Embryonic development and effect of water temperature on hatching of *Lophius litulon*

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Abstract

Most Lophiiformes including *Lophius* species are considered to spawn egg masses called an “egg veil” or “egg ribbon” composed of numerous mucoid chambers. However, *Lophius* eggs have been rarely collected in the field and thus little is known about their biological features. Here we examined the embryonic development of *Lophius litulon* and also the effects of water temperature on the embryonic development of eggs from egg veils collected in the field. Embryonic development was observed from the late cleavage stage to hatching. Low rates of mortality and deformity of embryos and early larvae were observed at 13–21ºC. The estimated appropriate water temperature range closely approximated the range of temperatures (12–20ºC) at which egg veils of *L. litulon* have been found in the field. Embryonic development accelerated with increased water temperatures. These results will enable estimation of the origin of and passive movement of egg veils and subsequently larvae, and will help to reveal the spatiotemporal distribution of the spawning and nursery grounds of *L. litulon*.

Key words: early development; goosefish; hatching process; larva; incubation temperature

Introduction

Pietsch and Arnold (2020) summarized information about Lophiiformes eggs. Most Lophiiformes are considered to spawn eggs encapsulated within a balloon-shaped or ribbon-shaped mucoid mass. Egg masses are formed by numerous mucoid chambers including eggs with seawater (Rasquin 1958) (Fig. 1a). There are few descriptions of the embryonic development of lophiiform fishes. Only *Histrio histrio* (Mosher 1954; Rasquin 1958; Fujita and Uchida 1959) and *Antennarius striatus* (Rasquin 1958) within the suborder Antennarioidei are recorded from fertilized ova to hatching. Descriptions of the embryonic development of species in Lophiodei are fewer than Antennarioidei. Unfertilized ova and the development from the gastrula stage of *Lophius americanus* was described by Everly (2002). However, other studies have reported only snippets of information like collection records or records over a short period of development (e.g., *L. piscatorius*: Laurenson (2006), *L. litulon*: Oh and Kim (2015)).

Lophiiformes species particularly in the genus *Lophius* are important fishery resources in regions throughout the world. However, their recruitment as well as landings often fluctuate significantly year by year (*L. americanus*: FAO (2020a), *L. budegassa*: ICES (2020), *L. litulon*: Takeya (2017), *L. piscatorius*: Solmundsson et al. (2010); FAO (2020b); ICES (2020), *L. vomerinus*: FAO (2020c)). Slight differences in survival rates during the early life stages have a large effect on fish stock fluctuations (Houde 1987). Thus, the mechanism of survival during the early life stages needs to be detailed to clarify the factors determining their population dynamics. However, information on the biological features of their early life stage is not sufficient to understand the mechanism of survival.

Lophius litulon is a commercially important demersal fish that is distributed in eastern Asia (Yoneda et al. 1997; Yoneda et al. 2001). Some of the reproductive ecology of *L. litulon* has been described. For example, spawning migrations have been shown in several regions (Yoneda et al. 2002; Iwasaki

et al. 2010; Takeya et al. 2013). At SST (sea surface temperature) of 9.0–16.3ºC, large numbers of pre-spawning individuals were caught in areas shallower than 60 m (Takeya 2017). They seem to have either a single (Yoneda et al. 2001; Takeya 2017) or double (Kim et al. 2020) period of spawning in a year. They spawn buoyant egg masses which are called an "egg veil" (Hoshino et al. 2006), adults have been suggested to rise to the surface layer to spawn. Egg veils have been reported around Japan from February to August (Mito 1963; Takeya et al. 2013). Oh and Kim (2015) described the morphological and molecular characterization of eggs preserved in ethanol solution using pre-hatching specimens. Although information about its reproduction is increasingly available in the literature, details of the embryonic development, embryonic period and appropriate water temperature range for eggs of *L. litulon* remain unclear.

Using *L. litulon* egg veils collected in the field, this study investigated (1) the embryonic development from early development stage eggs (2) the relationship between incubation temperature and rate of development (3) the appropriate temperature range determined from mortality and deformity rates of early larvae, to describe the morphology of eggs and determine the relationship between reproduction and water temperature in *L. litulon*. We then considered the embryonic features of the genus *Lophius* and the effect of temperature on their growth and survival during the early life stages in relation to recruitment success.

