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Comparison of larval hammerjaw (*Omosudis lowii*) (Pisces: Alepisauridae) from 3 oceans

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Abstract—The first detailed description of the larvae of hammerjaw (*Omosudis lowii*) from the western Indian Ocean is given. Errors in the description of larvae from the Atlantic Ocean are corrected: although the most comprehensive descriptions and illustrations of Atlantic specimens of *Omosudis* in previous reports have not mentioned or shown head ridges or spines, all larvae from the Atlantic, Pacific, and Indian Oceans examined in this study have preopercular spines and a dorsal ridge on the head. The results of this study provide further evidence that there are no species differences between specimens from the 3 oceans. The variability of peritoneal pigmentation is discussed. Morphological characteristics are provided for the reliable identification of larvae of *O. lowii*.

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The hammerjaw (*Omosudis lowii*) Günther, 1887 is a true oceanic species, rarely found on the continental shelf and distributed in tropical and temperate waters of the Atlantic, Indian, and Pacific Oceans (Rofen, 1966; Carpenter and Niem, 1999; Carpenter, 2002; Fricke et al., 2018). Günther (1887) described this species on the basis of 2 specimens from the Philippine Sea and off Madeira in the eastern Atlantic Ocean. Authors of subsequent reports often have used *lowei* as the spelling for the species name because it was a patronym in honor of Richard T. Lowe, but that spelling is an unacceptable emendation of the species name published by Günther (1887). In the early 20th century, 2 other species and 2 subspecies of *Omosudis* were described: *O. elongatus* Brauer, 1906; *O. brevis* Brauer, 1906; *O. lowei* var. *indicus* Brauer, 1906; and *O. lowei funchali* Roule, 1929. Ege (1958) determined that *O. elongatus* is a synonym of *Paralepis elongata* (Brauer, 1906), the elongate pikesmelt. Brauer's (1906) illustration of the larval example of *O. brevis* (15.3 mm total length [TL]?) clearly shows the dorsal-fin origin in line with the posterior edge of the gill cover and in line with the pectoral-fin base, indicating that *O. brevis* was based on a larval specimen of an *Alepisaurus* species. *Omosudis indicus* Brauer, 1906 and *O. funchali* Roule, 1929 remain as available names if there is more than 1 species in the genus. *Omosudis* is currently thought to be a monotypic genus, following revisions of the genus by Ege (1958) and Rofen (1966), a genus belonging to the family Alepisauridae (Baldwin and Johnson, 1996; Sato and Nakabo, 2002; Davis, 2010). As far as we know, no morphological differences have been found between adults from different locations of this widespread species (Ege, 1958; Rofen, 1966; Nielsen and Jespersen, 1986), but the situation is different for larvae of this species.

A number of illustrated descriptions of larvae of *Omosudis* from the Atlantic (Roule and Angel, 1930; Ege, 1958) and Pacific (Belyanina, 1982; Okiyama, 1984, 2014; Choi et al., 2020) Oceans have been published, and these descriptions indicate regional differences. According to these descriptions,

larvae from the Pacific Ocean differ markedly from larvae from the Atlantic Ocean in several morphological features: the presence of dorsal serrated ridges on the head, preopercular spines, and a caudal pigment band in Pacific larvae (absent in Atlantic larvae), as well as more intense pigmentation. Although it has been suggested that these characters were probably overlooked when Atlantic larvae have been described (Okiyama, 1984; Ditty, 2006), these differences, together with the discrepancy in the number of dorsal-fin rays between the South China Sea and North Atlantic populations (Ege, 1958), have led to the suggestion that there are more than 1 species within the genus *Omosudis* (Okiyama, 1984; Fahay, 2007). In a recent paper, Choi et al. (2020) discussed the problems of identifying larvae of *Omosudis* and used molecular genetics to suggest that Pacific larvae are *O. lowii*, but they did not resolve the issue of Atlantic larvae. They did not give the collection locality for the specimen from which the genetic sequence came that they used to identify their larva, creating an additional question about the relevance of their conclusions to the identity of *Omosudis* from the different oceans.

We have at our disposal larvae of *O. lowii* from the Indian Ocean, which have not been described before, as well as specimens from the Atlantic Ocean and the Pacific Ocean. The aim of this article is to describe the larvae of *O. lowii* from the Indian Ocean, to clarify the morphology of the larvae from the Atlantic Ocean and to identify differences, if any, between the larvae of this species from different regions of the world ocean.

