

Pigment that had previously been scattered regrouped in such a way that a pigment band formed on the middle of the tail, on the 12th to the 18th and most frequently on the 13th to the 15th myotomes (counting from the anus); in addition, a double row formed on the lower edge of the tail and above the intestine. The band that formed on the middle of the tail in the prolarval stage remained as one throughout the entire larval stage, with the difference that it became narrower and subsequently occupied only two or three (the 15th to the 16th, the 14th to the 16th, the 16th to the 17th, and the 16th to the 18th), and more frequently two (the 16th to the 17th), myotomes.

After the absorption of the yolk sac the large melanophores passed to the lower surface of the abdomen, on the middle ³⁵⁴ of which they formed a distinct pigment row that occasionally split in two. A few large, starry cells were located along both sides of this row. There was a row of cells on the isthmus. Towards the moment of formation of rays the band on the middle of the tail disappeared, and in its place there remained single large melanophores. Banded flounder larvae at this stage were fairly easily distinguished by a comparatively large number (11 to 13) of myotomes in the trunk, the absence of melanophores in the depth of the body above the chord and by a slight pigmentation on the lower edge of the tail.

The Arctic Flounder -- *Liopsetta glacialis* (Pallas)

Information on the development of the arctic flounder is extremely meager. Reports on the reproduction and egg sizes of

arctic flounder from the White Sea are available in a study by A.N. Nikolaev (1955). We have investigated artificially fertilized eggs which were kindly given to us by N.A. Pertsev, the Director of the White Sea Biological Station of Moscow State University, as well as three prolarvae from 3.7 to 6.6 mm long and twelve larvae from 6.53 to 7.89 mm long, caught with a plankton net from 21 July to 30 August 1946 in Kara Bay.

The above prolarvae and larvae have been described by L.A. Ponomareva (1949). A comparison of this limited material with that on the banded flounder is undoubtedly of great interest.

The eggs of the arctic flounder are pelagic, and at a salinity of 27 to 28‰ float in the open water. The membrane is thin and the yolk is colourless and transparent.

The diameter of ripe White Sea arctic flounder eggs, according to Nikolaev, varies from 1.2 to 1.6 mm. The diameter of fixed eggs that we examined ranged from 1.54 to 1.70 mm.

The perivitelline space in live eggs represented a narrow aperture, whose size after fixation increased as a result of the shrinking of the yolk.

Prolarvae (evidently recently hatched) 3.7 mm long (see fig. 51) had a large yolk sac. Their heads were straightened and separated from the yolk sac to the level of the forward edge and middle of the auditory capsule.

The pigmentation of the body was of an embryonic nature. Large melanophores were thickly scattered over the entire body of the prolarva, and there was a small quantity on the intestine and the yolk sac. The eyes were dark. Prolarvae from 6.35 to 6.66 mm long (see fig. 51, 2) had a fairly large yolk sac 0.90 to 1.29 mm long and 0.32 to 0.42 mm high. The tail was long and the distance from the end of the snout to the insertion of the anal fin represented 35.7 to 36.7% of the length of the body. The pectoral fins were small, and their ends reached the fourth myotome. To judge from the base, which was situated vertically, they were mobile.

There were 11 + 26 myotomes ^{in the body.} A mesenchymal accumulation was noticeable under the urostyle, in the place of the hypurals. The pigment lost its embryonic nature, and of it there remained a small number of cells scattered on the tail; the trunk was practically devoid of pigment. A somewhat indistinct accumulation of melanophores was noticeable on the tail around the 16th myotome, and there was a row of such melanophores on the lower edge of the tail.

In older larvae 6.53 to 7.12 mm long the yolk sac had been absorbed. The pigmentation changed little in comparison with the preceding stage: the number of scattered melanophores decreased on the tail and increased on the lower portion of the forward half of the intestine. In older larvae 7.89 (7.58 to 7.71) mm long, caught on 30 August 1946 at Ust'-Kara, the myotomes were sigmoid. The height of

the body represented 11.1 to 11.6% of its length. At the base of the dorsal and anal fin folds there appeared the 355 stripes of pterygiophores, from which there branched out fin rays, the length of most of which still did not exceed $1/3$ of the height of the fin folds. They [the fin rays] were best developed in the central area. Their number decreased progressively towards the front and the rear, and at the beginning and end of the fin folds they were entirely absent. There were 24 to 35 rays in the dorsal fin fold and 22 to 27 in the anal fold.

