



Title	The Embryonic and Larval Development, Growth, Survival and Changes in Body Form, and the Effect of Temperature on These Characteristics of the Smooth Lumpsucker, <i>Aptocyclus ventricosus</i> (Pallas)
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**The Embryonic and Larval Development, Growth, Survival and
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Aptocyclus ventricosus (Pallas)**

Kenichiro KYŪSHIN*

Abstract

Rearing experiment of eggs and larvae in the smooth lumpsucker were performed to examine the development, growth, survival and morphometrical changes and to detect the effect of temperature on these factors. In the southern Hokkaido the spawning season of this species is presumed to extend from early February to early April and spawning occurs on the rocky sea bottom of the coast at a depth of less than 10 m.

On February 28, 1968 artificial fertilization was carried out successfully and the fertilized eggs were incubated at a constant water temperature of 6°C. The eggs of smooth lumpsucker are demersal and adhesive and the only essential difference in the embryonic development in comparison with other teleostean species is the rapid development of the head and trunk portions and heavy pigmentation of the head and trunk in the latter embryonic stage. The incubation time required to 50% of hatching from fertilization was about 40 days and as high as 62% of the eggs hatched out.

The marked features of the newly hatched larvae lie in the tadpole-like body form and in the well-developed sucking disk, namely the ventral fins. In larval stage, the water temperature was kept 10°C throughout the experiment in Section I and was raised from 6°C in the first half to 10°C thereafter in Section II. During 116 days, the larvae grew to a length of 17.1-18.4 mm from 6.7 mm at hatching and to a range of 229-269 mg body weight from 3.2 mg at hatching. The growth inflection was recognized at a total body length of 7.6-7.9 mm. Examining the relative growth of eight body parts to the total body length by means of the allometric method, the body depth, the body width and the anteanal length demonstrated strong tachyauexesis or tachyauexesis throughout the experiment; the tail length showed almost no growth in the early larval stage and bradyauexesis thereafter. Thus, the larvae are gradually metamorphosed into the stocky body form. The effect of water temperature on the changes in body form was readily apparent: a high temperature expedited the growth of the anteanal length, the head length and the diameter of sucking disk in the phase before the relative growth inflection, in contrast, a low temperature operated to make the equilibrium constant of allometry large in the phase beyond inflection. The reverse results were obtained in the relative growth of the tail length. Among the body parts examined, the diameter of sucking disk was most influenced by temperature.

In this experiment the larvae lived far beyond the yolk-sac stage, and the survival rate at the 110th day after hatching was as high as 94-96% in the normal larvae and was 78-79% even in the deformed larvae which possessed a defective sucking disk. The survival was better in Section II, however the surviving

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biomass in Section I was always larger due to the rapid growth which more than made up the loss of biomass due to higher mortality. In Section II appreciable changes in growth, body form and survival were not recognized except for the relative growth of the sucking disk, although the water temperature was raised from 6°C to 10°C in the course of the experiment. The breaking inflection of the relative growth of the sucking disk appeared about a month after the time when the temperature was altered.

Introduction

Studies of eggs and larvae of marine fishes are potentially essential to evaluate the year-class strength which determines the population size, which has a great influence on the quantitative fluctuation of the population, as well as to detect the environmental factors affecting morphological characteristics.

The present study is one of a series of rearing experiments concerning the biology and morphology in the early life of marine fishes, and describes the embryonic and larval development, growth, survival, morphometrical changes and the effect of temperature on these characteristics of the smooth lumpsucker, *Aptocyclus ventricosus*.

In southern Hokkaido the smooth lumpsucker moves close to the rocky coast for spawning for the period from January to April only. The species is important to fishermen only as an incidental species and available as a food for human consumption. The smooth lumpsucker is not considered to be important commercially since the species is not abundant and its price is low. As a matter of fact, in Shikabe in the southern Hokkaido, annual commercial catches varied from 2 to 40 metric tons from 1960 to 1969 and it contributed less than 1% of the total annual weight of commercial catches. Although the catches are small, marked annual fluctuations are evident.

Before going further, the author is especially grateful to Mr. K. Sakamoto and Mr. K. Nakamichi, scientists of Hokkaido Hakodate Fisheries Experimental Station, who gave valuable help in providing specimens and photographs. The author acknowledges his debt to Mr. John P. Doyle, an associate professor of University of Alaska, for his critical review of the manuscript and invaluable advice. To Mr. Y. Kanno, an instructor of the Faculty of Fisheries of Hokkaido University, for his assistance to the present rearing experiment, the author is thankful.

Materials and methods

Materials for artificial fertilization, incubation of eggs and rearing of larvae

On February 28, 1968 the eggs and milt of the smooth lumpsucker were obtained from one ripe female and one ripe male (female: total body length 362 mm, diameter of sucking disk 54 mm; male: total body length 336 mm, diameter of

sucking disk 68 mm) captured by a demersal gill net on the shore of Shikabe at the entrance of Funka Bay, southern Hokkaido.

About 9 hours after catching, artificial fertilization was carried out by the ordinary wet method at a water temperature of 6°C in the laboratory of Biology of Fish Population. After thorough washing with sea water containing chloromycetin at 50 p.p.m., about 3,800 fertilized eggs were incubated in a glass vessel (the three dimensions: 22×29×29 cm) filled with 10 liters of sea water and reared at a constant water temperature of 6°C (Table 1). The water temperature in the incubator was indirectly adjusted by regulating the temperature in a tap water bath by means of a thermostat and heater. During incubation a vigorous stream of air was bubbled continuously in the incubator to stir the water and to supply the sea water with oxygen. One-half of the water in the incubator was changed daily with fresh sea water to keep the eggs free of contamination.

Table 1. *Incubative and rearing conditions of eggs and larvae.*

Exp. sect.	Number of rearing vessels	Number of eggs or larvae per vessel	Temperature (°C)		Chlorinity (‰)		Remark
			Mean	Range	Mean	Range	
Embryos	1	3820	6.06	5.8-6.5	18.63	18.52-18.92	
I	5	198-207	10.14	8.7-12.2	18.21-18.37	17.84-18.91	Number of vessels Normal larvae 3 Deformed larvae 2
Larvae II	6	194-205	April 9- May 24 6.11-6.13 June 9- Aug. 3 10.27-10.29	5.8-6.4 9.8-12.2	18.28-18.42	17.69-18.67	Number of vessels Normal larvae 4 Deformed larvae 2

When hatching occurred, air bubbling was stopped completely and the water was changed frequently every day during the hatching period. About 200 newly hatched larvae were transferred to each rearing vessel from the incubator making distinction between normal larvae and those in which the disk was deformed. The rearing experiment of the larvae was performed at two different temperatures, i.e. a constant temperature of 10°C throughout the larval stage in Section I and at a temperature of 6°C during the first half of Section II, increasing to 10°C for the latter half of Section II (Table 1). As during the incubation period, rearing vessels were immersed in a tap water bath, but water temperature was regulated by the use of cooling devices to control the rise of water temperature accompanied with the rising room temperature in the laboratory. Each vessel contained 10 liters of sea water and the larvae were reared in the condition of standing water

with faint aeration. The rearing vessels used for the larvae were the same size as the incubator, but their outsides were painted black to give a contrast between the food and the background to provide a possible better feeding condition for the larvae. One liter of sea water in each vessel was exchanged for fresh sea water daily. Nauplii of brine shrimp, *Artemia salina*, were provided as food for the larvae. Ample diets were supplied every day from the 6th day after hatching in Section I and the 8th day in Section II. The normal larvae in one vessel in Section II were reared without food for a starvation experiment. Every effort was made to keep the vessels clean by removing the dead bodies of brine shrimp and excrements using a glass siphon.

The water temperature was recorded daily and the chlorinity in the water was observed at weekly intervals throughout the embryonic and larval stages. The water average temperature was slightly higher than that projected at the beginning of the experiment (Table 1).