Materials and methods

Field samplings (egg collection)

Three egg veils were collected with surrounding water using a scoop net (50 cm diameter with 2 cm mesh and 60 cm long) and bucket (ca. 5 l) from below the sea surface in the coastal area (depth: 5–30 m) off Kazamaura, Aomori Prefecture (Fig. 1b, Fig. 2), on 17 June and 21 July 2020 (SST: 15–16ºC on 17 June, 18.7–20.7ºC on 21 July). A part of the egg veils (ca. 1 l volume) was kept in a plastic

bag (30 l volume) in seawater (ca. 10 l) with oxygen and then transported to Hokkaido University, Hakodate by truck and ship taking approximately for four hours.

Laboratory observation

Egg diameters from these egg veils were measured using a stereomicroscope (Table 1).

Two egg veils collected on 21 July were experimentally incubated at different temperatures for observation of embryonic development as follows: When we took out and observed these egg veils on 21 July, one egg veil was in the late cleavage stage (this egg veil was termed 1B), and the other egg veil was in the blastula stage (termed as 2B). The egg veils were cut with scissors into ca. 2–3 cm square sizes, containing approximately 100 eggs in each piece. Then, four pieces from each egg veil were kept in small-sized plastic tanks one each with 500 ml of the artificial seawater at 18–20ºC (Tetra Marine Salt Pro, Spectrum Brands Japan Inc; Japan, salinity: 32–33) (total 8 tanks). The tanks were put in incubators set at 13, 15, 18 and 21ºC to examine the difference in rate of development within the approximate water temperature range that egg veils of *L. litulon* have been collected in the field (12–14ºC: Oh and Kim (2015); 14.3ºC: Nakaya et al. (2017b); 15.9ºC: Mito (1963); 18.2ºC: Kim (1976); 19–20ºC: Hoshino et al. (2006) and this study (16–21ºC (Table 1)). Although, some eggs became detached from the pieces from the cut edge, they remained incubated in the tanks. A piece of the egg veils was carefully transferred to a petri dish, observations and photographs were taken of 20 to 30 individuals twice a day (7:00–8:00 and 15:00–16:00) using a stereomicroscope. Then, the piece of egg veils was returned to the experimental tanks and continued to be incubated. The experimental observations were conducted until 50% hatching (24–29 July). The process of embryonic development was divided roughly into 4 stages following Oozeki and Hirano (1985) and Kawabe (2005), and more precisely classified into 9 stages following the stages described for the closely related *Lophius americanus* as defined by Everly (2002). Everly (2002) characterized these 9 stages as follows.

111 Stage 8: Blastodisc comprised of cells 4–5 layers deep

112 Stage 9: Formation of germ ring and embryonic shield

113 Stage 10: Blastoderm advances to cover 33% of yolk

114 Stage 11: Blastoderm advances to cover 34% and 66% of yolk

115 Stage 12: Blastoderm advances to cover 67% and 90% of yolk

116 Stage 13: Blastoderm advances to cover 91% and 100% of yolk; blastopore closes

117 Stage 14: Caudal fin begins to develop, torsion of the caudal fin occurs at end of stage 14

118 Stage 15: Appearance of pectoral and pelvic fin buds

119 Stage 16: Flexure of brain begins at hatching

120 The appropriate temperature range for early development

121 Appropriate temperature range of early development of *L. litulon* was examined as follows: The
122 three egg veils collected on 17 June and 21 July were cut with scissors into ca. 2–3 cm squares
123 containing approximately 100 eggs in each piece. 10 or 12 pieces of egg veils containing only 1 or 0
124 dead eggs were selected from each egg veil. The selected pieces were maintained in a bucket with 1 l
125 of the artificial seawater (18–20ºC) for 1 hour to allow peripheral eggs along the cut edge to detach
126 from the egg veils. One piece from each egg veil was incubated in a small-sized plastic tank with 500
127 ml of the artificial seawater. Two replicate tanks were set in temperature incubators for each of the
128 three egg veils (total 6 tanks for each temperature but 4 tanks at 9ºC by absence of 1B). To cover the
129 range of water temperature that egg veils were collected in previous study ((12–14ºC: Oh and Kim
130 (2015); 14.3ºC: Nakaya et al. (2017b); 15.9ºC: Mito (1963); 18.2ºC: Kim (1976); 19–20ºC: Hoshino
131 et al. (2006)), incubation temperatures were maintained at 9, 13, 15, 18, 21 and 24ºC. The pieces of
132 egg veils were acclimated from 18–20°C to the adjacent temperature incubator every 1–2 hours so
133 that the experiment could be started within 12 hours. After all temperatures were adjusted gradually