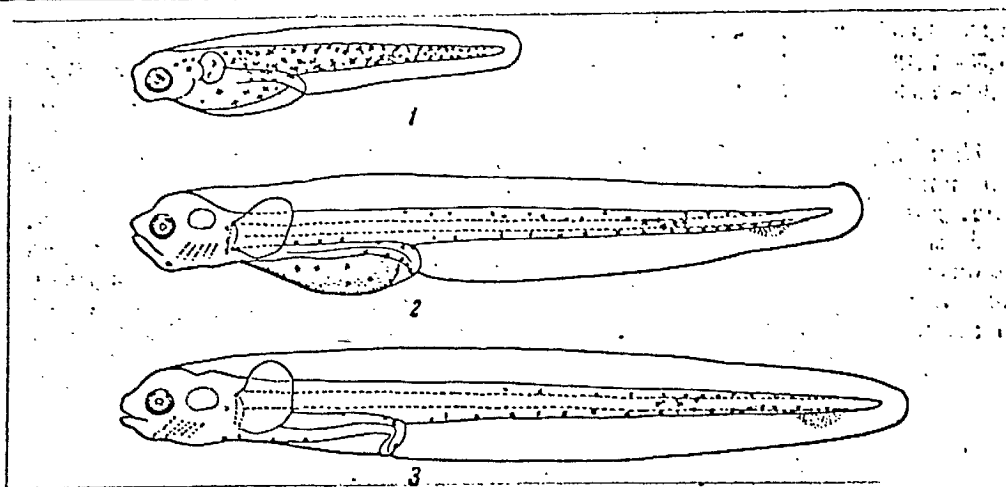


Figure 51- Prolarvae and larvae of L. glacialis.

1- 3.7 mm (after Ponomareva); 2- 6.7 mm; 3- 7.1 mm

The intestine formed a full loop, which was still small and situated in the rear portion of the abdominal cavity. The urostyle was curved slightly upwards, and under it were outlined the hypurals and the tail fin rays.

Pigment was for the most part still of a larval nature, with the difference that the number of scattered melanophores decreased on the upper portion of the tail and

the pigmentary cells themselves became much larger. The melanophores which had been under the urostyle extended along the length of the outlined tail fin rays.

In larvae 7.96 (6.98) mm long the height of the body increased to 18.3% of its length. The fin rays, with the exception of the first and last three to four in the dorsal and anal fins, were differentiated. They were noticeably longer than in the preceding stage and fell slightly short of the edges of the fin folds. There were about 50 rays in the dorsal fin and about 38 in the anal fin. Eight or nine fin rays were outlined in the tail.

The intestinal loop filled the entire rear half of the abdominal cavity. The end of the rectum was pulled somewhat forward as compared with its position in the preceding stage.

The pigmentation of the right and left sides was asymmetrical. On the right side there was a large number of small, scattered melanophores on the head and the forward portion of the trunk, and a few larger starry cells in various areas of the tail.

The first spot of the upper row of the tail was outlined and was also visible on the left side.

The left side of the body, with the exception of one pigmentary cell remaining from a band on the middle of the tail, and a few cells on the end of the intestine and the lower edge of the tail, was devoid of pigment.

The change in the proportions of the body in the course of development of the prolarvae and larvae that have been described is shown in Table 53.

Table 53 1356

The Correlation of Body Parts of Prolarvae and Larvae of *L. glacialis*

Length, in mm	Number of specimens	Percentage of length of body				Percentage of length of head	
		aA	H	lc	O	aO	
6,35—6,66	2	35,7—36,7	4,16—4,7	13,75	28,5—33,0	16,4—16,6	
6,53—7,12	9	33,3—37,7	4,5—5,1	13,25—14,6	27,1—27,6	15,1—19,0	
6,98—7,89	3	37,4—41,0	11,1—18,3	18,45—23,2	19,74—22,1	17,45—19,1	

As may be seen from the data in Table 53, during the period of development the following changes take place in the parts of the bodies of larvae: the distance from the end of the snout to the insertion of the anal fin, the height of the body, the length of the head, and the length of the snout increase, and the eyes decrease in size.

