



Title	Embryonic development and effect of water temperature on hatching of <i>Lophius litulon</i>
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Citation	Environmental biology of fishes, 105(1), 77-86 <a href="https://doi.org/10.1007/s10641-021-01195-4">https://doi.org/10.1007/s10641-021-01195-4</a>
Issue Date	2022-01
Doc URL	<a href="http://hdl.handle.net/2115/87848">http://hdl.handle.net/2115/87848</a>
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Type	article (author version)
File Information	210918 Ishikawa et al Egg dev.pdf



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

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**Declarations**

**Funding:** No funding was received for conducting this study.

**Conflicts of interest/Competing interests:** The authors have no relevant financial or non-financial interests to disclose.

**Availability of data:** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

**Ethics approval:** All procedures and experiments were carried out in accordance with the experimental guidelines set by Hokkaido University.

**Code availability:** Not applicable

**Consent to participate:** All of the authors have approved the contents of this paper and have agreed to the Environmental Biology of Fishes 's submission policies.

**Consent for publication:** All of the authors have agreed to the Environmental Biology of Fishes's article publishing agreement.

26

### Abstract

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

38

39 **Key words:** early development; goosfish; hatching process; larva; incubation  
40 temperature

41

## 42 **Introduction**

43 Pietsch and Arnold (2020) summarized information about Lophiiformes eggs. Most Lophiiformes  
44 are considered to spawn eggs encapsulated within a balloon-shaped or ribbon-shaped mucoid mass.  
45 Egg masses are formed by numerous mucoid chambers including eggs with seawater (Rasquin 1958)  
46 (Fig. 1a). There are few descriptions of the embryonic development of lophiiform fishes. Only *Histrio*  
47 *histrio* (Mosher 1954; Rasquin 1958; Fujita and Uchida 1959) and *Antennarius striatus* (Rasquin  
48 1958) within the suborder Antennarioidei are recorded from fertilized ova to hatching. Descriptions of  
49 the embryonic development of species in Lophiodei are fewer than Antennarioidei. Unfertilized ova  
50 and the development from the gastrula stage of *Lophius americanus* was described by Everly (2002).  
51 However, other studies have reported only snippets of information like collection records or records  
52 over a short period of development (e.g., *L. piscatorius*: Laurenson (2006), *L. litulon*: Oh and Kim  
53 (2015)).

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

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

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

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

## 82 **Materials and methods**

### 83 Field samplings (egg collection)

84 Three egg veils were collected with surrounding water using a scoop net (50 cm diameter with 2  
85 cm mesh and 60 cm long) and bucket (ca. 5 l) from below the sea surface in the coastal area (depth:  
86 5–30 m) off Kazamaura, Aomori Prefecture (Fig. 1b, Fig. 2), on 17 June and 21 July 2020 (SST: 15–  
87 16°C on 17 June, 18.7–20.7°C on 21 July). A part of the egg veils (ca. 1 l volume) was kept in a plastic

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

90 Laboratory observation

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

92 Two egg veils collected on 21 July were experimentally incubated at different temperatures for  
93 observation of embryonic development as follows: When we took out and observed these egg veils on  
94 21 July, one egg veil was in the late cleavage stage (this egg veil was termed 1B), and the other egg  
95 veil was in the blastula stage (termed as 2B). The egg veils were cut with scissors into ca. 2–3 cm  
96 square sizes, containing approximately 100 eggs in each piece. Then, four pieces from each egg veil  
97 were kept in small-sized plastic tanks one each with 500 ml of the artificial seawater at 18–20°C (Tetra  
98 Marine Salt Pro, Spectrum Brands Japan Inc; Japan, salinity: 32–33) (total 8 tanks). The tanks were  
99 put in incubators set at 13, 15, 18 and 21°C to examine the difference in rate of development within  
100 the approximate water temperature range that egg veils of *L. litulon* have been collected in the field  
101 (12–14°C: Oh and Kim (2015); 14.3°C: Nakaya et al. (2017b); 15.9°C: Mito (1963); 18.2°C: Kim  
102 (1976); 19–20°C: Hoshino et al. (2006) and this study (16–21°C (Table 1)). Although, some eggs  
103 became detached from the pieces from the cut edge, they remained incubated in the tanks. A piece of  
104 the egg veils was carefully transferred to a petri dish, observations and photographs were taken of 20  
105 to 30 individuals twice a day (7:00–8:00 and 15:00–16:00) using a stereomicroscope. Then, the piece  
106 of egg veils was returned to the experimental tanks and continued to be incubated. The experimental  
107 observations were conducted until 50% hatching (24–29 July). The process of embryonic development  
108 was divided roughly into 4 stages following Oozeki and Hirano (1985) and Kawabe (2005), and more  
109 precisely classified into 9 stages following the stages described for the closely related *Lophius*  
110 *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 (18–20°C) 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 9°C by absence of 1B). To cover the  
129 range of water temperature that egg veils were collected in previous study ((12–14°C: Oh and Kim  
130 (2015); 14.3°C: Nakaya et al. (2017b); 15.9°C: Mito (1963); 18.2°C: Kim (1976); 19–20°C: Hoshino  
131 et al. (2006)), incubation temperatures were maintained at 9, 13, 15, 18, 21 and 24°C. 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