Observation of the embryonic and larval development and the measurement of the larvae

Microscopic observations were frequently made on the living eggs to determine the stage of development. The larvae were anaesthetized with 5 mg percent solution of MS 222-Sandoz before observation and measurement. For the studies of larval growth and changes in body form measurements were carried out under a microscope with micrometer eyepiece to determine the total body length (*TL*), the anteanal length (*AL*), the head length (*HL*), the body depth (*BD*), the body width (*BW*), the eye diameter (*ED*) and the diameter of sucking disk (*SD*) (Fig. 1). The head length was defined as the distance from the tip of the snout to the posterior edge of the opercle along the forizontal axis of the body. The body depth and width were measured at the level of the marginal edge of the opercle. The tail

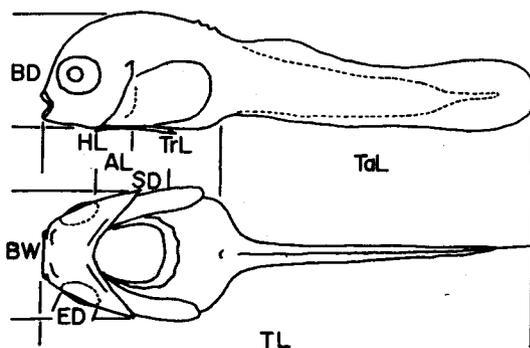


Fig. 1. A diagram of the various measurements made of the larvae of smooth lump sucker.

length (TaL) was obtained by subtracting the anteanal length from the total body length. Similarly the trunk length (TrL) obtained by subtracting the head length from the anteanal length. The larvae were weighed in a wet condition by means of a torsion balance. Furthermore, the number of fin rays in dorsal, anal, pectoral, ventral and caudal fins were counted to examine the development of the meristic characteristics.

During the larval stage, five living larvae were taken out randomly from each experimental section every 4 days for these measurements. After observations and measurements, the larvae were preserved in a 3% formalin solution for further studies of the larval development.

Dead larvae were removed, counted and preserved daily for the studies of larval survivorship.

Materials of adult fish for the length composition, the overy fecundity and the meristic characters

Four samples, totalling 59 fish, were obtained from the commercial catch in Shikabe in February and March 1969; of these, 37 were female and 22 male. The total body length, the diameter of sucking disk, the body weight and the gonad weight were measured before fixation in a 10% formalin solution. Fecundity was estimated by the gravimetric method. The number of fin rays in dorsal, anal, pectoral and caudal fins were counted to contrast with those of the larvae obtained from rearing experiment in the previous year.

In addition, the total body lengths of 329 fish randomly sampled from the commercial catch in the same period and in the same locality mentioned above were recorded with distinction of sex to analyze the length frequency distribution of the spawning population in the smooth lumpsucker.

Result

Length composition of adult fish and fecundity in ripe female

The frequency distributions of the total body length in mature females and males taken from the spawning population were almost normal (Fig. 2). The mean total body length was 35.1 cm with a range of 31 to 39 cm for females; 30.8 cm with a range of 26 to 36 cm for males. When testing the homogeneous of variance in these distributions, the difference between them was not significant ($F_0=1.068$, df. 171 and 156, $P>0.05$). But the difference of mean between sexes was highly significant ($t_0=21.186$, df. 327, $P<0.001$), thus female has a larger mean and the difference between sexes will lie in the interval between 3.80 and 4.87 cm with 99% confidence. Consequently, the length composition combined the sexes formed a bimodal distribution. Since the age of the smooth lumpsucker was not determined in the present study, it is left unsolved whether

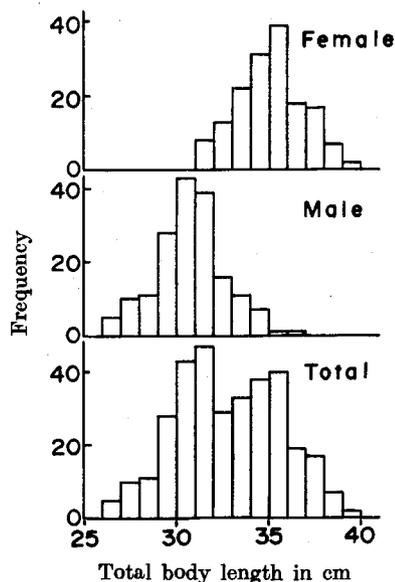


Fig. 2. Frequency distribution of the total body lengths of mature fish.

the differences in the length composition and in the mean total body length were attributable to the disparity of age composition or growth by sex.

Mature females have very fat ovaries weighing from 384 to 726 g - 30.2 to 48.8% of the body weight within the total body length from 32 to 39 cm. In contrast, males have small testes weighing 29.3 to 57.2 g - 3.4 to 5.2% of the body weight within the total body length from 27 to 37 cm. The number of ovarian eggs varied from 45,500 to 80,000 within above total body length (Table 2). The correlation coefficient between the total body length and the number of ovarian eggs is +0.583 with a 95% confidence interval between +0.32 and +0.76, accordingly the number of ovarian eggs is proportional to the total body length.

Eggs and embryonic development

The mature eggs of the smooth lump sucker are spherical in shape, measuring 2.38 mm in average diameter with a range of 2.32 to 2.42 mm. The chorion is about 50 μ in thickness. Clear oil globules ranging from 50 to 720 μ in diameter form a mass on the upper side of the yolk and on the opposite side in the yolk many granular materials are in a group (Pl. Fig. A). Conspicuous sculptures are not observed on the surface of the chorion. The yolk has a faint pink color and the chorion is a light milky white. The eggs are demersal and adhere solidly to one another after coming in contact with sea water.

Five hours after fertilization, the blastodisc, lenticular in shape, was fully formed by the accumulation of the egg cytoplasm toward the animal pole (Pl.

Table 2. The number of ovarian eggs.

N	Total body length (cm)		Egg number (10^3)	
	Range	Mean	Range	Mean
8	32-34	33.2	45.5-65.6	54.2
18	34-36	35.1	46.2-74.5	58.7
9	36-38	36.9	53.4-79.3	62.5
2	38-39		73.2-80.0	

Fig. B). The perivitelline space is very narrow. Two and half hours after this stage, two cell stage was completed by the first cleavage and subsequent divisions occurred at about four hour intervals (Pl. Fig. C). Eggs developed into the morula stage in about 44 hours (Pl. Fig. D) and reached the gastrula stage at about 70 hours after fertilization (Pl. Fig. E). Fifteen hours after the previous stage, the germinal ring which extended about one-fifth of the way around the yolk sphere was clearly observed. At the 150th hour, the germinal ring was almost equatorial in position and an embryo was distinguishable as a bulging on the yolk (Pl. Fig. F). At the 190th hour, the blastopore completely closed, the embryo extended over one-third of the circumference around the yolk sphere, Kupffer's vesicle had finally appeared near the posterior end of the embryo and five pairs of somites could be counted in the middle part of the embryo (Pl. Fig. G). No constriction of the yolk by the germinal ring was observed until the closure of the blastopore as has been observed in *Hemitripterus villosus*¹⁾. At the 238th hour, the optic vesicles and auditory vesicles were well defined and 12-13 pairs of somites were apparent.

At the 264th hour, the embryo had encircled approximately a half of the yolk sphere, Kupffer's vesicle had disappeared, the tail had started to grow free from the yolk sac, 15-16 pairs of somites were counted and melanophores appeared on the marginal part of the optic vesicles (Pl. Fig. H). By this stage, the oil globules coalesced into a larger globules, the largest of which was prominent on the yolk just front of the head. At the 294th hour, the heart appeared as a slight bulge below the nape and 20 hours later it was beating quite slowly and regularly.