In fingerlings 28 mm long, caught on 11 August 1945 with a fingerling trawl in Baidarata Bay, both eyes were on the right side, and the fingerlings' metamorphosis had evidently long been completed. Juvenile fish 98 mm long had the appearance of adults.

The Black Flounder -- *Liopsetta obscura* (Herzenstein)

We have given a brief outline of the structure of black flounder eggs in published keys to the pelagic eggs

of fish of Peter the Great Bay (Pertseva-Ostroumova, 1955).

The development of prolarvae and larvae from 3.5 to 58 mm in length under artificial conditions has been traced by Kurata (1956).

We studied embryonic and postembryonic development in series obtained through the artificial fertilization and incubation of eggs. Brood stock was taken from fyke nets set out under the ice in the region around Vladivostok, off Cape Burnyi and in the area adjacent to the 19th kilometre station of the Maritime Railway, as well as by fishing with Danish seines of the Tafaun Fish Combine in Ussuri Bay and Anna Bay. A total of seven series with five subseries was obtained from 2 to 19 March 1953 (see Table 54).

Out of seven series of artificially fertilized eggs, development in four was cut short at the prolarva stage, larvae were obtained in three and in the remaining [groups] the eggs died at the cleavage and gastrula stages.

In addition to the larvae obtained from artificial fertilization, two larvae 8.23 to 8.67 (7.97 to 8.16) mm long, caught on 3 and 4 July 1948 in Amur Bay, were also examined.

In the first and second series, experiments were set up on the effect of salinity fluctuations on the development of eggs, prolarvae and larvae.

We have described the course of development mainly from the material in the second series of experiments, in which the water temperature was nearest to that under natural conditions.

Eggs fertilized on 2 March 1953 at 2:25 pm were placed in sea water at a temperature of $+1.2^{\circ}$; temperatures subsequently fluctuated from -1.0 to $+8.6^{\circ}$ and averaged $+2.4^{\circ}$. The water temperature in the sea in the spawning region was about -1.0° .

The development of eggs in water of normal salinity at a water temperature averaging $+2.4^{\circ}$ is shown in Table 55, while abbreviated outlines of development at another temperature are given in Table 56.

As may be seen, the first prolarvae hatched in 21 days and 5 hours. The hatching process took place fairly slowly; mass hatching began only a day later, i.e., 22 days and 5 hours after fertilization. After 23 days the bulk of the prolarvae hatched. Prolarvae, however, continued to hatch from isolated eggs in the course of the next 1357 several days, while some of the embryos whose membrane was covered with a thick bacterial film, never could free themselves from it and subsequently died.

Prolarvae that hatched at various times developed to differing degrees: the later they hatched, the more they were developed and vice versa. Cases were not infrequent in which late prolarvae hatched with pigmented eyes, pectoral fins that had grown to a considerable extent, an open mouth and a noticeably shrunken yolk sac.

As may be seen from the data in Table 56, at average water temperatures of +5.5 to 7.7° embryonic development proceeded much more rapidly.

In comparing data from observations in the second and third series of experiments, we attempted to calculate the temperature threshold of development and the number of degree-days necessary for completion of the embryonic development of the black flounder. Substituting our data in Reibisch's formula, we obtained a temperature threshold of -2.2° and a required number of 97 degree-days.

The figures obtained through calculation are evidently close to true values, since at this temperature water changes to ice, and in nature, eggs do not, of course, develop under such conditions.

Taking into account the fact that eggs develop under natural conditions at an average temperature of 0°, we deduce that the period of embryonic development lasts for 42 days. Consequently, from eggs laid from the middle to the end of March prolarvae should hatch at the end of April and beginning of May.

Ripe, live unfertilized black flounder eggs are transparent and on the whole are of a light yellowish-greyish hue.

