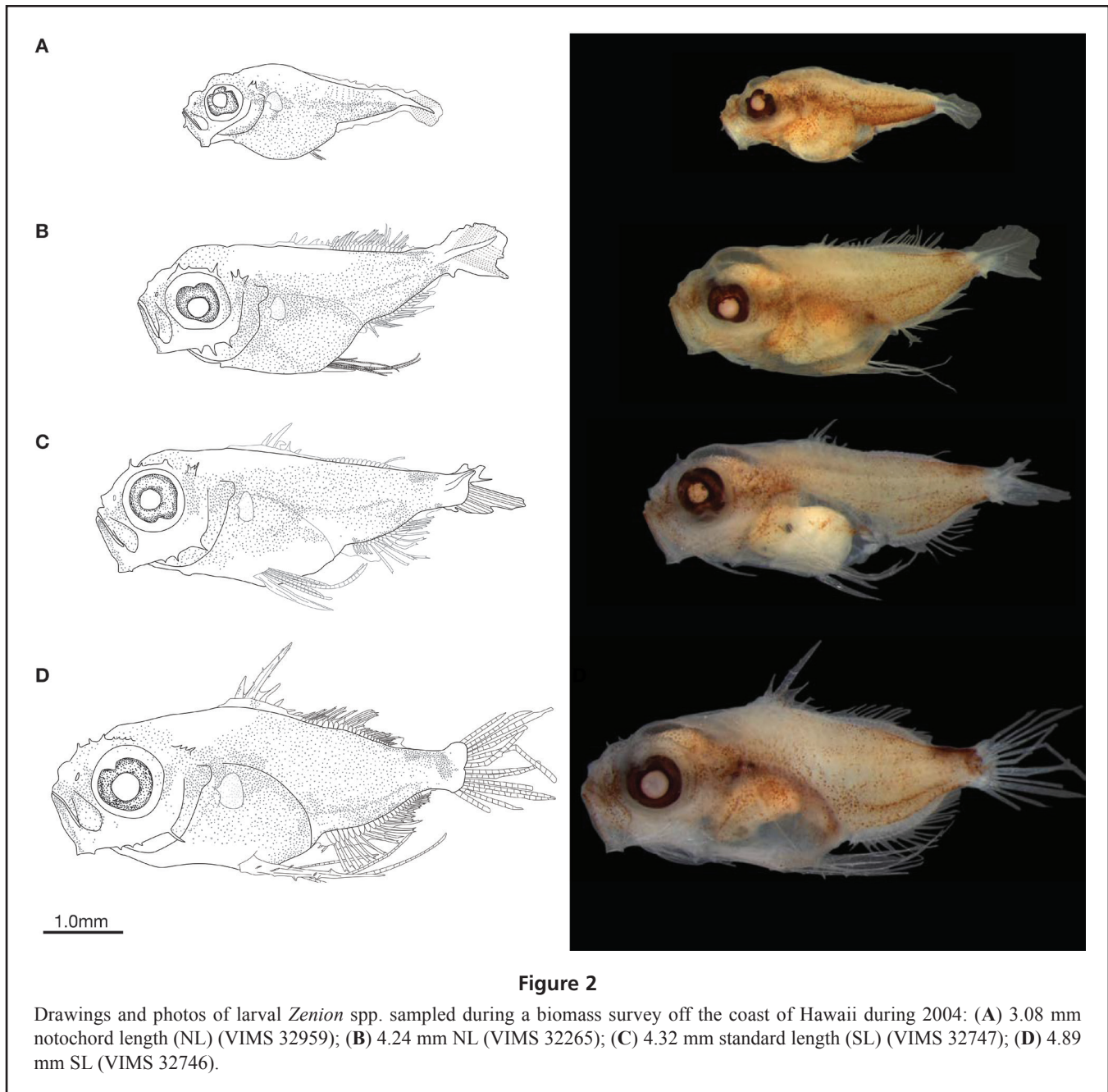


Figure 1 was generated using the QGIS, vers. 3.30.1 (QGIS Development Team, 2023).