Materials and methods

The work was carried out on specimens from the Shirshov Institute of Oceanology, Russian Academy of Sciences. A total of 20 larvae of *O. lowii*, with a range in standard body length (SL) of 7.7–28.0 mm, from the Atlantic (9 specimens), Indian (4 specimens), and Pacific (7 specimens) Oceans were directly examined (Table 1). Catalog numbers are provided for stained specimens and those used for figures. Atlantic Ocean: R/V *Akademik Vavilov*, expedition no. 43, SL 7.7 mm (catalog no. IORAS 04993), 17 October 2016, station (sta.) 2632, 19°34′N, 36°52′W, Bogorov-Rass (BR) net, 200–1000 m; 10.0 mm SL (IORAS 04994), 20 October 2016, sta. 2647, 11°26′N, 41°01′W, BR net, 200–800 m; 11.0 mm SL, 18 October 2016, sta. 2636, 16°37′N, 38°13′W, BR net, 200–900 m; R/V *Akademik Ioffe*, expedition no. 29, 16.5, 17.0, and 23.0 mm SL, 7 November 2009, sta. 2171, 4°06′S, 12°25′W, midwater trawl (MWT), 0–1250 m; R/V *Akademik Ioffe*, expedition no. 67, 15.5 mm SL, 29 July 2024, sta. 4507, 25°19′N, 23°43′W, MWT, 0–1125 m; 11.2 and 11.7 mm SL, 31 July 2024, sta. 4510, 27°15′N, 23°45′W, MWT, 0–1006 m. Indian Ocean: R/V *Vityaz*, expedition no. 31, 11.0 mm SL, 13 March 1960, sta. 4679, 7°31′S, 40°19′E, MWT, 0–2300 m; R/V *Vityaz*, expedition no. 36, 12.0 mm SL (IORAS 04995), 20 November 1964, sta. 5315, coordinates unknown (central Indian Ocean), MWT, 0–4500 m; R/V *Vityaz*, expedition no. 17, 14.2 mm SL, 6 January 1989, sta. 2789, 12°02′S, 60°37′E, MWT, 0–1000 m; R/V *Akademik Kurchatov*, expedition no. 36, 14.8 mm SL, 11 April 1983, sta. 3750, 10°36′S, 50°01′E, MWT, 2950–3450 m. Pacific Ocean: R/V *Vityaz*, expedition no. 57, 11.0 mm SL, 14 February 1975, sta. 7200, 10°27′N, 126°24′E, MWT, 0–1000 m; R/V *Vityaz*, expedition no. 29, 11.2 mm SL, 22 November 1959, sta. 4548, 6°31′S, 100°07′E, Perlon ring trawl, 0–3115 m; R/V *Vityaz*, expedition no. 57, 13.2 mm SL, 9 May 1975, sta. 142, 29°20′N, 142°40′E, MWT, 0–1000 m; R/V *Akademik Mstislav Keldysh*, expedition no. 22, 15.0 mm SL, 3 September 1990, sta. 2342, exact coordinates unknown (near Hawaiian Islands), BR net, 750–1000 m; R/V *Vityaz*, expedition no. 25, 22.0 mm SL, 19–20 August 1957, sta. 3689, 11°20′N, 142°10′E, hamseros conical net, 0–1000 m; R/V *Vityaz*, expedition no. 27, 25.0 and 28.0 mm SL, 16 May 1958, sta. 3993, 2°00′N, 174°83′W, hamseros conical net, 0–1000 m.

Additionally, 4 larvae of *Alepisaurus* from the Atlantic Ocean were examined: 3 shortnose lancetfish (*A. brevirostris*) Gibbs, 1960, R/V *Akademik Ioffe*, expedition no. 29, 13.0 and 16.5 mm SL (IORAS 04997), 7 November 2009, sta. 2171, 4°06′S, 12°25′W, MWT, 0–1250 m; R/V *Akademik Ioffe*, expedition no. 67, 13.5 mm SL, 31 July 2024, sta. 4511, 28°54′N, 23°26′W, MWT, 0–1170 m; and 1 longnose lancetfish (*A. ferox*) Lowe, 1833, R/V *Akademik Ioffe*, expedition no. 67, 15.0 mm SL (IORAS 04996), 5 August 2024, sta. 4525, 35°25′N, 20°22′W, MWT, 0–1175 m.

Most of the samples are stored in a 4% formaldehyde solution; the samples from expedition no. 67 of R/V *Akademik Ioffe* are stored in a 96% ethyl alcohol solution. The 7.7-mm-SL larva (IORAS 04993) and 15.0-mm-SL larva of *A. ferox* (IORAS 04996) were stained with alizarin according to the standard method (Taylor and Van Dyke, 1985). The following specimens were photographed by using a Leica S6 E stereomicroscope (Leica Microsystems[1], Wetzlar, Germany) equipped with a Canon EOS 1200D camera (Canon Inc., Tokyo, Japan): 3 larvae of *O. lowii*, 7.7 mm SL (IORAS 04993), 10.0 mm SL (IORAS 04994), and 12.0 mm SL (IORAS 04995); larva of *A. ferox*, 15.0 mm SL (IORAS 04996); and larva of *A. brevirostris*, 16.5 mm SL (IORAS 04997). Details of the specimens of *O. lowii* from all localities, such as meristic features, proportions, and number of peritoneal patches, are given in Table 1. In addition, all descriptions and illustrations of larvae currently available in the literature were studied and are considered in the "Discussion" section (Roule and Angel, 1930; Ege, 1958; Belyanina, 1982; Okiyama, 1984, 2014; Choi et al., 2020).