Table 55

The Course of Embryonic Development of *L. obscura* at a
Water Temperature Averaging +2.4°

Stage of development	Age		Pigmentation
	days	hours	
2 to 4 blastomeres.....	--	18	--
8 blastomeres.....	1	--	--
128 blastomeres.....	1	22	--
Blastomere blastula.....	2	22	--
Epithelial blastula.....	4	20	--
Beginning of gastrula.....	5	20	--
Blastoderm covers half of yolk.....	7	21	--
Blastoderm covers 3/4 of yolk. Embryonic stripe.....	8	21	--
Blastopore closes. Rudiments of optic vesicles.....	10	21	--
Optic vesicles fully formed. 8 to 9 myotomes in the body. Kupfer's vesicle. Embryo envelops 2/3 of the yolk.....	11	21	--
17 myotomes.....	11	23	--
1 bud has formed. Eye cups. 20 to 22 myotomes. Embryo envelops 3/4 of yolk.....	13	7	Dark melanophores and yellow chro- matophores have appeared.

Table 55 (cont'd)

Stage of development	Age		Pigmentation
	days	hours	
Beginning of separation of tail. 25 myotomes. Kupfer's vesicle...	15	--	Same
End of tail almost touches head. 10 to 12 myotomes in the tail.....	16	--	Same
19 to 21 myotomes in the tail. Heart beats.....	17	--	Embryo heavily pigmented
End of embryo's tail proceeds beyond the head to the middle of the eye. Hatching glandulae..	18	--	Same
End of tail reaches auditory capsule.....	19	--	"
End of tail reaches pectoral fins. 11 to 12 myotomes in trunk and 26 to 27 in tail.....	19	10	"
Prolarvae begin to hatch.....	21	5	"
Mass hatching.....	22	5	"
Mass hatching completed.....	23	--	"

The membrane of the egg was thick and sticky and gathered in a large number of folds intersecting in various 358 directions; it was usually closely attached to the yolk.

The sizes of such ovarian eggs ranged from 0.69 to 0.90 mm. Live, developing eggs were transparent, and swelled very slightly in the water; the reticular structure of the membrane was retained throughout the entire period of development. The sizes of live and fixed eggs practically did not differ and ranged in different series from 0.78 to 0.94 mm, averaging

0.86 to 0.90 mm. The yolk was homogeneous, and after fixation shrank considerably, became hard and assumed a bright yellow colour. Its size in live eggs varied from 0.71 to 0.87 mm, and in fixed eggs, from 0.51 to 0.78 mm. The perivitelline space, from measurements of live and fixed eggs, was small (see fig. 52), and in live specimens represented only 4.1 to 7.6%, and an average of 5.5%, of the diameter of the egg. The corresponding percentage in fixed eggs increased to 5 to 21%, averaging 10.5 to 16.3%, as a result of the shrinking of the yolk. The membrane of the egg was comparatively thick and viscous; because of this, the eggs not infrequently stuck together in lumps and adhered to the wall and bottom of the vessel. The adhesiveness of the membrane decreased in 1/360 proportion to development, and the lumps separated into individual eggs, which came loose from the substrate. The blastodisc was high, and reached its greatest height at the morula stage. Its base at this time completely covered the yolk from above, and its height represented about $1/3$ of the diameter of the latter. In its abundance of plasma and the character of its blastodisc the black flounder egg approximated a type of polyplasmatic egg. At the epithelial blastula stage the height of the blastodisc decreased and reached its minimum at the beginning of gastrulation. The base of the gastrula completely covered the upper portion of the yolk surface. In the stage of development at which there were 20 to 22 myotomes in the trunk, and the embryo enveloped more than $3/4$ of the yolk, on the body there appeared lemon-yellow chromatophores and less noticeable dark chromatophores, single