At the 342nd hour, the embryo had extended over a half of the circumference of the yolk sphere, rudimentary pectoral fins were observed on the postero-ventral region of the auditory vesicles, a transparent, narrow fin fold appeared on the tail part and there were 27-28 pairs of somites (Pl. Fig. I). The embryo showed movement occasionally twisting its body. By this stage, the oil globules coalesced to a large single globule and it protruded strikingly on the yolk. The embryo at the 381st hour extended about two-thirds of the circumference of the yolk sphere and the intestine was differentiated below the ventral side on the embryo. The optic vesicles became increasingly dark, but not yet completely dark. At the 432nd hour, melanophores were apparent as minute spots on the mid-region of the body in the vicinity of the pectoral fin and on the yolk sac near the intestine. The head had become considerably broaden. At the 528th hour, the pigmented area spread toward the crown on the head, the chromatophores appeared on the pectoral fins and the optic vesicles were now completely dark. The blood could be seen running through the blood vessels on the yolk sac and along the notochord and the mouth was differentiating. The body had greatly

increasing in bulk.

It was very difficult to count the number of somites after the 381st hour stage, because of the enlarged head and trunk of the embryo and the heavy pigmentation. The increase in number of somites from the 190th hour stage to the 342nd hour stage was proportional to the time elapsed: the relationship between them is expressed in the linear equation, $S=0.146 t-22.53$, where S is the number of somites and t the hours after fertilization.

At the 672nd hour, the embryo had grown so that now the tip of the tail reached the snout completely encircling the yolk sac (Pl. Fig. J). The twitching movement of the embryo became vigorous. By this stage, the yolk sphere had considerably decreased in size, while the cephalic region and the trunk of embryo had rapidly increased in bulk and now filled a great part of the egg. Because of the much broadened head and the heavy pigmentation, the profile of the auditory vesicles became indefinite.

Through the incubation period, the author missed seeing the differentiation and the development of the ventral fins that perform an essential function for the life of the smooth lumpsucker.

The embryos first began to hatch out at 931 hours or about 39 days after fertilization and hatching continued for the next three days. Hatching rate was 62% but the deformed larvae which had the defective ventral fins accounted for 35% of all hatched larvae.

Larval development

The average total body length of the newly hatched larvae was 6.69 mm with a range of 6.5 to 7.0 mm. The average body weight was 3.2 mg. The body form bore a striking resemblance to the tadpole of *Batrachia*: the head and trunk of the larvae was very thick, gradually tapering toward the tail (Pl. Fig. K). The vent was situated at about one-third of the total body length from the snout. The head length was 19% of the total body length. The sucking disk, united ventral fins, measuring 0.9–1.1 mm in its horizontal diameter, was well developed on the ventral side of the trunk. The broad transparent fin fold had its origin far posteriorly to the nape and extended continuously to posterior to the vent surrounding the tail. There were 20 incipient pectoral fin rays which is the same as in adults, and 6 in the ventral fins. The ray formation was not complete dorsally, ventrally and caudally.

As mentioned above, the most striking feature of the larvae of this species was very thick and wide body form like the tadpole and well developed sucking disk on the ventral side of the larvae. The pigmentation was also a remarkable characteristic of the larvae: the pigmentation by melanophores and reddish brown chromatophores was quite heavy over the body except for the tail portion which

turned faint yellow. As a result, the total number of somites could not be counted and the remaining yolk and other internal organs were never observed in any side view of the body. An oil globule about 0.8 mm in diameter was measured under a proper light source but with much effort. Some chromatophores were also present on the dorsal margin of the 8th from the last somite. The pigmentation pattern on the head and the trunk differed considerably between larvae.

The newly hatched larvae were well developed. Immediately after hatching they held fast to the wall of the rearing vessel by the use of their sucking disk and were able to swim by vigorous fluttering of their tail and fanning of their pectoral fins. Though quite small in number, some larvae were at a standstill, floating upside down as if they were adhering to the air water interface by the sucking disk.

The following description of the development of normal larvae is based on observations of Section I where the larvae were reared at a constant water temperature of 10°C.

Eight days after hatching, the larvae measured 7.35 mm in average total body length with a range of 7.11 to 7.60 mm and 6.4 mg in average body weight. The head and the trunk of the larvae had become more enlarged and widened, gaining solidity. The tail began to turn upward. The fin fold had 10-11 incipient rays dorsally and 7-8 rays ventrally. The five dorsal spiny rays appeared as small tubercular processes and were the full complement as in adults. They were situated just anterior to the origin of the fin fold. The caudal fin possessed 9-10 incipient rays. The pigmentation pattern remained essentially the same as in the hatching stage except for heavier pigmentation on the head and the trunk.

Sixteen days after hatching, the larvae attained an average total body length of 8.06 mm with a range of 7.77 to 8.74 mm and an average body weight of 9.24 mg. The gill opening began to close by the adhesion of the opercle to the body, retaining a small opening at its upper part. The number of fin rays were 10-11 in the second dorsal, 7-9 in the anal and 10-11 in the caudal fins. Four days after this stage, melanophores were apparent as a longitudinal band on the basal part of the caudal fin.

Thirty-three days after hatching, the larvae reached an average total body length of 9.64 mm with a range of 9.33 to 9.92 mm and an average body weight of 20.6 mg. The scattered minute specks of melanophores, developing along the dorsal and ventral sides of the tail, became dentritic or stellate. A few reddish pigments were observed on the tail. Fin rays in the second dorsal and anal fins had already reached their maximum at the 24th and 20th day respectively, and now there were 12 caudal fin rays, the same number as in the adults. From the 41st day after hatching, the dorsal spiny rays began to bury under the skin and the burying was accomplished by the 50th day.

After this stage, few changes were evident except the growth of the body, the development of pigmentation on fin rays and on the fin fold and rapid changes of outlines in the fin fold. One hundred and sixteen days after hatching, the larvae grew to 18.42 mm in average total body length with a range of 18.01 to 19.35 mm and 269.3 mg in average body weight (Pl. Fig. L).

The increase in number of the dorsal, anal and caudal fin rays are summarized in Figure 3. The pectoral fins whose rays were already developed to their full adult number at hatching and the ventral fins where the visible ray numbers were always 6 throughout the larval stage were omitted in this figure. The numerical increase of fin rays was rapid during the first few days after hatching: there were 5 spines in the first dorsal fin by the 8th day, 8-9 fin rays in the anal fin by the 20th day, 11-12 in the second dorsal fin by the 24th day and 12 in the caudal fin by the 33rd day, thereafter the appreciable increase were not recognized. The total body length when fin rays attained the full number was about 7 mm in the first dorsal fin, about 7.5 mm in the anal fin, about 8 mm in the second dorsal fin and about 9 mm in the caudal fin. Accordingly, the organogenesis of fin rays proceeded in the order of the pectoral fin or ventral fin, the first dorsal fin, the anal fin, the second dorsal fin and the caudal fin as to either the lapse of time or the

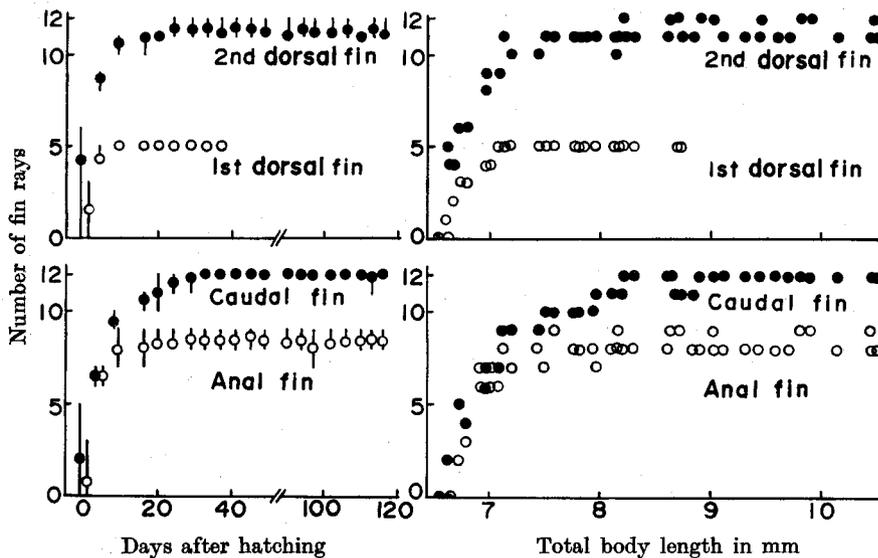


Fig. 3. Changes in number of dorsal, anal and caudal fin rays with the lapse of time from hatching and with the increase of total body length.