(0.1–2.0ºC per hour), the experiment started. Incubation water was renewed 50% every two days and with gentle aeration (10–80 ml/min). Twice a day (8:30–9:30 and 14:30–15:30), emerged larvae and dead individuals were collected and counted the number of them and then emerged larvae were preserved in 90% ethanol solution. Deformity rate was determined by observing specimens, using a stereomicroscope. Deformed individuals were characterized from the bending of the notochord against the abdominal cavity and the stunting of the notochord as well as the stunting of the jaw. Percentage of NDL (normal developing larvae i.e., non-deformed live larvae) to the total collected individuals was calculated.

Results

Morphology of eggs

The eggs were spherical or slightly oval spherical, the diameter range was 1.51 to 1.98 mm (Table 1). Each egg had a single colorless and transparent yolk. The perivitelline space was extremely narrow. Color of the oil globule is orange, and becomes nearly colorless by the time to hatch. Eggs mainly had a single oil globule, some had small double or triple globules (1B: 24.1% at Stage 9–11, 2B: 2.1% at Stage 9–10) that had fused during development. Melanophores appeared sparsely on the blastoderm from three quarters epiboly.

Embryonic development

Embryonic development of *L. litulon* was recorded as Cleavage stage, Blastula stage, Gastrula stage and Embryo stage, and from Stage 8 through to Stage16 as defined by Everly (2002) (Fig. 3). Each stage was characterized as follows.

Cleavage Stage (Egg veil 1B was at this stage just before the experiment)

Stage 8

Small blastomeres, and marginal periblast between the blastoderm and the yolk were observed.

Blastula Stage (Egg veil 2B was at this stage just before the experiment)

Stage 9

The central part of the blastoderm became transparent. The blastoderm started to spread over the yolk.

Gastrula stage (Period, 13ºC: 28h; 21ºC: 16h）

Stage 10

The blastoderm became mostly transparent. The embryonic shield was observed. Epiboly advanced, and the blastoderm covered approximately 30% of the yolk.

Stage 11

The blastoderm became transparent completely. The length of the embryonic shield was 20% of the circumference of the yolk. The blastoderm covered approximately 50% of the yolk.

Embryo stage (Period, 13ºC: 100 h; 21ºC: 40 h)

Stage 12

Optic vesicles and the notochord were observed. Melanophores appeared on the blastoderm. The embryo extended to 30% of the circumference of the yolk. The blastoderm covered approximately 70% of the yolk.

Stage 13

The lens, somite and Kupffer's vesicle appeared. Oil globule was located at the tip of the tail. The melanophores increased in size by aggregating. The embryo extended to 40% of the circumference of the yolk. The blastoderm completely covered the yolk.

Stage 14

Heart was visible clearly and started beating. The yolk around the tip of the tail somewhat became hollow. The embryo extended to 50% of the circumference of the yolk.

Stage 15

The coloration of the embryo became mostly black. Melanophores covered the head, abdominal region, a part of yolk behind the abdominal and the tip of the tail. The embryo greatly increased in size and extended to 60% of the circumference of the yolk.

Hatching

Stage 16

The oil globule located posterior of the yolk. The vent located behind the yolk. The mouth is still closed.

Effect of water temperature on incubation period and survival

Percentage of NDL at 9, 13, 15, 18, 21 and 24ºC were 17 ± 14.8%, 64 ± 12.2%, 71 ± 14.5%, 71 ± 13.5%, 81 ± 7.0% and 33 ± 14.8% (mean ± standard deviation), respectively (Fig. 4). The relationship between incubation temperature and rate of NDL was explained by a convex upward quadratic curve approximation

$y = -0.91x^2 + 31.74x - 196.19$ ($r^2 = 0.660$, $p < 0.001$, $n = 34$)

where the vertex located at 17.4ºC, and straight lines connecting the mean rate of NDL between adjacent incubation temperatures. The curve and polyline showed that over 50% rate of NDL were between 11.6ºC and 23.2ºC, and 11.8ºC and 23.0ºC, respectively.