Counts and measurements follow the standard practice (Leis and Carson-Ewart, 2000; Richards, 2006; Fahay, 2007). Information for the following features are included in the descriptions: SL (distance from the tip of the snout to the posterior margin of the hypural plate in postflexion larvae), head length (HL), body depth at pectoral-fin base (BD), distance from snout to anal-fin origin (Sn-AO),

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Meristic characters and proportions of the postflexion larvae of hammerjaw (*Omosudis lowii*) collected during research expeditions at stations in the Atlantic, Pacific, and Indian Oceans between 1957 and 2024. A plus sign (+) indicates that the ray formation is not complete, a dash (–) indicates that the rays have not yet formed or that it is not possible to count the number of rays or the number of vertebrae, and the symbol x indicates that the feature is damaged. Lengths are given in millimeters.

Character or proportion	Station number																			
	Atlantic Ocean									Pacific Ocean							Indian Ocean			
	2632	2647	2636	4510	4510	4507	2171	2171	2171	7200	4510	7402	2342	3689	3993	3993	4679	5315	2789	3750
Standard body length (SL)	7.7	10.0	11.0	11.2	11.7	15.5	16.5	17.0	23.0	11.0	11.2	13.2	15.0	22.0	25.0	28.0	11.0	12.0	14.2	14.8
Vertebrae	39	39	41	39	40	40	–	40	–	–	41	39	40	41	–	40	40	40	41	–
Dorsal-fin rays	8+	9+	9	9	9	9	10	10	x	9	8	9	9	10	9	10	9+	8+	10	9
Anal-fin rays	14	14	13	14	15	14	14	13	14	13	15	14	14	13	14	14	14	13	14	13
Pectoral-fin rays	–	–	–	–	–	9+	8+	7+	13	–	5+	8+	–	12+	13	13	4+	–	7+	5+
Pelvic-fin rays	–	4+	–	–	5+	4+	8	7	8	–	–	–	6+	x	8	8	–	–	–	3–4+
Caudal-fin rays	9–5	4+9–9+3	6+9–9+5	3+9–9+3	6+10–9+6	5+9–10+6	6+9–10+5	8+9–10+7	8+9–9+8	x	6+9–9+6	5+9–8+5	6+9–10+5	7+9–9+8	8+9–9+8	9+9–9+8	5+9–9+6	5+9–9+5	7+9–10+5	6+9–9+5
Number of peritoneal patches	2	3	3	3	x	3	4	4	4	2	3	3	3	3	4	3	2	3	x	4
Head length (HL), % SL	43.6	40.2	42.9	40.2	36.8	36.8	33.3	32.3	36.1	42.7	40.2	37.9	43.3	35.5	33.2	32.1	40.9	37.5	38.7	40.5
Body depth, % SL	32.9	28.9	29.2	32.4	x	29.0	29.1	28.0	29.1	31.8	29.8	30.3	31.3	28.1	26.8	25.0	34.5	30.8	28.2	30.4
Snout length, % HL	41.1	36.8	41.0	35.5	34.9	40.4	32.7	36.6	36.1	38.3	33.3	36.0	38.4	35.9	37.3	38.8	40.0	42.2	41.8	35.0
Vertical eye diameter, % HL	25.0	23.8	26.6	26.6	27.9	24.6	27.3	25.5	25.3	27.6	28.8	28.0	27.7	25.6	26.5	30.0	28.8	28.8	28.8	28.3
Horizontal eye diameter, % HL	14.7	19.0	17.7	15.5	18.6	21.1	21.8	23.6	25.3	19.1	20.0	18.0	23.1	21.8	26.5	25.5	24.4	22.2	23.1	23.3
Predorsal length, % SL	65.4	61.7	59.0	62.5	64.1	61.3	65.5	60.0	63.9	63.6	59.8	60.6	66.6	61.3	61.2	60.7	63.6	61.6	60.5	64.2
Snout to anal-fin length, % SL	74.4	75.5	75.5	76.7	76.9	74.2	71.5	73.5	76.5	77.2	75.9	75.8	76.6	73.2	74.0	75.0	77.3	76.6	73.9	74.3
Snout to anus length, % SL	x	70.5	68.0	65.2	64.9	63.7	x	x	65.6	66.3	x	64.4	63.6	63.6	62.3	66.1	x	65.0	66.2	61.6

snout-to-anus distance (Sn-A), predorsal length (PDL), snout length (SnL), horizontal diameter of the eye (ED_1), vertical diameter of the eye (ED_2), number of rays in dorsal fin (D), number of rays in anal fin (A), number of rays in pectoral fin (P_1), number of rays in pelvic fin (P_2), number of gill rakers on the upper and lower parts of the first gill arch (GR), number of vertebrae (V), and number of branchiostegal rays (Br).