134 (0.1–2.0°C per hour), the experiment started. Incubation water was renewed 50% every two days and  
135 with gentle aeration (10–80 ml/min). Twice a day (8:30–9:30 and 14:30–15:30), emerged larvae and  
136 dead individuals were collected and counted the number of them and then emerged larvae were  
137 preserved in 90% ethanol solution. Deformity rate was determined by observing specimens, using a  
138 stereomicroscope. Deformed individuals were characterized from the bending of the notochord against  
139 the abdominal cavity and the stunting of the notochord as well as the stunting of the jaw. Percentage  
140 of NDL (normal developing larvae i.e., non-deformed live larvae) to the total collected individuals  
141 was calculated.

## 142 **Results**

### 143 Morphology of eggs

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

### 150 Embryonic development

151 Embryonic development of *L. litulon* was recorded as Cleavage stage, Blastula stage, Gastrula stage  
152 and Embryo stage, and from Stage 8 through to Stage 16 as defined by Everly (2002) (Fig. 3). Each  
153 stage was characterized as follows.

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

#### 155 Stage 8

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



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

158 Stage 9

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

161 Gastrula stage (Period, 13°C: 28h; 21°C: 16h)

162 Stage 10

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

165 Stage 11

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

168 Embryo stage (Period, 13°C: 100 h; 21°C: 40 h)

169 Stage 12

170 Optic vesicles and the notochord were observed. Melanophores appeared on the blastoderm. The  
171 embryo extended to 30% of the circumference of the yolk. The blastoderm covered approximately  
172 70% of the yolk.

173 Stage 13

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

177 Stage 14

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

180 Stage 15

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

184 Hatching

185 Stage 16

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

188 Effect of water temperature on incubation period and survival

189 Percentage of NDL at 9, 13, 15, 18, 21 and 24°C were  $17 \pm 14.8\%$ ,  $64 \pm 12.2\%$ ,  $71 \pm 14.5\%$ ,  $71 \pm$   
190  $13.5\%$ ,  $81 \pm 7.0\%$  and  $33 \pm 14.8\%$  (mean  $\pm$  standard deviation), respectively (Fig. 4). The relationship  
191 between incubation temperature and rate of NDL was explained by a convex upward quadratic curve  
192 approximation

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

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

197 The higher water temperature, the shorter time to hatch at 13–21°C (Fig. 5). Incubation period  
198 ranged 2.8–7.1 days for Stage 8 to Stage 16 depending on water temperature. Time from stage 10 to  
199 50% hatch at 13, 15, 18 and 21°C were  $128 \pm 11.3$  hours,  $100 \pm 5.7$  hours,  $72 \pm 0.0\%$  and  $56 \pm 0.0$   
200 (mean  $\pm$  standard deviation) hours, respectively.