The higher water temperature, the shorter time to hatch at 13–21ºC (Fig. 5). Incubation period ranged 2.8–7.1 days for Stage 8 to Stage 16 depending on water temperature. Time from stage 10 to 50% hatch at 13, 15, 18 and 21ºC were 128 ± 11.3 hours, 100 ± 5.7 hours, 72 ± 0.0% and 56 ± 0.0 (mean ± standard deviation) hours, respectively.

Discussion

Embryonic development

203 The eggs from the three egg veils were confirmed as *L. litulon* from the descriptions of
204 morphological features of eggs (Oh and Kim 2015). Embryonic development from late cleavage stage
205 through to hatch in *L. litulon* were observed. Information on egg or embryonic development of two
206 species of *Lophius* has been reported (*L. americanus*: Fahay (1983); Everly (2002), *L. piscatorius*:
207 Laurenson (2006)). Observations in this study have shown that eggs of *L. litulon* resembled that of *L.*
208 *americanus* more than that of *L. piscatorius*. The most remarkable differences between *L. piscatorius*
209 and the other two species were the egg diameter and rate of development. Egg diameter of *L. litulon*
210 in this study was 1.51–1.98 mm. In comparison, the egg diameter of *L. americanus* was described as
211 1.61–1.84 mm (Fahay 1983), whereas egg diameter of *L. piscatorius* as approximately 3 mm
212 (Laurenson 2006), twice larger than that of the others. In this study, *L. litulon* took 56 hours from stage
213 10 to hatching at 21ºC. In comparison, *L. americanus* took approximately 75 hours from stage 10 to
214 hatching at 20ºC (Everly 2002), whereas *L. piscatorius* took approximately 120 hours from stage 12
215 to stage 14 at 7ºC (Laurenson 2006). Rate of embryonic development of *L. litulon* is as rapid as that
216 of *L. americanus* at almost the same temperatures, but that of *L. piscatorius* is slower at lower
217 temperature. The eggs of *L. piscatorius* seemed to be collected under 10ºC (Laurenson 2006), and
218 subsequently the embryonic period of *L. litulon* and *L. americanus* would be much shorter than that
219 of *L. piscatorius* in the field. The embryonic development process of eggs in *Lophius* seem to be
220 common with that observed in this study because the appearances of the eggs in the three species are
221 quite similar, however, eggs in other *Lophius* species remain poorly known.
222 Period of egg from fertilization to late cleavage stage is still unknown in *L. litulon* because eggs just
223 after being spawned are difficult to collect. The embryonic period of related species such as *Histrio*
224 *histrio* took 16.5 hours from fertilization to 30% epiboly, and 48.3 hours from fertilization to hatching
225 at 26.8–27.4ºC (Fujita and Uchida 1959). In other words, time from fertilization to 30% epiboly

accounted for 34% of the whole embryonic period at stable water temperature in *Histrio histrio*. Eggs in *L. litulon* could be estimated to take 3.5–8.1 days from fertilization to hatch at estimated appropriate temperature range 13–21ºC extrapolating from rate of development in *Histrio histrio*.

Effect of temperature on embryo

Incubation temperatures affected the mortality and the deformity rates for embryos because the rate of NDL was higher than 50% between 11.6ºC and 23.2ºC or 11.8ºC and 23.0ºC. Deformity in larvae can worsen their growth and survival (Andrades et al. 1996; Cobcroft and Battaglene 2009) and thus appropriate water temperature range was demonstrated at 12 to 23ºC. This result is supported by the suggestion that areas under 12ºC may be inappropriate as nursery grounds (Nakaya et al. 2017b). The appropriate temperature range almost covered the water temperature range that egg veils have been collected in previous studies (12–14ºC: Oh and Kim (2015); 14.3ºC: Nakaya et al. (2017b); 15.9ºC: Mito (1963); 18.2ºC: Kim (1976); 19–20ºC: Hoshino et al. (2006) and this study (16–21ºC (Table 1)). *L. litulon* may spawn within the appropriate water temperature range for eggs and early larval stage (at 12 to 23ºC).