Circles and vertical lines represent mean values and ranges of fin ray numbers respectively in the relation between the number of fin rays and days after hatching. A circle shows the number of fin rays of one larva in the relation between the number of fin rays and total body length.

increase of the total body length. The numerical character of fin rays in the adult fish is described for the sake of contrast as follows: the number of fin spines ranges from 4 to 5 with a mode at 5 in the first dorsal, and fin rays from 10 to 13 with a mode at 11 in the second dorsal, from 8 to 10 with a mode at 9 in the anal, from 11 to 12 with a mode at 12 in the caudal and from 18 to 21 with a mode at 20 in the pectoral.

A conspicuous feeding behaviour was observed throughout the larval stage. The larvae darted forward rapidly from their attached position and the moment the larvae took the food, they attached to the wall of the vessel again. The distance of one dash for feeding was, at longest, within their own body length. The larvae never preyed while swimming. Biting behaviour was rarely observed in the late larval stage in this experiment.

Growth of larvae

During 116 days, the larvae grew to an average total body length of 18.4 mm in Section I and to 17.1 mm in Section II; the larvae attained an average body weight of 269.3 mg in the former and 229.2 mg in the latter. These lengths and weights were about 2.8 and 2.6 times the length of 6.69 mm at hatching and about 84 and 72 times the weight of 3.2 mg at hatching respectively. One larva reached a maximum length of 19.4 mm in Section I at the final measurement of the experiment.

In the larval growth appreciable inflection of the growth curve was apparent

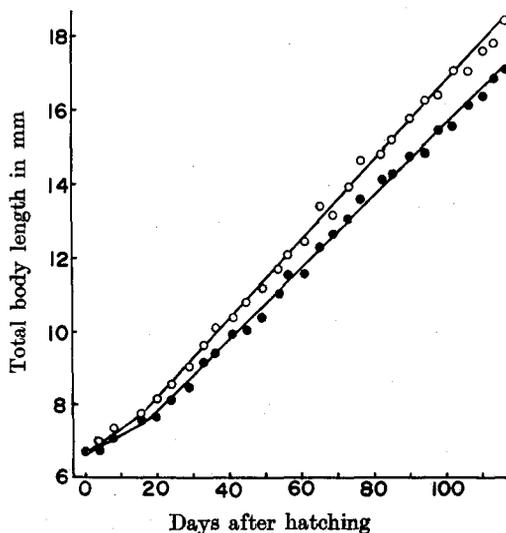


Fig. 4. Growth in total body length. Open circles and closed circles represent Section I and Section II respectively.

in each experimental section. Growth appeared to be linear before and after the inflection point and could be expressed as $L=c+at$, where L is the total body length in mm and t the days after hatching. The constants a and c were calculated by the least squares method (Fig. 4). The growth was better in Section I in which the water temperature was kept at 10°C throughout the experiment. The growth coefficient, a , was significantly larger in the period after inflection than before inflection in each experimental section (Table 3). The daily growth increment changed from 0.057–0.085 mm (the interval estimate at 0.05 level of significance) to 0.103–0.109 mm after the growth inflection in Section I and from 0.034–0.064 mm to 0.096–0.101 mm in Section II. The growth inflection appeared when the larvae reached a length of 7.9 mm in Section I and 7.6 mm in Section II. In Section II the water temperature was raised during the period from the 46th to the 61st day after hatching from 6°C in the initial to 10°C, however the growth curve was expressed as a straight line in the stage after the growth inflection as there was no recognizable change in growth rate.

The body weight increased exponentially with the time elapsed (Fig. 5). Similarly to the growth of length, the growth of weight was better in Section I as it is evident from Figure 5. Commonly, the exponential growth law, $W=Ce^{dt}$, where W is the body weight, t the days after hatching, and C and d are the constants in this regression, is associated with such growth. But, in this experiment the

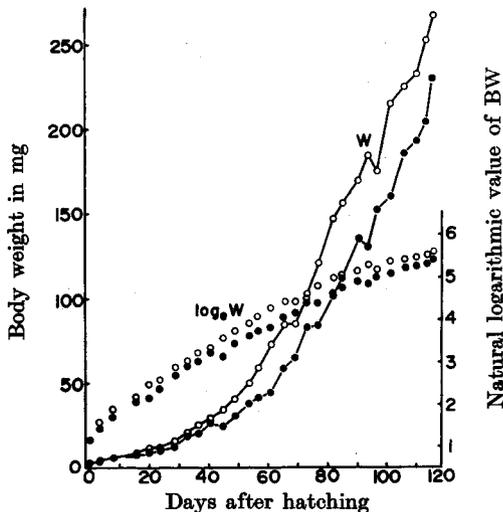


Fig. 5. Growth in body weight and the relationship between natural logarithmic value of body weight and days after hatching. Notations are the same as those in Fig. 4.

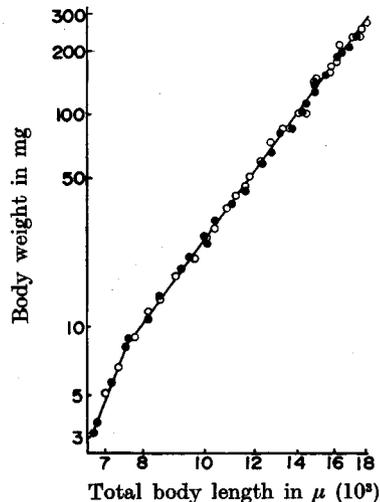


Fig. 6. Relationship between total body length and body weight. Notations are the same as those in Fig. 4.

KYŪSHIN: The embryonic and larval development of *Aptocyclus ventricosus*

Table 3. Comparison of the growth coefficient and the adjusted mean in the growth curve of larvae between experimental sections and between the growth phases before and after growth inflection.

Exp. sect.	a	c		F-test for slope			F-test for adjusted mean			Remark
				df	F ₀	P	df	F ₀	P	
I	0.071	6.708		1, 6	11.18	0.025-0.01	1, 7	9.73	0.025-0.01	Before inflection
	0.106	6.110		1, 45	13.05	0.005>				
II	0.049	6.681		1, 25	7.09	0.025-0.01				Before inflection
	0.098	5.787		1, 26	19.87	0.005>				

Table 4. Comparison of the increasing coefficient and the adjusted mean in the weight-length relationship of larvae between experimental sections and between the phases before and after inflection.

Exp. sect.	f	log g		F-test for slope			F-test for adjusted mean			Remark
				df	F ₀	P	df	F ₀	P	
I	6.783	-25.421	>1, 4	0.07	>0.50	1, 5	0.08	>0.50	Before inflection	
II	7.118	-26.694								
I	4.114	-15.043	>1, 45	1.09	0.50-0.25	1, 46	0.15	>0.50	After inflection	
II	4.042	-14.754								
Combined	6.833	-25.608	>1, 53	46.54	0.005>				Before inflection	
		4.082								-14.914

relationship between $\log_e W$ and t exhibited a curvilinear regression in each experimental section, and the decrease in the relative rate of increase of the body weight with the time elapsed was evident (Fig. 5).