Results

Identification

We established the developmental series of the 5 *Zenion* species larvae (3.08 mm NL, 4.89 mm SL) as belonging to the order Zeiformes by myomere count, the heavy pigmentation, and the sequence of fin develop-

ment, the almost vertical mouth, and the large rostral cartilage. To identify the larvae to the family Zeniontidae and the genus *Zenion*, we noted the less compressed body shape similar to that of *Parazen*, which is generally uncommon for Zeiformes, pelvic fins that originate posterior to the pectoral fins, and the characteristic saddle of melanophores between the dorsal and caudal fins (Fig. 2). Pigment pattern, myomere count, and head spination linked the larvae. We used the dorsal, anal, and pelvic-fin ray counts of the 4.89-mm-SL postflexion larva, VIMS 32746 (Table 2), to ascertain the order, family, and species.

Table 2

Meristic characters from the literature for the *Zenion* species, the zeiform species known from the region of the Hawaiian Ridge, and the 5 Virginia Institute of Marine Science (VIMS) specimens described in this paper. The meristic characters include vertebrae/myomere count (V/M; vertebrae and myomeres counts are identical), dorsal fin (D), anal fin (A), pectoral fins (P), and pelvic fins (V). Meristic counts that are underlined indicate overlap with the meristic counts of the largest larva described in this paper. ()=genus level; -=not present; ?=not documented; NL=notochord length; SL=standard length.

Species	V/M	D	A	P	V	Source
<i>Zenion hololepis</i>	27	VI-VII, 26-31	II, 23-29	16-18	I, 6	Tyler et al. (2003)
	(27)	VI-VII, 25-28	I, 23-28	16	I, 6	Smith and Heemstra (1986)
	?	VI-VII, 26	?, 23	16	I, 6	Goode and Bean (1896)
	25-27	VI-VII, 25-31	I-II, 23-28	15-17	I, 6	Heemstra (2016)
	?	VI, 28	I, 26	15-17	I, 6	Martins et al. (2012)
<i>Zenion</i> sp. VIMS32959 (3.08mm NL)	28-29	-	-	-	I, 2	This study
<i>Zenion</i> sp. VIMS32264 (4.10mm NL) not pictured	28-30	VI, ≈19	I, ≈15	-	-	This study
<i>Zenion</i> sp. VIMS32265 (4.24mm NL)	?	VI, ≈17	I, ≈15	-	I, 6	This study
<i>Zenion</i> sp. VIMS32747 (4.32 mm SL)	28-30	VI, ≈18	I, ≈16	-	I, 6	This study
<i>Zenion</i> sp. VIMS32746 (4.89mm SL)	28-30	VI, 23	I, 23	-	I, 6	This study
<i>Zenion japonicum</i>	27-28	VI-VII, 23-29	I, 23-26	15-17	I, 5-6	Okiyama (2014)
	?	VII, 27-28	I, 23-24	17	I, 6	Kamohara (1934)
	?	VI-VII, 23-28	I, 6-7	15-17	I, 5-6	Machida (1984)
<i>Zenion leptolepis</i>	27	VI-VII, 27-31	II, 22-31	16-18	I, 6	Tyler et al. (2003)
	(27)	VI-VII, 28-31	I, 28-32	15-17	I, 6	Smith and Heemstra (1986)
	?	VII, 28	I, 32	15	I, 5	Gilchrist and von Bonde (1924)
<i>Zenion longipinnis</i>	?	VI, 28-29	I, 25-26	?	?	Uyeno et al. (1983)
	26	VI, 29	I, 26	16	I, 6	Kotthaus (1970)
<i>Zenion</i> sp.		VI, 30	I-II, 26-28	16-17	I, 6	Uyeno et al. (1983)
<i>Cyttomimus stelgis</i>	28-30	VII-VIII, 22-24	II, 22-26	14-15	I, 6	Tyler et al. (2003)
<i>Stethopristes eos</i>	32-33	VI-VII, 27-28	I, 27-28	13-14	9	Tyler et al. (2003)
<i>Grammicolepis brachiusculus</i>	28-30	VI-VII, 32-34	II, 33-35	14-15	I, 6-7	Tyler et al. (2003)
<i>Zenopsis nebulosus</i>	34-36	VIII-IX, 25-27	III, 24-26	11-12	6	Tyler et al. (2003)
<i>Alloctytus folletti</i>	40	V-VII, 30-33	III, 30-32	19-21	I, 6	Tyler et al. (2003)

Table 3

Measurements in percent of body length or head length of 4 of the *Zenion* larvae sampled during a biomass survey off the coast of Hawaii during 2004. A=anal-fin length; BD=body depth; BL=standard or notochord length; DL=dorsal-fin length; ED=eye diameter; HD=head depth; HL=head length; PAL=preanal length; NL=notochord length; SL=standard length.