In this study, the rate of embryonic development in *L. litulon* was accelerated with the increase in incubation temperature between 13 and 21°C. Such a result has been typically shown and generally recognized in teleosts (e.g., Kamler 2002; Morehead and Hart 2003; Kawabe 2005; Yang and Chen 2005; Peña et al. 2014; Hu et al. 2017; Nakaya et al. 2017a). The origin and destination of egg veil in the field could be estimated by the relationship between stage of egg and water temperature, passive transport of egg veil by ocean currents or waves are being conducted to this end. Variation in water temperature coming with the changes of years and seasons will change period to hatch and then affect transportation of eggs and larvae in *L. litulon*.

This study found that water temperature affects growth and survival of eggs and early larval stage

of *L. litulon*. Takeya (2017) described a positive correlation between PDO (Pacific Decadal Oscillation) and reproductive success of *L. litulon* off Aomori Prefecture including this study area, and suggested that a cold regime can enhance their abundance. Solmundsson et al. (2010) described that the abundance and distribution of *L. piscatorius* off Iceland increased rapidly in the decade concurrent with increasing seawater temperature. These tendencies imply that spatiotemporal changes of water temperature by climatic conditions could alter the survival rate in any of the life stages until recruitment. For example, eggs can be exposed to inappropriate temperature if steep SST gradient is formed around spawning area. Survival rate in each life stage of *Lophius* is unknown. However, variation in recruitment of fish is known to be determined by survival during the early life stage (Hjørt 1914). Thus, variation in water temperature during the egg and early larval stage is considered to effect their passive transport or growth and then recruitment success in *Lophius* e.g., "Stage duration hypothesis" (Houde 1987), "Transport hypothesis" (North and Houde 2003; Suzuki et al. 2019) and "Growth-predation hypothesis" (Litvak and Legget 1992; Takasuka et al. 2003). Information that we gained in this study is important to clarify the spatiotemporal distributions of spawning and nursery ground of *L. litulon* and the effect of temperature on recruitment success in the field. However, further research is needed to examine the passive transport of egg veils and larvae like the previous study in *L. piscatorius* conducted by Hislop et al. (2001).

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Fig. 1 Yellow goosefish *Lophius litulon*. a: egg veil chambers and ova, b: egg veil floating in the sea

Fig. 2 Location of the sampling site off Kazamaura

Fig. 3 Embryonic development of yellow goosefish, from late cleavage stage to newly hatched larva. Stages used are as defined by Everly (2002). V or L with stage number indicates ventral or lateral view

Fig. 4 Relationship between incubation temperature and rate of normal developing larvae (NDL) in yellow goosefish. The relationship is explained by a quadratic curve approximation (solid line) and a line graph (broken line). The dashed line indicates the 50% rate of normal developing larvae

Fig. 5 Relationship between mean water temperature and mean time from Stage 10 (Everly 2002) to 50% hatch in *Lophius litulon* eggs. Closed circle and cross mark indicate different egg veils, respectively

Table. 1. Summary of egg diameter in yellow goosefish collected around Tsugaru Strait

	Date collected	SST [*1] (ºC)	Stage [*2]	*n*	Egg diameter (mm)	
					Mean ± s.d.[*3]	Range
Egg veil A	17 June 2020	16–18	14	30	1.8 ± 0.06	1.73–1.98
Egg veil B	21 July 2020	19–21	14	30	1.6 ± 0.07	1.51–1.80
Egg veil C	21 July 2020	19–21	15	30	1.8 ± 0.07	1.62–1.88

*1 SST is sea surface temperature at the sampling.

*2 Stages used are as defined Everly (2002). Stage is at the measurement.

*3 s.d. indicates standard deviation.