Results

In this section, we provide a description of the larvae of *O. lowii* from the Indian Ocean (Fig. 1). The meristic characters of 4 larvae, 11.0, 12.0, 14.2, and 14.8 mm SL, are as follows: D: 9–10, A: 13–14, P_1: 7+, P_2: 4+ (rays not fully formed), V: 40–41, GR: 0, Br: 8.

The larval body is quite massive and short. It tapers smoothly toward the tail (Fig. 1). The maximum body depth of the larvae is observed at the level of the posterior edge of the preopercle (BD 28.2–34.5% SL). The head is large and deep (HL 37.5–40.9% SL), the upper profile of the head is almost straight or slightly convex, and the snout is long (SnL 35.0–42.2% HL). On top of the head, there are 3 pairs of serrated ridges: 1 pair supraocular and 2 pairs frontal. The eyes are oval (ED_1 22.2–24.4% HL, ED_2 28.3–28.8% HL). The mouth is large, and the jaw length is 81–84% HL; the posterior ventral edge of the dentate is jagged. The jaws are strongly toothed. On the premaxilla, there are 1–2 small curved teeth, followed posteriorly by a longer, usually straight tooth (0.5 mm long—this length and the other tooth lengths given in this paragraph are for the 12.0-mm-SL larva). Behind these 2 (sometimes 3) anterior teeth are 7–13 smaller teeth of varying lengths (0.1–0.25 mm). On the palatine, there is a very large, straight canine tooth (1.2 mm), followed by a large canine tooth (1.1 mm) and a small canine tooth (0.3–0.5 mm) that are directed posteriorly. The last small teeth are sometimes absent on one or both sides. The number and size of teeth do not depend on the size of the larva. There are 6–8 curved teeth on the lower jaw not uniform in size; the 4th canine is noticeably larger than the other teeth on the lower jaw (0.9 mm). There are no gill rakers on the first arch of the gills. There are 3–4 large (4—very rare, additional spine ventral to other spines) and 1–2 small spines on the preopercle anterior to the large spines. The upper large spine branches from the base into 2 spines, and when the larva is 10–11 mm long, the upper part of the spine splits into 2 apices at the end. The number of large spines does not depend on the size of the larva, and small spines become invisible when the larva is >22 mm SL.

The dorsal and anal fins are short; the origin of the dorsal fin is at the level of the anus (PDL 60.5–64.2% SL). The origin of the anal fin and the adipose fin are located on the same vertical line (Sn-AO 73.9–77.3% SL). There is a distance between the anus and the anal-fin origin (Sn-A 61.6-66.2% SL) that is comparable to the length of the base of the dorsal fin. The pectoral fins are small, low at the level of the articular joint of the jaw; in the 14.8-mm-SL larva, the rays are not fully developed. The pelvic fins are located just in front of the anus, and the rays in these fins are also not fully formed in the 14.8-mm-SL larva. The intestine is short, sac-like, and the abdomen of larvae is often swollen with food.

The larvae are moderately pigmented. Melanophores on the head are concentrated in the parietal region, between the dorsal ridges, on the preopercle, in the upper part of the opercle, along the edge of the orbit, and at the end of the snout. A row of melanophores extends along the entire length of the upper and lower jaws. The vomer and parasphenoid areas are pigmented. The gular region is uniformly pigmented with dot-like melanophores. The epaxial part of the anterior myomeres 27–32 is covered with large

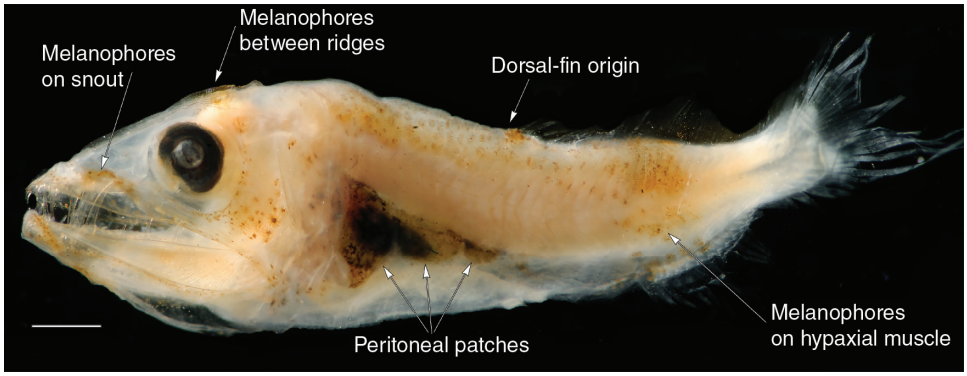

Figure 1

A larva of *Omosudis lowii* (hammerjaw), 12.0 mm standard body length, caught in the Indian Ocean during the 36th expedition of the R/V *Vityaz* in 1964 at station 5315 (catalog no.: IORAS 04995). Arrows point to distinctive features used to identify this larva as *Omosudis lowii*. The scale bar indicates a length of 1 mm.