Species	HL/BL	HD/BL	ED/HL	BD/BL	PAL/BL	DE/BL	A/BL
<i>Zenion</i> sp. VIMS32959 (3.08mm NL)	29.2	27.2	46.5	38.3	59.61	–	–
<i>Zenion</i> sp. VIMS32265 (4.24mm NL)	31.8	29.6	51.3	35.9	62.7	38.4	20.0
<i>Zenion</i> sp. VIMS32747 (4.32 mm SL)	32.1	30.7	53.0	37.3	64.8	41.0	24.3
<i>Zenion</i> sp. VIMS32746 (4.89mm SL)	35.4	30.4	48.3	38.5	64.5	44.1	24.3

External morphology

Shape

The 5 larvae share a moderately laterally compressed body, a large head (29.2–35.4% BL), and a compact gut venting at midbody (59.6–64.8% BL) in all stages (Fig. 2, Table 3). The lower jaw closes to a near vertical position, which is characteristic for larval zeiforms.

Head spination

Posttemporal spines are present in all larvae examined (Fig. 2). Three posterior-oriented preopercular spines are present on all but the smallest specimen (Fig. 2, B–D). The supraocular crest of the frontal dorsally of the eye is present on all but the smallest larva (Fig. 2). The anterior-most spine is the largest in the preflexion and late flexion larvae (Fig. 2, B and C) but is similar in size to the more posterior spine in the 4.89-mm-SL postflexion larva (Fig. 2D).

Meristic data and fin development

Myomere counts range between 28 and 30 (Table 2). The elongated pelvic fin originates at the midbody and has completed development (I, 6) by the preflexion stage (Fig. 2B). The pelvic spine is serrated, and the longest ray (2nd) reaches the caudal peduncle in the largest postflexion larva (Fig. 2D).

The pectoral fin is already present in the smallest preflexion larva, but the fin rays remain undifferentiated in all our specimens (Fig. 2).

Six spines are present in the first dorsal fin in all but the 3.08-mm-NL preflexion larva, the second spine being the longest and serrated in the 4.89-mm-SL postflexion larva (Fig. 2, Table 2). The median fins in the larg-

est specimen have VI, 23 dorsal-fin elements and I–II, 23 anal-fin elements completed (see section on anal-fin spines in the Discussion).

Pigmentation

The larvae are heavily pigmented with patterns matching the 2 larvae of *Z. japonicum* described and illustrated by Okiyama (2014).

Head

The pigment on the head is concentrated on the lower jaw of the early preflexion 3.08-mm-NL larva, with some melanophores on the anterior part of the upper jaw, between the nostril and the eye, the pterotic region toward the dorsal part of the preopercle, and the frontal and parietal regions (Fig. 2). Pigment on the lower jaw is present along the dentary, the anguloarticular (forming the jaw joint) and retroarticular, with denser pigmentation closer to the symphysis (Fig. 2). Pigment on the upper jaw is initially visible on the premaxilla and maxilla (Fig. 2A) and extends distally on the maxilla in the later stages (Fig. 2, B–D) but is less pronounced than that proximally. The area of the lateral ethmoid, between the eye and the nostril, is pigmented but remains unpigmented around the rostral cartilage in all stages (Fig. 2). A dense melanophore patch is present on the otic region between the eye and the preopercle (Fig. 2), forming a stripe with the pigmentation anterior to the eye. The parietal and the posterior part of the frontal are covered with melanophores, which slightly increase in density with size (Fig. 2). The ventral area of the preopercle and cleithrum of the 3.08-mm-NL and 4.24-mm-NL larvae, including the area of the branchiostegal rays, is heavily pigmented (Fig. 2A, B), with pigment becoming restrict-

ed to the dorsal area of the preopercle in the 4.47-mm-NL flexion and 4.89-mm-SL postflexion larvae (Fig. 2, C and D).