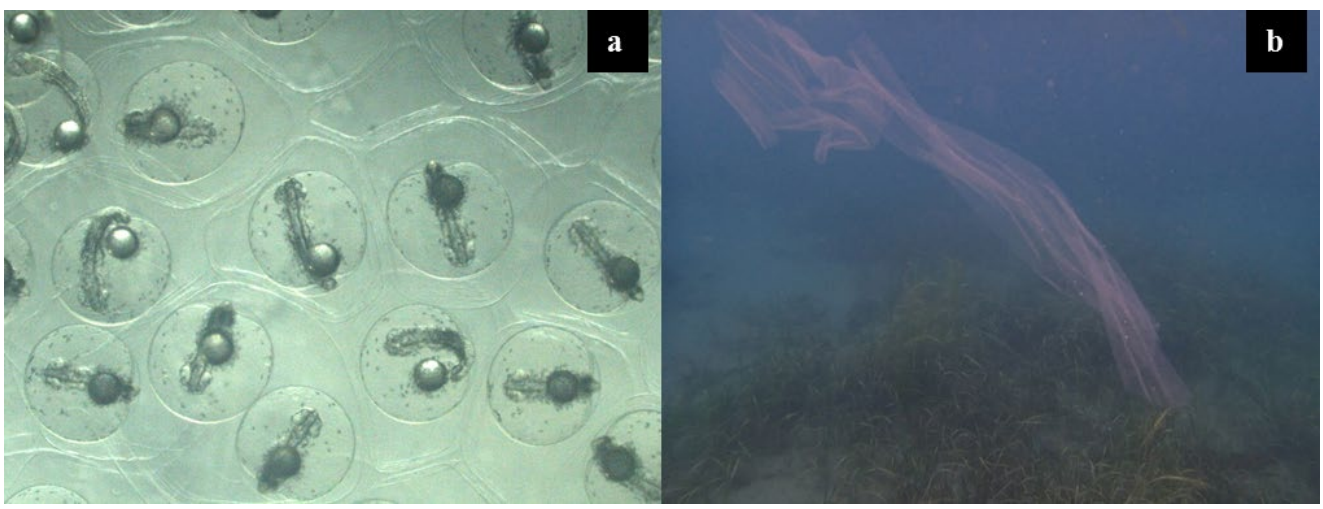
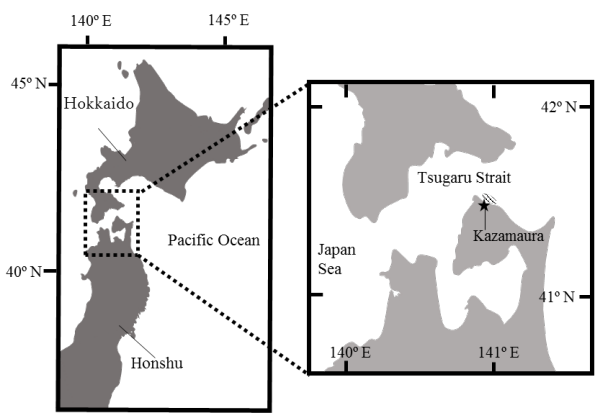


Fig. 1 Ishikawa et al.