## 201 Discussion

202 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 21°C. In comparison, *L. americanus* took approximately 75 hours from stage 10 to  
214 hatching at 20°C (Everly 2002), whereas *L. piscatorius* took approximately 120 hours from stage 12  
215 to stage 14 at 7°C (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 10°C (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 *Histrion*  
224 *histrion* took 16.5 hours from fertilization to 30% epiboly, and 48.3 hours from fertilization to hatching  
225 at 26.8–27.4°C (Fujita and Uchida 1959). In other words, time from fertilization to 30% epiboly

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

229 Effect of temperature on embryo

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

240 In this study, the rate of embryonic development in *L. litulon* was accelerated with the increase in  
241 incubation temperature between 13 and 21°C. Such a result has been typically shown and generally  
242 recognized in teleosts (e.g., Kamler 2002; Morehead and Hart 2003; Kawabe 2005; Yang and Chen  
243 2005; Peña et al. 2014; Hu et al. 2017; Nakaya et al. 2017a). The origin and destination of egg veil in  
244 the field could be estimated by the relationship between stage of egg and water temperature, passive  
245 transport of egg veil by ocean currents or waves are being conducted to this end. Variation in water  
246 temperature coming with the changes of years and seasons will change period to hatch and then affect  
247 transportation of eggs and larvae in *L. litulon*.

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

249 of *L. litulon*. Takeya (2017) described a positive correlation between PDO (Pacific Decadal  
250 Oscillation) and reproductive success of *L. litulon* off Aomori Prefecture including this study area, and  
251 suggested that a cold regime can enhance their abundance. Solmundsson et al. (2010) described that  
252 the abundance and distribution of *L. piscatorius* off Iceland increased rapidly in the decade concurrent  
253 with increasing seawater temperature. These tendencies imply that spatiotemporal changes of water  
254 temperature by climatic conditions could alter the survival rate in any of the life stages until  
255 recruitment. For example, eggs can be exposed to inappropriate temperature if steep SST gradient is  
256 formed around spawning area. Survival rate in each life stage of *Lophius* is unknown. However,  
257 variation in recruitment of fish is known to be determined by survival during the early life stage (Hjørt  
258 1914). Thus, variation in water temperature during the egg and early larval stage is considered to effect  
259 their passive transport or growth and then recruitment success in *Lophius* e.g., “Stage duration  
260 hypothesis” (Houde 1987), “Transport hypothesis” (North and Houde 2003; Suzuki et al. 2019) and  
261 “Growth-predation hypothesis” (Litvak and Legget 1992; Takasuka et al. 2003). Information that we  
262 gained in this study is important to clarify the spatiotemporal distributions of spawning and nursery  
263 ground of *L. litulon* and the effect of temperature on recruitment success in the field. However, further  
264 research is needed to examine the passive transport of egg veils and larvae like the previous study in  
265 *L. piscatorius* conducted by Hislop et al. (2001).

266

## 267 **Acknowledgments**

268 We are grateful to Dr. Y. Takeya (Aomori Prefectural government), Dr. K. Noro and Mr. R. Suzuki  
269 (Aomori Prefectural Industrial Technology Research Center Fisheries Institute) for their support and  
270 valuable suggestions. We thank to Mr. Y. Kindaichi (Kazamaura fisheries cooperative association), Mr.  
271 G. Komamine (Komamine Corporation) the staff of Kazamaura Village Government, Laboratory of

272 Marine Bioresources Ecology of Hokkaido University Faculty of Fisheries and crew of the T/S Ushio-  
273 maru of Hokkaido University, Faculty of Fisheries for their kind assistance in collection of specimens.  
274 This work was conducted under permits from Hokkaido University Manual for Implementing Animal  
275 Experimentation.

276

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**Fig. 1** Yellow gosefish *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 gosefish, 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 gosefish. 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

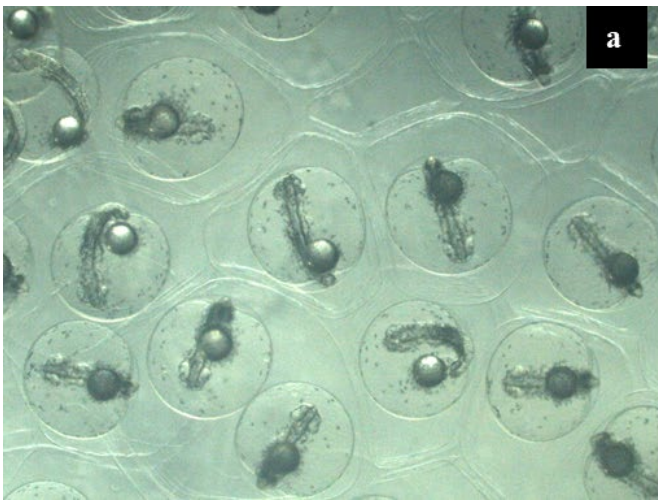
Table. 1. Summary of egg diameter in yellow gosefish collected around Tsugaru Strait