The parabolic equation, $\log W = \log g + f \log L$, was fitted to the body weight-total body length relationship, since the regression between their logarithmic values was expressed by two straight lines with an inflection in each experimental section (Fig. 6). Significant differences between slopes and between adjusted means from each experimental section were not recognized, and combining the measurements of both sections the slope was calculated as 6.83 before inflection and as 4.08 after inflection (Table 4). The slope in the phase before inflection was significantly larger than that in the phase after inflection. The inflection point appeared at a total body length of 7.7 mm and a body weight of 9.0 mg in Section I and a total body length of 7.6 mm and a body weight of 8.6 mg in Section II. These lengths correspond closely to the respective length at the growth inflection in $L-t$ relation.

Relative growth

To investigate the changes in body form in the larval stage, the relative

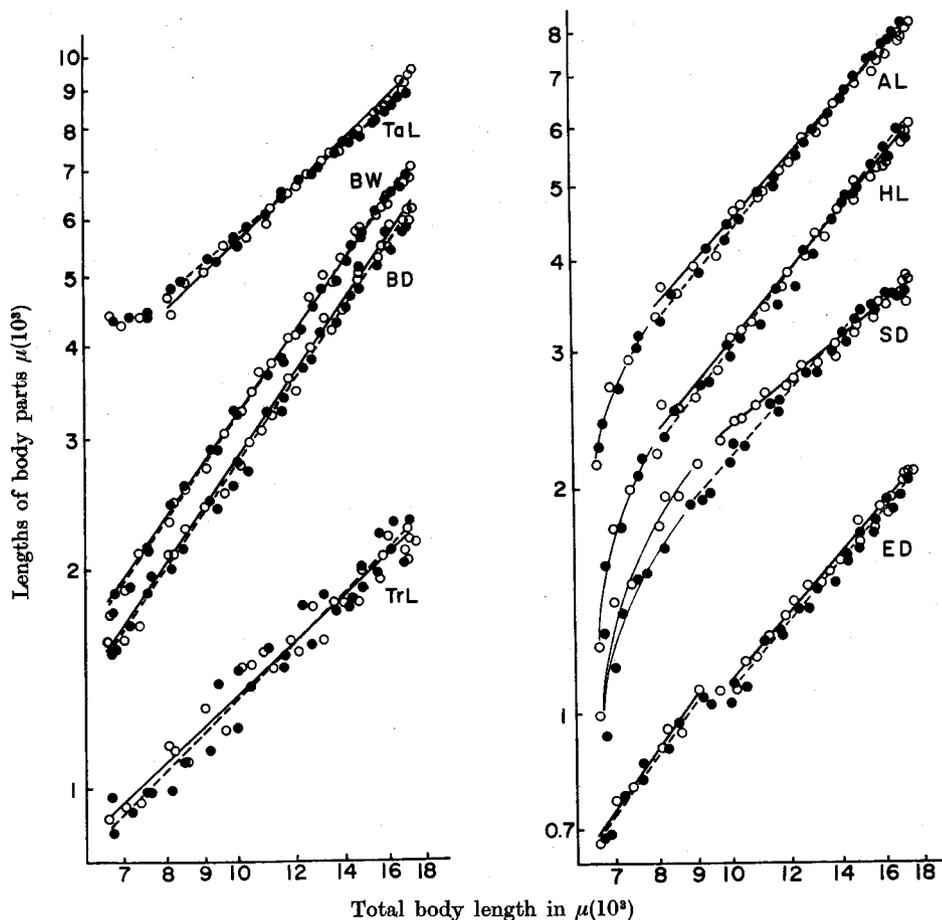


Fig. 7. Relative growth of eight body parts in relation to total body length. The calculated values of constants in allometric equation of each line are presented in Table 5. Notations are the same as those in Fig. 4.

growth, that is the regressions of the anteanal length (*AL*), the tail length (*TaL*), the head length (*HL*), the trunk length (*TrL*), the body width (*BW*), the body depth (*BD*), the eye diameter (*ED*) and the diameter of sucking disk (*SD*) to the total body length (*TL*), were examined by an allometric equation. The equation is specified as $\log y = \log b + k \log x$, where y is the length of body part in μ , x the total body length in μ , k the equilibrium constant in allometry and b the initial index. The pattern of the relative growth may be divided broadly into three categories (Fig. 7).

1. *Linear relation*

A linear regression could be adopted to the relations of *BW*, *BD* and *TrL* to

KYŪSHIN: The embryonic and larval development of *Aptocyclus ventricosus*

Table 5. Values of equilibrium constant k and another constant $\log b$ in the allometric equation, and comparison of k and the adjusted mean between experimental sections. Figures in parentheses represent 95% confidence intervals of k .

Relation	Exp. sect.	k	F-test	$\log b$	Adjusted mean (μ)	F-test	Remark
<i>AL-TL</i>	I	1.092 (1.06-1.13)	$F_0=18.93$ df:1, 45	-0.719	5795	$F_0=0.16$ df:1, 46	After inflection
	II	1.185 (1.16-1.21)	$P < 0.005$	-1.103	5781	$P > 0.50$	
<i>TaL-TL</i>	I	0.938 (0.91-0.97)	$F_0=28.17$ df:1, 45	-0.006	6971	$F_0=0.02$ df:1, 46	After inflection
	II	0.844 (0.82-0.86)	$P < 0.005$	0.376	6967	$P > 0.50$	
<i>HL-TL</i>	I	1.182 (1.14-1.22)	$F_0=5.56$ df:1, 45	-1.239	4112	$F_0=0.41$ df:1, 46	After inflection
	II	1.253 (1.21-1.30)	$0.02 > P > 0.01$	-1.532	4093	$P > 0.50$	
<i>TrL-TL</i>	I	0.914 (0.85-0.98)	$F_0=2.67$ df:1, 54	-0.526	1562	$F_0=0.20$ df:1, 55	
	II	1.002 (0.91-1.09)	$0.25 > P > 0.10$	-0.885	1541	$P > 0.50$	
<i>BW-TL</i>	I	1.436 (1.40-1.47)	$F_0=0.34$ df:1, 54	-2.233	4079	$F_0=0.69$ df:1, 55	
	II	1.448 (1.42-1.48)	$P > 0.50$	-2.286	4018	$0.50 > P > 0.25$	
<i>BD-TL</i>	I	1.464 (1.42-1.51)	$F_0=0.14$ df:1, 54	-2.411	3537	$F_0=3.45$ df:1, 55	
	II	1.453 (1.41-1.50)	$P > 0.50$	-2.372	3447	$0.10 > P > 0.05$	
<i>ED-TL</i>	I	1.426 (1.16-1.69)	$F_0=0.06$ df:1, 11	-2.610	858	$F_0=0.90$ df:1, 12	Before inflection
	II	1.391 (1.17-1.62)	$P > 0.50$	-2.478	847	$0.50 > P > 0.25$	
	I	1.153 (1.09-1.21)	$F_0=0.19$ df:1, 37	-1.566	1593	$F_0=12.52$ df:1, 38	After inflection
	II	1.172 (1.10-1.24)	$P > 0.50$	-1.660	1549	$P < 0.005$	
<i>SD-TL</i>	I	0.783 (0.74-0.83)	$F_0=56.14$ df:1, 35	0.247	2893	$F_0=4.83$ df:1, 36	After inflection
	II	1.097 (1.02-1.18)	$P < 0.005$	-1.051	2812	$0.05 > P > 0.025$	

TL throughout the experiment. The equilibrium constant, k , was 1.44-1.45 in *BW* and 1.45-1.46 in *BD*, all demonstrated strong tachyauexsis, while 0.91 or 1.00 in *TrL* showed bradyauexsis or isauexsis. In the relative growth of these three body parts, the difference between experimental sections was not significant (Table 5).

2. *Linear relation with inflection*

There appeared a strong inflection in *TaL* at about the total body length of 7.8 mm. Before inflection, the equilibrium constant could not be calculated because of a small number of measurements but *TaL* is considered to be almost no growth up to a total body length of 7.8 mm as pointed out from Figure 7. *TaL* showed bradyauxesis after inflection and the difference in *k* between experimental sections was highly significant (Table 5).