melanophores, the intensity of pigmentation decreases dorsoventrally, and there is an unpaired large melanophore at the dorsal-fin origin. The hypaxial musculature is only covered with melanophores in the area above the anal fin. In the caudal section, at the level of myomeres 20–32, the melanophores form a band. This band ends at the level of the middle of the anal fin, after which the pigment is absent. The peritoneum in the dorsolateral part is black, and the pigmented part is divided into 2–4 peritoneal sections (2 sections: 2.4 and 1.5 mm wide in the 11.0-mm-SL larva; 3 sections: 1.6, 0.8, and 0.7 mm wide in the 12.0-mm-SL larva; and 4 sections: 1.1, 0.4, 0.6, and 0.7 mm wide in the 14.8-mm-SL larva). The posterior half of the area between the anus and anal-fin origin is covered with melanophores. The rays of all fins are unpigmented. The dorsal-fin base and anterior half of the anal-fin base are covered with melanophores; there are several melanophores on the pectoral-fin base. The intensity of pigmentation increases with larval growth.

Discussion

Uncertainty about the species composition of *Omosudis* arises primarily from differences in the descriptions of larvae. Günther (1887) based his description of *O. lowii* on an 82.55-mm-TL (3.25-in) specimen from the Philippine Sea (BMNH 1868.5.13.6), but he also referenced (p. 202) a damaged, "somewhat smaller example" found floating at the surface at Magdalena, Madeira (in the eastern North Atlantic Ocean) (BMNH 1887.12.7.220). He did not comment on possible species differences in these specimens from the different oceans, the Pacifc and Atlantic Oceans. The 2 specimens are listed as syntypes by Fricke et al. (2024).

Omosudis lowei var. *indicus* was described from 6 larval and juvenile specimens, 0.5–1.8 cm TL, collected in the eastern Atlantic Ocean (Gulf of Guinea), at Cocos Island in the Indian Ocean, in the western Indian Ocean between the Seychelles and Zanzibar, and near the Chagos Archipelago (SMF 2064; ZMB 17555–17556; ZMB 22579). These specimens are listed as syntypes by Fricke et al. (2024). Brauer (1906) published a very poor illustration of *O. lowei indicus* that shows 2 blunt spines on the lower edge of the preopercle and what may have been a ridge on top of the snout and over the eye. It is not clear from his paper which specimen was illustrated. In Brauer's (1906) key, *Omosudis* species are distinguished by a difference of 1 ray in the count for the anal fin and by differences in body depth that may have been due to allometric changes with development. Parr (1928) examined specimens from near the Bahamas and Bermuda and concluded that Brauer's (1906) descriptions of *O. loweii* and *O. loweii indicus* fell within the range of variation for *O. lowei* and that there is only 1 species of *Omosudis*. Ege (1958) and Rofen (1966) agreed with Parr in their revisions of the genus. Roule (1929) described another subspecies, *O. lowei funchali* from Madeira. Rofen (1966) listed *O. funchali* as a synonym of *O. lowii*.

Beebe (1932) described and illustrated 6.58- and 10.00-mm-SL larval *O. lowii* (as *O. lowei*) from Bermuda. From the pigment pattern, his 6.58-mm-SL specimen may have been an *Alepisaurus*. He did not illustrate head ridges or spines for these larvae, but made this statement in his text (p. 72) about these larvae: "The head is set sharply off as a series of elongate, bracing bones, strongly ossified, and forming a nearly perfect equilateral triangle, the corners being the posterior borders of the frontals, the snout and the quadrate."

Ege (1958) recognized only 1 species in the genus, *O. lowei*, excluding *O. elongatus* and *O. brevis* from the genus and including *O. lowei indicus* as a synonym of *O. lowei*. He did not mention *O. lowei funchali*. His study included larvae and juveniles, 5–75 mm body length (BL), from the Atlantic, Indian, and Pacific Oceans. Ege (1958) described the morphometrics, meristics, pigment, and dentition of his specimens in detail, but he did not mention or illustrate spines or ridges on the heads of his specimens. The absence of any mention of spines or ridges in Ege's (1958) paper is the basis for the uncertainty about the number of species in the genus.

In the next review of *Omosudis*, Rofen (1966) also recognized only 1 species, accepting Ege's (1958) taxonomic conclusions and also including *O. lowei funchali* in the synonymy of *O. lowei*. He examined 158 specimens, mostly from the western central Atlantic Ocean but also from the Gulf of America, near Borneo, and from the Pacific Ocean. He reprinted the figures of larvae and juveniles from Ege (1958) and compared the early stages to those of *Alepisaurus*. Unfortunately, Rofen cited only the illustrator and not Ege's paper in his captions for the reproduced figures, leading to confusion about their source in later papers. Like Ege (1958), Rofen did not mention head spines for larvae of either genus, but he noted (p. 476) "a high vertical ridge on frontal bones" for larvae of *Alepisaurus* 11–17 mm BL.