Trunk

The pigment on the anterior trunk region between the nape and the mid-section of the second dorsal fin is absent in the smallest early preflexion larva (Fig. 2A) but is gradually filled in with melanophores in the older stages until it reaches about the third dorsal-fin spine in the largest specimen (Fig. 2, B–D). The pigmentation on the caudal peduncle in the 4.24-mm-NL preflexion larva (Fig. 2B) is more concentrated dorsally and becomes a dark pigment patch, which extends ventrally in the 4.89-mm-SL postflexion larva (Fig. 2D). The 4.24-mm-NL and the 4.32-mm-SL specimens show a smaller pigment patch on the caudal peduncle ventrally (Fig. 2, B and C), which is already indicated in the 3.08-mm-NL specimen but is less prominent in the 4.89-mm-SL specimen (Fig. 2, A and D). The caudal fin is unpigmented in all 5 larvae (Fig. 2). The cleithrum area is entirely covered in melanophores in the preflexion and flexion larvae examined (Fig. 2, A–C), whereas it is unpigmented on the ventral third in the postflexion larva (Fig. 2D). The pigment along the lateral line in the 2 preflexion larvae continues as a thin stripe toward the caudal peduncle. Internal pigment is present over the gut in all 5 larvae examined (Fig. 2). External pigment over the gut is present laterally and ventrally in the preflexion larvae (Fig. 2, A and B) but is absent over the ventral surface in the flexion and postflexion larvae (Figs. 2, C and D).

Discussion

Species identification

A combination of several meristic characters (Table 2) and proportional measurements (Table 3) distinguishes larvae of the family Zeniontidae from other zeiforms from the area. The meristic counts of *Cyttomimus stelgis* overlap strongly with *Zenion*, but in *Cyttomimus stelgis*, the caudal peduncle is longer and narrower, and the body is more compressiform (Gilbert, 1905).

Although the margin of difference is narrow, the dorsal and anal fins provide the only variables useful for species identification (Table 2). The number of dorsal-fin elements of VI, 23 for our largest specimen is on the lower end of the spectrum of counts for the genus and overlaps only with *Z. japonicum*. The number of anal-fin elements with I–II, 23 overlaps with *Z. japonicum* and *Z. hololepis*; however, the number of dorsal-fin rays is at least 25 or more in the latter (Table 2). The anal-fin ray count also overlaps with *Z. leptolepis* (Tyler et al., 2003); however, we exclude that species as a possibility

because of the lack of geographical overlap (see Introduction). An anal-fin element count of I, 6–7 was given for the specimen of *Z. japonicum* described by Machida (1984) (Table 2), which is an unusually low number for zeniontids, and we assume, based on the photo of the specimen (Machida, 1984, plate 103), that the count is incorrect.

Anal-fin spines

Tyler and Santini (2005) documented 2 anal-fin spines for *Z. hololepis* and *Z. leptolepis*, and Uyeno et al. (1983) reported one or 2 for the genus. In contrast, all other references (see Table 2) document a single spine. In the identification key of zeiform families and genera, Tyler et al. (2003:44) described the “second anal-fin spine below the surface of skin and not visible externally... for the genus *Zenion*.” Since Tyler et al. (2003) used cleared, stained, and dried material to analyze the osteology, the second anal-fin spine was likely overlooked by those listed in Table 2 and by us in this study. However, it was impossible, without damaging the specimens, to identify a second spine in the anal fin in our specimens.

Conclusions

Early life stages of fishes of the order Zeiformes are exceptionally rare and unknown for some families (Table 1). *Zeus faber* is the only exception, with early larval stages described by Schmidt (1908) and Sanzo (1931). Identification of the larval *Zenion* to species is challenging based on a) the available meristic data, which show a high degree of overlap (see Table 2); b) the sympatry of *Z. japonicum* and *Z. hololepis*; and c) the uncertainty of the number of valid species. However, based on the pigmentation of the 5 specimens and the complete meristic data of the largest specimen, we identified the 5 larvae as *Z. japonicum*.

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