In *ED-TL* relation the discontinuous point of relative growth was readily apparent at about the total body length of 9.5 mm, therefore a straight line was fitted to each regression before 9.1 mm and after 9.8 mm respectively. *ED* indicated strong tachyauxesis in the former and tachyauxesis in the latter. Comparing between experimental sections, the adjusted mean in Section I was significantly larger than that in Section II in the relative growth beyond 9.8 mm (Table 5).

3. *Relation composed of curve and straight line*

The relations of *AL*, *HL* and *SD* to *TL* were expressed as a parabolic curve in the early larval stage. The linear regression in *AL* and *HL* was obtained in the relative growth beyond the total body length of 7.8 mm and that in *SD* beyond 9.3 mm in Section I and beyond 8.5 mm in Section II. Because *AL* and *HL* in each experimental section and *SD* in Section II showed tachyauxesis in the linear regression phase, these three body parts in the early growth stage express marked tachyauxesis though the allometric equation could not be fitted because of the curvilinear growth. In both linear phases of *AL* and *HL* the equilibrium constant in Section II was significantly larger than that in Section I (Table 5).

In the case of *SD* the relative growth is more complicated. There was difference between experimental sections not only in the total body length at the gradual inflection from a curve to a straight line but also in the size of sucking disk: the total body length and the sucking disk at the gradual inflection were markedly large in Section I as compared with those in Section II. Furthermore, in the linear phase *SD* showed bradyauxesis in Section I in contrast to tachyauxesis in Section II, and the difference in the equilibrium constant between experimental sections was highly significant (Table 5). Consequently, two regression lines from each experimental section intersected in a *TL* of 13.61 mm and a *SD* of 3.05 mm. In Section II the breaking inflection was recognizable at about the total body length of 14.8 mm, but the allometric equation after this inflection was not calculated due to insufficient measurements.

The length of body parts at hatching and that computed from the allometric equation are shown in Table 6. For the estimate of the length of various body parts, the value of the intercept in the allometric equation was adjusted by the

Table 6. Size of body parts at hatching* and that computed from the allometric equation at given total body length. Figures in parentheses represent percentage of the size of body parts to total body length.

Body part	Exp. sect.	Total body length (mm)			
		6.69*	9	13	17
AL	I		3.97(44.1)	5.93(45.6)	7.94(46.7)
	II	2.21(33.0)	3.83(42.6)	5.92(45.6)	8.14(47.9)
TaL	I		5.03(55.8)	7.09(54.5)	9.10(53.5)
	II	4.48(67.0)	5.19(57.6)	7.07(54.4)	8.87(52.2)
HL	I		2.73(30.3)	4.21(32.4)	5.77(33.9)
	II	1.26(18.8)	2.65(29.4)	4.20(32.3)	5.88(34.6)
TrL	Combined	0.95(14.2)	1.21(13.4)	1.72(13.3)	2.22(13.1)
BW	Combined	1.75(26.2)	2.77(30.8)	4.71(36.2)	6.94(40.8)
BD	Combined	1.57(23.5)	2.39(26.6)	4.07(31.3)	6.02(35.4)
ED	I		1.06(11.8)	1.50(11.5)	2.04(12.0)
	II	0.68(10.2)		1.46(11.2)	2.00(11.7)
SD	I		—	2.95(22.7)	3.63(21.4)
	II	0.96(14.3)	1.94(21.5)	2.90(22.3)	—

following approximation, $\log b + 1.15 [(n-1)/n] S^2$, where n is the number of measurements and S^2 the residual variance of regression, to correct the bias attributable to the logarithmic transformation. As a matter of course, the ratios of the length of body parts which indicate tachyauexis in relation to the total body length increase with the growth of larvae and conversely decrease in the case of bradyauexis (Table 6). For example, *HL* showing tachyauexis in relation to the total body length is 1.26 mm at hatching and it is about 19% of the total body length. The ratio of *HL* to the total body length increases to 29–30% at the total body length of 9 mm, further to 34–35% at 17 mm. Another example which is bradyauexis in relation to the total body length indicates that *TaL* decreases gradually from 67% at hatching to 52–54% at 17 mm.

Survival of eggs and larvae

The number of survivors and the mortality rate in the embryonic stage are shown in Table 7. The survival of embryos began to decrease, consequently the mortality rate began to increase from the 30th day after fertilization, and it attained 13.4% at the 35th day. Since hatching occurred on the 39th day after fertilization and the rate of hatching was 62%, the critical period for the embryos might be in the hatching stage.

Survival curves for larvae are given in Figure 8. In the fed group normal larvae began to die from the 20th day after hatching and the survivors decreased linearly thereafter. The instantaneous mortality coefficient was 0.000655 in Section I and 0.000437 in Section II, between which a significant difference was

Table 7. Survivors, original number of eggs being 1,000, and mortality rate every five days in embryonic stage.

Days after fertilization	Survival of eggs	Mortality rate (%)
0	1000	
5	995.5	0.45
10	993.2	0.23
15	989.5	0.37
20	989.0	0.05
25	988.5	0.05
30	972.8	1.59
35	842.1	13.44

recognized ($F_0=81.71$, df. 1 and 90, $P<0.005$). Converting this coefficient into the survival rate, it is 99.94% in Section I and 99.96% in Section II. The ratio of the survivors at the 110th day after hatching to the initial numbers was 94.1% in Section I and 96.1% in Section II. On the contrary, in the non-fed group of Section II the mortality rate began to increase rapidly from the 28th day and all larvae starved to death by the 42nd day after hatching. The time required from hatching to the 50% death was as long as 31 days at a water temperature of 6°C.

The mortality of the deformed larvae was observed from the 10th day after hatching. The pattern of the survival curve was rather complex, so the mortality coefficient could not be computed simply (Fig. 8). The survival rate in the deformed larvae was considerably less than that in the normal larvae. The difference in mortality between the normal and deformed larvae became greater with elapsed time. The ratio of the survivors of deformed larvae at the 110th day after hatching to the initial numbers was 78.4% in Section I and 79.3% in Section II.

Survivorship expressed as the relation between the survivors and the total body length was examined to analyse the survival throughout the growth processes. As it is clear from Figure 9, the curves are composed of two phases. One is the phase before the inflection point, where the mortality is completely negligible. Another is the decreasing phase after inflection and the reduction coefficient was 0.0061 in Section I and 0.0044 in Section II. Similarly the coefficient in Section I was significantly higher than that in Section II ($F_0=38.63$, df. 1 and 46, $P<0.005$).

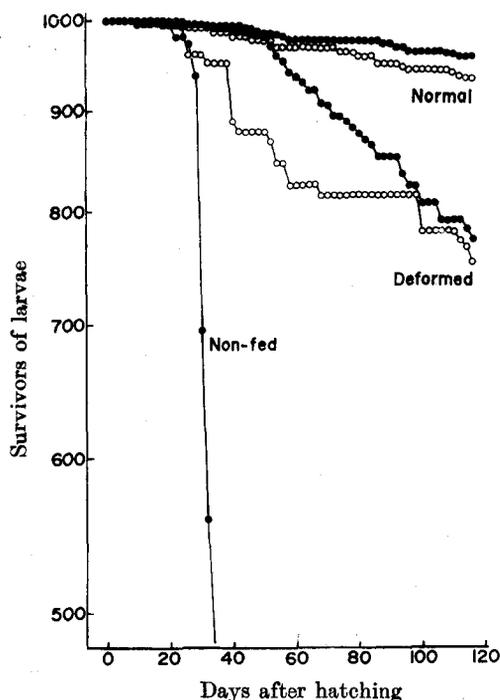


Fig. 8. Survival curves in larval stage, original number of larvae being 1,000. Notations are the same as those in Fig. 4.