Belyanina (1982) described and illustrated an 11.5-mm-BL *Omosudis* from the western Pacific Ocean. She showed head ridges and spines for the first time. Okiyama (1984, 216) wrote for the Omosudidae that "a single mesopelagic species, *Omosudis lowei*, constitutes this cosmopolitan family." However, later on the same page, he stated, "The presence of two larval types is in sharp contrast to the current concept of a monotypic family. In this connection, Ege's comments (1958) on the significant differences in dorsal ray numbers between populations in the South China Sea and north Atlantic are of particular interest." An illustration of a 22.5-mm-SL larva from the western Pacific Ocean and Ege's (1958) figure of an 11.8-mm-BL larva, as reprinted in Rofen (1966), were provided as examples.

Okiyama's (1984) suggestion has been repeated in subsequent identification guides. Ditty in Richards (2006, 367) wrote, "The Alepisauridae is currently comprised of three species: *Alepisaurus brevirostris*, *A. ferox* and *Omosudis lowii* (Sato & Nakabo 2002), although another larval type of *Omosudis* has been found in tropical waters of the western Pacific (Okiyama 1984)." He commented (p. 372),

"Ege 1958 figures inadequately illustrates [*sic*] preopercular spines & spinous ridges on head." Similarly, Fahay (2007, 384) commented, "Well-developed ridges on head and spines along edge of preopercle best displayed in specimen from tropical western Pacific. . .[P]igment also better developed than described for larvae from the Atlantic; these differences, and differences in meristic characters, suggest possibility of more than a single species in *Omosudis*." In the second edition of his identification guide, Okiyama (2014, 307) wrote that, with respect to the larvae and juveniles described by Ege (1958), Belyanina (1982), and himself (1984, 2014), he would identify his specimens only as *Omosudis* sp. and that a taxonomic reconsideration of the species in the genus seems necessary.

Nielsen and Jespersen (1986) examined 450 juvenile and adult specimens of *Omosudis*, investigating variability in color, meristics, and morphometrics. They found 5 specimens that were markedly different from the others in color and body depth. With histological examination of the ovotestes, they concluded that these differences among the specimens were due to maturation state and were not indicative of the existence of more than 1 species in the genus.

Choi et al. (2020) described a 7.8-mm-BL larval *Omosudis* from near Chuuk in the Caroline Islands. They included a detailed explanation of the taxonomic confusion involving discrepancies in the descriptions of larvae by Ege (1958) and later accounts, concluding that (p. 241) "[g]iven these disputes, it was difficult to determine the species of our larva based on morphological characteristics alone." They identified their specimen genetically as *O. lowei* by comparing their sequence to one from a specimen of *O. lowei* attributed to A. Kawaguchi, M. Miya, and M. Nishida. Although no collection data were given for the specimen from which the sequence was obtained, it seems likely that the specimen was collected in the western North Pacific.

Comparison

The Pacific larvae of *O. lowii*, with sizes of 11.0–28.0 mm SL, from our collections are practically indistinguishable in morphology from the Pacific larvae previously described in the literature (Belyanina, 1982; Okiyama, 1984, 2014; Choi et al., 2020) and from the Indian Ocean larvae described in the "Results" section. The pigment belt is formed at the level of myomeres 21–32 and extends to the level of the middle of the anal fin. This pattern is typical for larvae less than 22 mm SL. With increasing length, the melanophores extend further caudally. The number of peritoneal patches varies from 2 (1 specimen) to 4 (1 specimen), with 3 sections (5 specimens) being the most common.

Results of a study of Atlantic larvae of *O. lowii*, with sizes of 7.7–23.0 mm SL, indicate that they have characteristic features not noted in the original description (Ege, 1958): there are 3 pairs of serrate ridges dorsally on the head, and there are 3 large and 1–2 small spines on the preopercle (Fig. 2). The pigmentation is similar to that described in the "Results" section for the Indian Ocean larvae: clusters of melanophores in the parietal region, between the ridges, on the preopercle, along the jaws, and at the end of the snout. The dorsal part of the body is also pigmented. At the level of myomeres 22–33 (for larvae <23 mm SL), a pigment belt is formed. It is located in the same area as the belt on larvae from other locations. The smallest of the Atlantic larvae is rather light-coloured compared to the Pacific larva of the same size (Choi et al., 2020)—the melanophore groups on the head are present in the same positions, and the belt is at about the same level (myomeres 20–30); however, the dorsal pigment in the Atlantic larva is represented by a paired row of melanophores at the top of the myomeres but in the Pacific larva is expanded ventrally. The pigmented part of the