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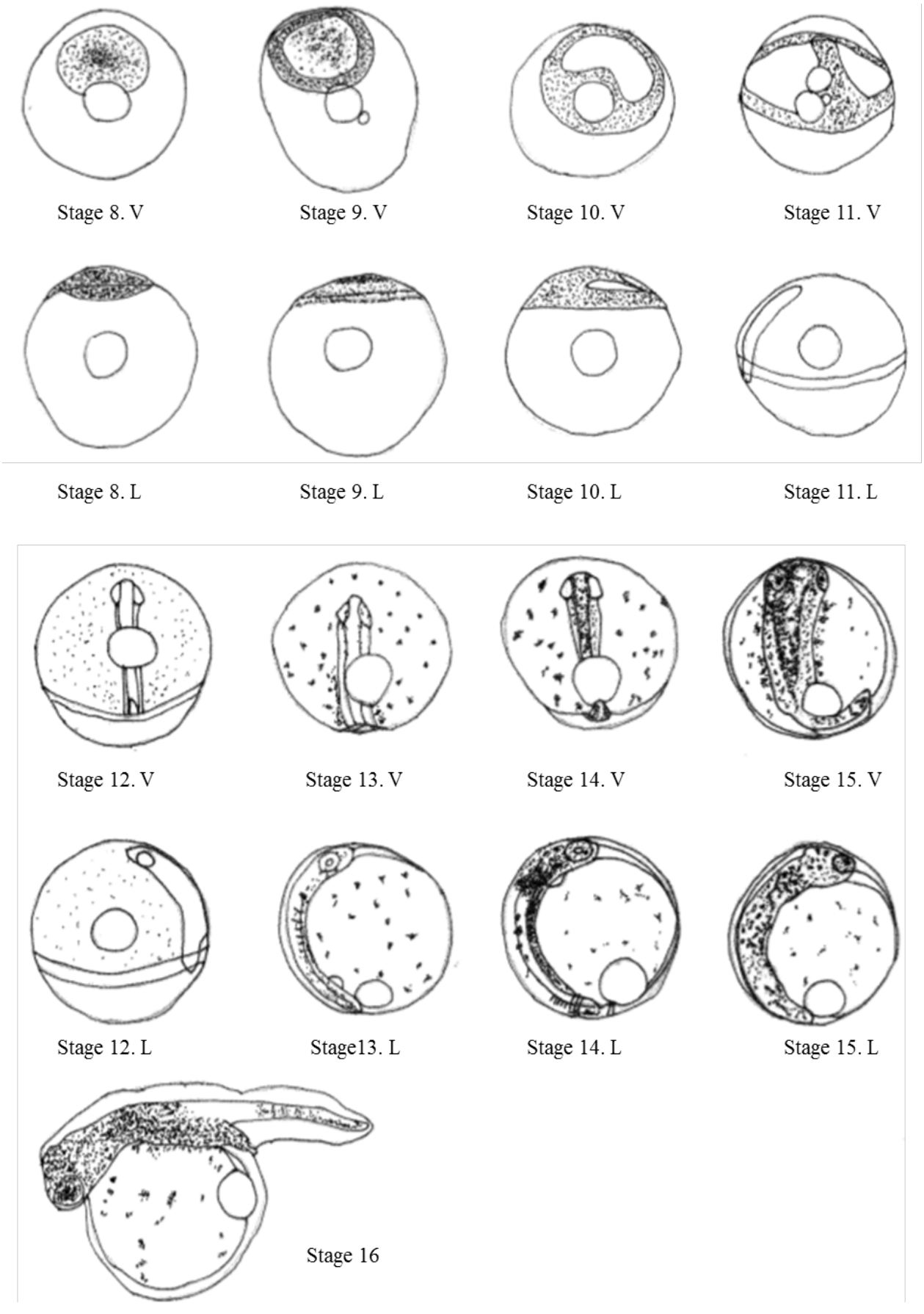

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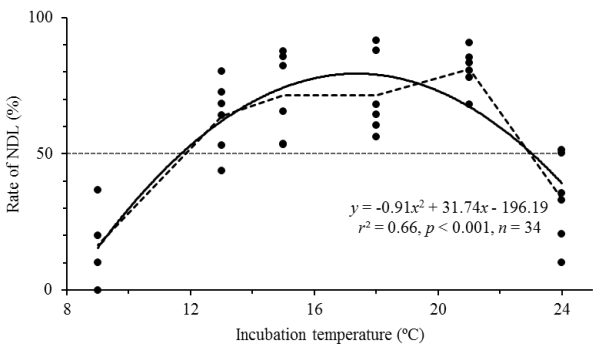

Fig. 4 Ishikawa et al.

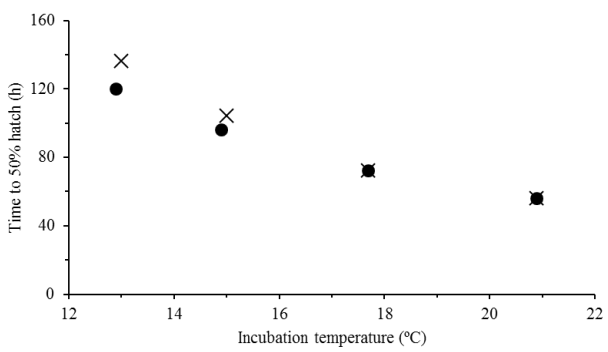

Fig. 5 Ishikawa et al.