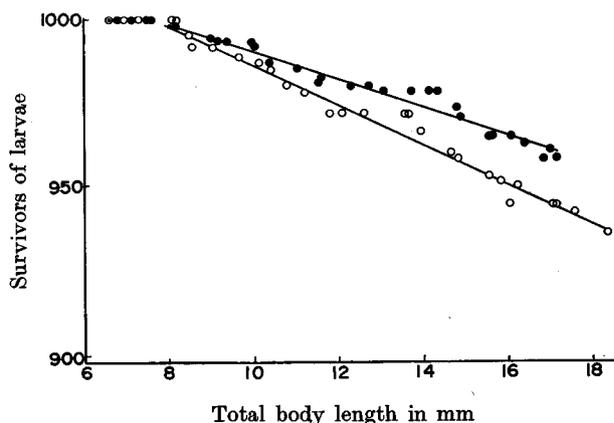


Fig. 9. Relation of number of survivors to total body length in the normal larvae, original number of larvae being 1,000. Notations are the same as those in Fig. 4.

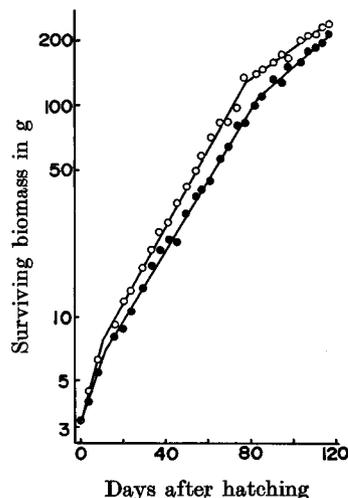


Fig. 10. Surviving biomass of larvae. Notations are the same as those in Fig. 4.

The ratio of the survivors at a total body length of 17 mm to the initial numbers was 94.4% in Section I and 96.0% in Section II. The inflection point in survivorship appeared at the total body length of 7.5–8.0 mm, which almost coincides with that at the inflection of the growth curve.

The surviving biomass in the experimental population (the product of the mean body weight and the number of survivors as the initial numbers being 10^3) is shown in Figure 10. The biomass increased throughout the larval stage from 3.2 g at hatching to 245.0 or 219.4 g at the end of the experiment, the weight of Section I was always larger. However, the relative rate of increase of the biomass has the tendency of stepwise reduction as is evident from Figure 10.

Discussion

The smooth lump sucker approaches the coast for spawning and is caught commercially during the period from January to April in the southern Hokkaido. In Shikabe the species is presumed to spawn from early February to early April, because mature fishes are captured and the artificial fertilization can be accomplished successfully in this season. In the spawning population the female is larger than the male and the general color of the female is conspicuously blackish blue and the male has a drab appearance, therefore the sex of mature fishes is distinguishable from external features. The most obvious morphometrical difference between sexes lies in the size of sucking disk as emphasized by Kobayashi²⁾: the male possesses a remarkably larger sucking disk than the female. According to the



Fig. 11. A picture showing a lump of eggs of the smooth lumpsucker collected in Toi, southern Hokkaido. (Photographed by K. Sakamoto)

author's observations, the ratio of the diameter of sucking disk to the total body length ranges from 21 to 26% in male, in contrast, from 14 to 18% in female, the distributions of *SD-TL* ratio from both sexes never overlap by each other.

The peak fishery for the smooth lumpsucker is between February and March every year and the fishes are abundant on rocky ground less than about 10 m in depth during this period. On May 1, 1968 a lump of eggs which adhered to the lower surface of a rock was collected by K. Sakamoto by hand at neap tide in Toi, southern Hokkaido (Fig. 11). The development had proceeded to the latter embryonic stage and a few days after the collection the larvae of smooth lumpsucker commenced to hatch out in the laboratory of Hokkaido Hakodate Fisheries Experimental Station.

From this information the spawning of this species probably occurs on the rocky sea bottom in the shallow water of the coast.

The water temperature at the sea bottom in water about 10 m in depth is about 3–5°C in February and about 4–6°C in April in the vicinity of Shikabe, thence gradually rises to 6–7°C in early May and 7–8°C in early June, then rapidly rises to 14–15°C by early July.^{3,4,5)} By taking cumulative temperature required to hatching in the present study into account, the hatching season in nature is estimated to extend from early April to early May. In the natural environment the embryonic development of the species progresses under rising temperatures.

As mentioned above, eggs of the smooth lumpsucker are demersal and adhesive and there is no essential difference in the embryonic development between the species and other teleostean species except the rapid growth of the head and trunk portions and the heavy pigmentation on these body parts in the latter embryonic stage of the smooth lumpsucker. The striking features of the newly hatched larvae lie in the tadpole-like body form and in the well-developed sucking disk, the ventral fins, on the ventral side of the body. According to the laboratory observations, it is a biological characteristic of the smooth lump-

sucker that the larvae live an attached life by their sucking disk except during rapid, forward darting movement for feeding or the swimming to shift the attached position.

The rearing experiment of the larvae was performed for a long period of 116 days. During this period, the larvae grew to an average total body length of 17.1–18.4 mm from 6.7 mm at hatching. The growth inflection appeared at a total body length of 7.6–7.9 mm, which nearly coincided with the length at the inflection of the weight-length relationship. Feeding began on the 6th–8th day after hatching and the total body length at the stage of yolk-absorption is estimated to be about 8.8 mm, therefore it is hard to associate the growth inflection directly with such biological or physiological phenomena. Since the length at the inflection of the growth curve coincides well with relative growth inflection, it probably has close relation to the changes in body form which implicate the biological consequences. The growth rate was more rapid in Section I in which the larvae were subjected to a constant temperature of 10°C. Although the water temperature in Section II was raised from 6°C to 10°C in the period from the 46th day to the 61st day after the beginning of the rearing experiment of larvae, any changes in growth were not recognized. The appropriate considerations to the cause could not be determined in this experiment.

On July 25, 1969 three wild larvae of the smooth lumpsucker were introduced to the rearing tank set in the laboratory of Hokkaido Hakodate Fisheries Experimental Station by means of the sea water drawing pipe which has an opening 200 m offshore where the water depth is about 3 m. They were dipped up, preserved and offered to the present study by K. Nakamichi. The larvae measured 23.9, 22.8 and 15.9 mm in total body length at the time of collection. From the growth process observed in the rearing experiment, evidently they were derived from the 1969 year class. The range of the total body length of the wild specimens overlaps that in the 24th of July in Section I of this experiment, namely 16.1–17.9 mm at the 106th day after hatching. Probably such a wide range as 15.9–23.9 mm in the collection is due to the extended hatching period attributable to a long period of the spawning season and to the variety of the environmental condition in nature. As far as the author knows, there is no published information concerning the larvae of smooth lumpsucker in the vicinity of Hokkaido except for this collection. Although it was impossible to trace the larval growth in natural conditions, it may be suggested that the growth in nature is better than that obtained from this experiment, as the lengths of two specimens from the natural collection are far larger than the larvae artificial reared.

Examining the changes in body form by means of the relative growth of body parts to the total body length, it was elucidated that the head, trunk and sucking disk made remarkable development, while the tail portion had no growth in

the early larval stage. The body depth, the body width and the anteanal length demonstrated strong tachyauexesis or tachyauexesis throughout the experiment, and the tail length thus showed non-growth or bradyauexesis. Consequently the larvae of smooth lumpsucker are gradually metamorphosed into the stocky body form suitable to the demersal, attached life, in another meaning inept for active swimming. These are just the striking characteristics of morphological changes in the smooth lumpsucker larvae differing from *Hexagrammos otakii*⁶⁾ and *Hemitripterus villosus*¹⁾ whose larvae live an active swimming life, and are considered to be the morphological adaptation for such a specific living in the larval stage.