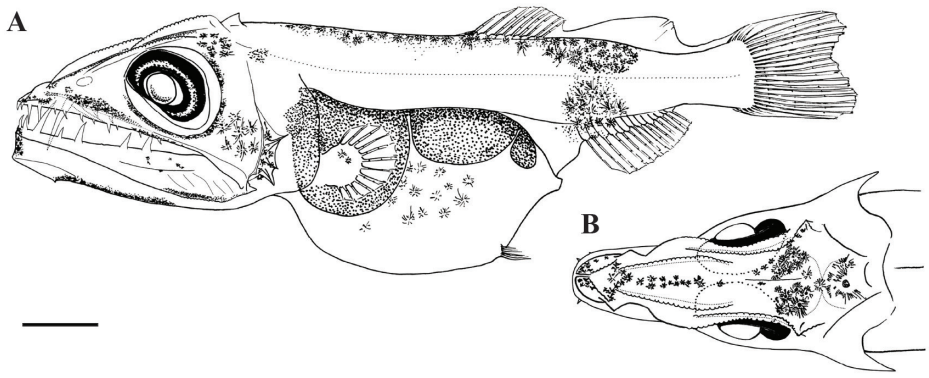

Figure 2

Illustrations of a larva of *Omosudis lowii* (hammerjaw), 10.0 mm standard body length, caught in the Atlantic Ocean during the 43rd expedition of the R/V *Akademik Vavilov* in 2016 at station 2647 (catalog no.: IORAS 04994): (**A**) lateral view, and (**B**) dorsal view of the head. The scale bar indicates a length of 1 mm.

peritoneum of the larvae that we have is similarly represented by 2 (1 specimen), 3 (4 specimens), or 4 sections (3 specimens).

Peritoneal patches are of primary importance for identifying early developmental stages in the related family Paralepididae. Extreme variability in the number and rate of development of peritoneal patches has been observed among closely related species (Okiyama, 1984; Okamoto et al., 2007). For example, the white barracudina (*Arctozenus risso*) (Bonaparte, 1840) has 1 patch in the preflexion stage, increasing to about 9 sections in the postflexion stage and up to 12 sections in transforming and early juvenile specimens, whereas a closely related species, *Notolepis coatsorum* Dollo, 1908 (originally named "*coatsi*," but Fricke et al. (2024) noted a spelling error in the species name and suggest using "*coatsorum*"), has only 1 patch in its early larval stages, and that patch increases in size with growth (Okiyama, 1984). The character of the peritoneal pigmentation of larval *O. lowii* from all collection areas is quite similar—the pigmented part for all specimens comprises 2–4 sections. When there are 2 sections, the patches are usually large and of comparable size; when there are 3 or 4 sections, the first section is large and the subsequent part of the pigmented peritoneum is divided into smaller sections. In larvae of *O. lowii* <14.2 mm SL, 2 or 3 sections are more common, whereas in larvae >14.2 mm SL, division into 3 or 4 sections predominates. Most likely, with increasing size of larval *O. lowii*, the number of peritoneal sections increases, as it does in larvae of *Arctozenus*, *Lestidiops*, and *Stemonosudis*, all genera of the family Paralepididae (Okamoto et al., 2007), and the sizes of the second and subsequent sections decrease. Ege (1958) noted that the peritoneal pigment of *O. lowii* that were 44.1 and 75.2 mm SL was not divided into sections; apparently, when the length of the larvae is >28 mm SL, the peritoneal sections begin to merge into one. In summary, the variation in the number of peritoneal sections represents ontogenetic variation and not interspecific or interpopulation variability.

There is a wide overlap of plastic characteristics between specimens from all 3 oceans, allowing us to assume that they all belong to the same species of *Omosudis*. We, therefore, followed morphometric changes during early ontogeny in a series of larvae ranging from 7.7 to 28.0 mm SL (Table 1). The length of the head and the body depth decrease slightly. During growth, there is little change in the PDL, Sn-AO, and Sn-A. The size of the eye gradually increases, with the length and width of the eye becoming more or less equal at 17 mm SL. The SnL has a fairly wide range (32.7–42.2% SL) but remains almost unchanged as the larva grows.

Identification

Early stages of *O. lowii* can easily be confused with *Alepisaurus ferox* because of similarities in body shape, dentition, external pigmentation, and the presence of ridges on the head. Some sources state that larvae of *A. brevirostris* lack ridges on the head and spines on the preopercle (Ambrose, 1996; Ditty, 2006; Fahay, 2007). However, all of the specimens of both *Alepisaurus* species we examined had ridges (the serration on them is less prominent than on larvae of *O. lowii*) and spines (not as strong as in *O. lowii*—in the form of a plate with 3–4 pointed tips) (Figs. 1, 3, and 4). Therefore, these characters are common to larvae of the family Alepisauridae and cannot be used to distinguish larvae of different species within the family. Some of the characters used to distinguish the early developmental stages of larvae of *Omosudis* and *Alepisaurus* include head shape, tooth size, pectoral-fin size and pigmentation, sequence of fin formation, and body pigmentation (Okiyama, 1984; Ditty, 2006; Fahay, 2007). Some of these characters are relative to and strongly dependent on the size of the larva and the degree of deformation. We have identified the most distinctive features for the separation of the larvae of these 2 genera (Figs. 1, 3, and 4):