	Date collected	SST <sup>*1</sup> (°C)	Stage <sup>*2</sup>	<i>n</i>	Egg diameter (mm)	
					Mean ± s.d. <sup>*3</sup>	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

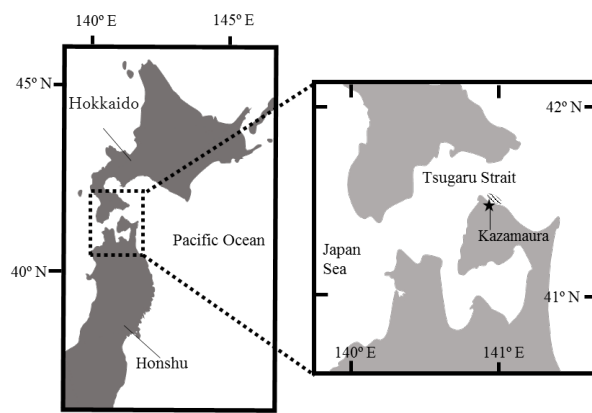
\*1 SST is sea surface temperature at the sampling.

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

\*3 s.d. indicates standard deviation.



**Fig. 1** Ishikawa et al.



**Fig. 2** Ishikawa et al.



Stage 8. V



Stage 9. V



Stage 10. V



Stage 11. V



Stage 8. L



Stage 9. L



Stage 10. L



Stage 11. L



Stage 12. V



Stage 13. V



Stage 14. V



Stage 15. V



Stage 12. L



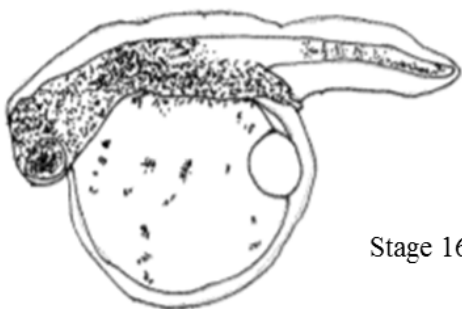
Stage 13. L



Stage 14. L

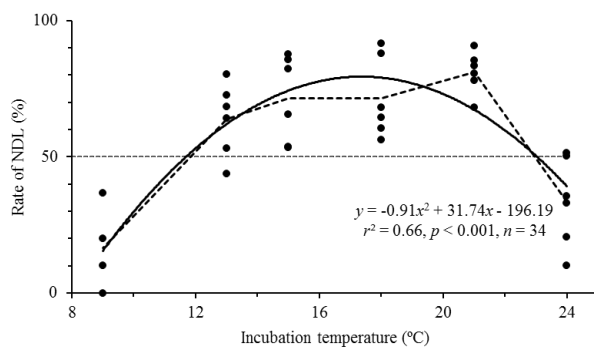


Stage 15. L



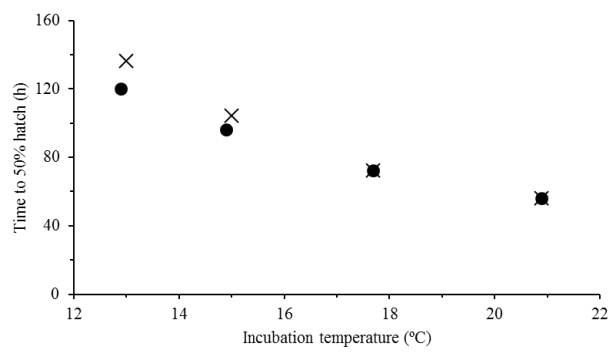
Stage 16

**Fig. 3** Ishikawa et al.



**Fig. 4** Ishikawa et al.





**Fig. 5** Ishikawa et al.