The effects of water temperature on the changes in body form are recognized. A high temperature expedites the growth of the anteanal length, the head length and the diameter of sucking disk in the stage before relative growth inflection, but a low temperature apparently operates to make the equilibrium constant larger after inflection; the reverse results are obtained in the tail length. In the case of the eye diameter a high temperature made the adjusted mean of the allometric equation larger after inflection, viz. the eyes of the larvae which were reared under high temperature throughout the experiment are larger. Among the body parts examined, the size of sucking disk is subjected to the potent influence of temperature, but the biological meaning involved in the temperature effect remains unknown. A fact of some interest is that any changes in relative growth were not recognized in Section II contrary to the author's expectation though the temperature was raised from 6°C to 10°C in the course of the experiment. It is not clear from the results of this experiment whether a temperature of 6°C in the first half regulates the subsequent relative growth or the body form obtained in the past temperature condition is sustained for a period until the morphological characteristic for the latter condition is revealed. In Section II the breaking inflection in the relative growth of the sucking disk was recognizable at a total body length of 14.8 mm. The inflection appeared about a month after the time when the temperature was raised from 6°C to 10°C. This result may be suggestive of a change in the relative growth of the sucking disk with a time lag due to the alteration of the temperature.

As mentioned above, considerable variation in the relative growth due to the temperature effect is apparent between body parts within the same species and between species.^{1,6,7,8)}

In this experiment the author succeeded in a long series of rearing of the smooth lumpsucker larvae beyond the yolk-sac stage and a high survival was achieved: the survival rate of the normal larvae at the end of the experiment, namely at the 110th day after hatching, was as high as 94-96%. This reason is probably due to that the larvae of smooth lumpsucker have a long period of yolk-sac stage, as much as 31 days under a water temperature of 6°C, as con-

trasted with the greenling⁶⁾ and the Alaska pollack⁶⁾ whose yolk-sac stage are about 15 days under the temperature of 6-8°C. In the rearing experiments of the greenling and the Alaska pollack, high mortalities occurred at the yolk absorption stage and no larvae survived to metamorphosis. Accordingly, it is probable that the long yolk-sac stage of the smooth lumpsucker enabled the larvae to have an extended opportunity for feeding. Another reason for high survival in this experiment is considered to lie in that the nauplii of brine shrimp was a suitable food for the larvae throughout the experiment.

The existence and the exact nature of a critical period of mortality in the larval stage of fishes has been a subject of debate for a long time. In the rearing experiments of marine fishes the high mortality more or less occurs prior to or following yolk absorption.^{1,6,8,9,10,11)} However, it is never recognizable in any larval stage of the smooth lumpsucker, the conceivable causes of this must be involved in the reasons mentioned above. The mortality was higher in Section I in the survival curve and in the relation between the survivors and total body length. Nevertheless, the surviving biomass in Section I was always larger than Section II in consequence of the increases in biomass brought about by the rapid growth which made up for the loss of biomass by the higher mortality. In Section II any changes of mortality due to the rise of water temperature were not appreciable.

Although the survival of the deformed larvae was considerably low as compared with the normal larvae, yet it was as high as 78-79%. However, it can not be expected that the deformed larvae which possess a defective sucking disk live long under the severe environment in nature, since the sucking disk fills the indispensable biological function for the smooth lumpsucker.

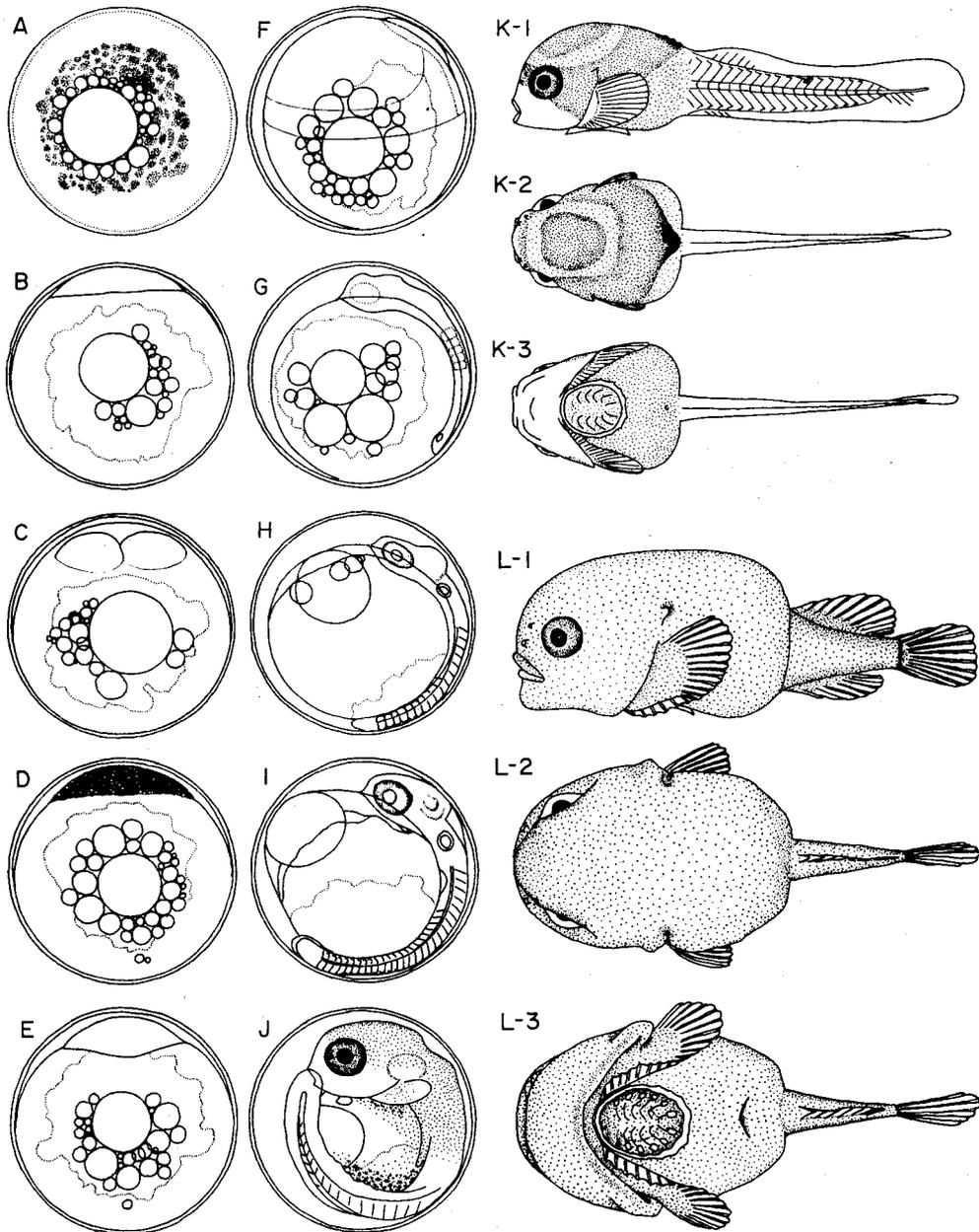
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Explanation of Plate

- Fig. A. Mature egg before fertilization, top view.
Fig. B. Protoplasmic germ disc, 5 hours, top view.
Fig. C. 2-cell stage, 7.5 hours, top view.
Fig. D. Morula stage, 44 hours, top view.
Fig. E. First gastrula stage, 70 hours, top view.
Fig. F. Germinal ring attains to an equatorial position, 150 hours, top view.
Fig. G. Embryo over one-third circle, 190 hours, lateral view.
Fig. H. Embryo in about half circle, 264 hours, lateral view.
Fig. I. Embryo over half circle, 27-28 pairs of somites, 342 hours, lateral view.
Fig. J. Embryo forming nearly a circle, 672 hours, lateral view.
Fig. K. Newly hatched larva, 6.79 mm long in total body length.
K-1: lateral view, K-2: dorsal view, K-3: ventral view.
Fig. L. 116 days old larva, 18.87 mm.
L-1: lateral view, L-2: dorsal view, L-3: ventral view.



KYŪSHIN: The embryonic and larval development of *Aptocyclus ventricosus*