- –The dorsal fin of *O. lowii* is short (D: 8–10) and located approximately in the middle of the body (PDL 59.0–66.6% SL), whereas *A. ferox* and *A. brevirostris* have a long dorsal fin (D: 39–42 and 42–45, respectively) that begins just behind the head (PDL 37.3–42.1% SL). This fin character is not visible before the postflexion stage (at a size of about 7–8 mm SL).
- –In larvae of *Alepisaurus*, the pigment on the hypaxial muscles of the caudal peduncle is absent or very weakly expressed (in contrast to the relatively strong expression in *O. lowii*), and there are no melanophores on the rostrum or between the head ridges (melanophores are present in *O. lowii*). These characters are also present only after flexion.
- –The pigmented part of the peritoneum in *O. lowii* is divided into 2–4 peritoneal sections, whereas in *Alepisaurus*, the peritoneum is uniformly pigmented with large melanophores.
- –The eye of *O. lowii* is oval to about 17 mm SL, whereas the eye of larvae of *Alepisaurus* is round or nearly round from at least 6.58 mm SL (Beebe, 1932). The ED_1 of the eye of *O. lowii* is smaller than that of *Alepisaurus* (14.7–26.5% HL versus 24.4–31.4% HL, respectively).

Given that larvae of *A. brevirostris* do have ridges on the head and spines on the preopercle, it will be useful to point out how the 2 species of *Alepisaurus* can be separated in light of the new data. *Alepisaurus ferox* has a cluster of melanophores anterior to the anal-fin origin at a size ≥10 mm SL, absent in *A. brevirostris*, and *A. ferox* has significantly larger eyes (31.4% HL versus 24.4–27.9% HL, respectively).

Conclusions

The results of this study indicate that any differences between larvae of *Omosudis lowii* from different regions of the world reported in the literature are the result of incomplete or inaccurate descriptions. The few differences

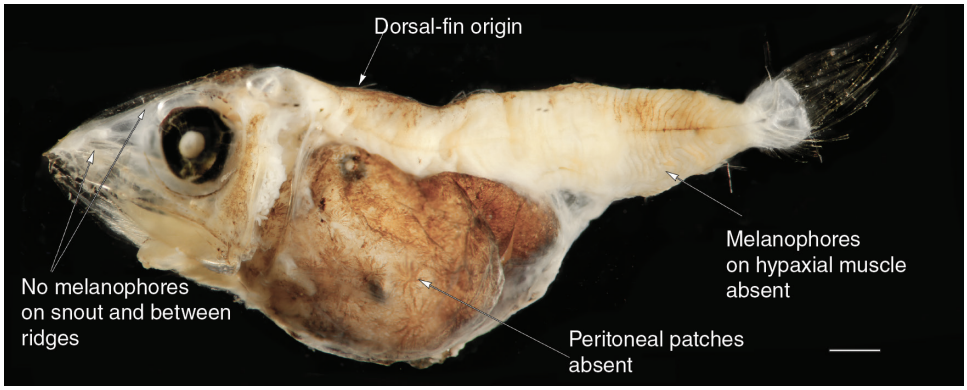

Figure 3

A larva of *Alepisaurus brevirostris* (shortnose lancetfish), 16.5 mm standard body length, caught in the Atlantic Ocean during the 29th expedition of the R/V *Akademik Ioffe* in 2009 at station 2171 (catalog no.: IORAS 04997). Arrows point to distinctive features used to identify this larva as *Alepisaurus brevirostris*. The scale bar indicates a length of 1 mm.

Figure 4

A larva of *Alepisaurus ferox* (longnose lancetfish), 15.0 mm standard body length, caught in the Atlantic Ocean during the 67th expedition of the R/V *Akademik Ioffe* in 2024 at station 4525 (catalog no.: IORAS 04996). Arrows point to distinctive features used to identify this larva as *Alepisaurus ferox*. The scale bar indicates a length of 1 mm.

in larval specimens from the Atlantic, Pacific, and Indian Oceans found in this study are smaller than those expected from the literature and most likely represent natural variability between individuals rather than between species.

Resumen

Se presenta la primera descripción detallada de las larvas de *Omosudis lowii* del Océano Índico occidental. Se corrigen errores en la descripción de larvas del Océano Atlántico: aunque las descripciones e ilustraciones más completas de especímenes atlánticos de *Omosudis* en informes anteriores no han mencionado o mostrado crestas o espinas en la cabeza, todas las larvas de los Océanos Atlántico, Pacífico e Índico examinadas en este estudio tienen espinas preoperculares y una cresta dorsal en la cabeza. Los resultados de este estudio aportan pruebas adicionales de que no existen diferencias de especie entre los especímenes de los 3 océanos. Se discute la variabilidad de la pigmentación peritoneal. Se aportan características morfológicas para la identificación confiable de larvas de *O. lowii*.

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