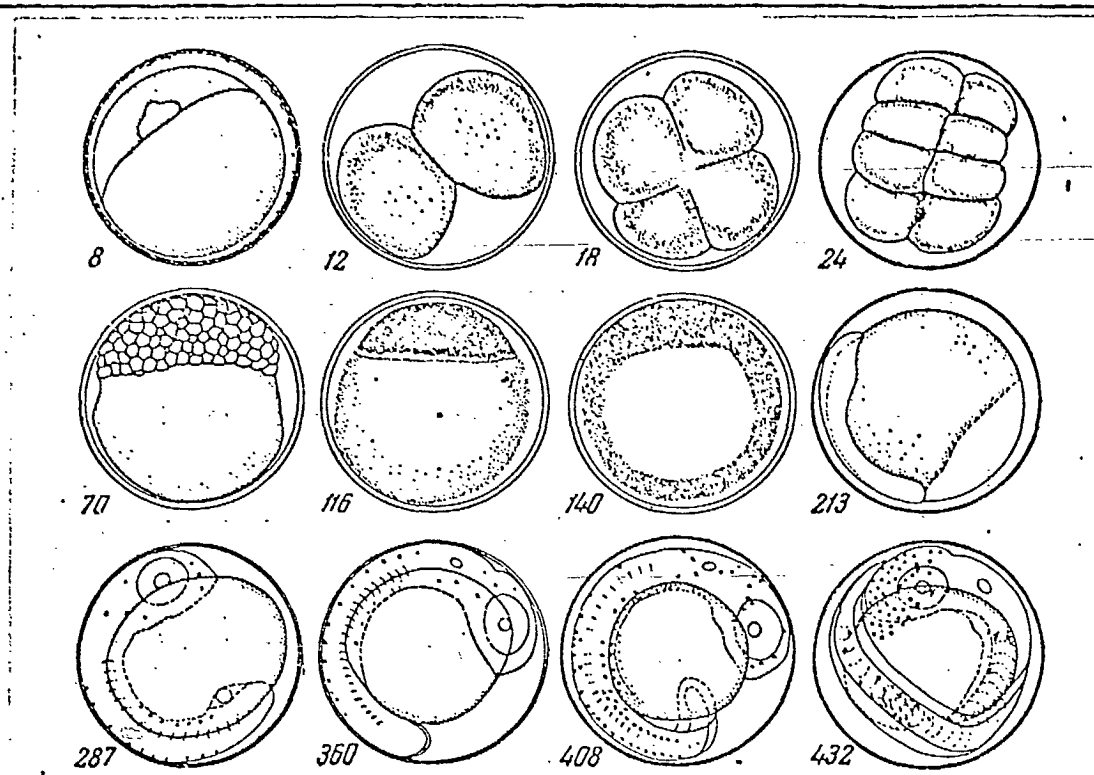


Figure 52- The development of eggs of *L. obscura* at an average water temperature of $+2.4^{\circ}$.

The figures under the illustrations designate hours of development

cells of which were visible in the postorbital region and were unevenly scattered on the body, and particularly thickly in its forward quarter. Yellow chromatophores bordered the eyes, were thickly scattered on the head and grouped noticeably behind the eyes. On the body they were situated in more or less regular rows, of which there were two in the forward half and four in the rear. Subsequently, a large number of scattered cells appeared on the forward half of the tail, and an accumulation was outlined on the middle of the latter. The end of the tail was free from pigment. The melanophores were branched, and pale-coloured, and, in the same way as the yellow chromatophores, were scattered on the head and trunk and were arranged in an unusual pattern on the tail, forming four rows, of which two

Table 56

The Course of Development of Eggs of *L. obscura*

Stage of development	Temperature, in °C			Age		Temperature			Age		
	from	to	average	days	hours	from	to	average	days	hours	
4 to 8 blastomeres											
Morula											
Blastula -- beginning	-2,0	+2,0		0	13						
Blastula -- end	-1,8	+2,7		0	13	+6,0	+6,0		13		
Gastrula	+2,7	+3,4		+0,6	19						
Blastopore closed, optic vesicles have appeared	+3,4	+6,1		+1,3	2	13	+6,0	+10,0	+8,0	1	13
	+5,4	+6,1		+1,8	3	15	+8,0	+11,0	+9,0	2	13
	+3,0	+8,5		+3,3	5	15	+3,8	+9,2	+8,0	4	13
Formation of tail bud	+4,1	+10,0		+4,4	7	19					
	+7,5	+10,5		+5,1	8	22					
Tail almost touches head	+7,1	+10,5		+5,5	9	22	+3,8	+6,8	+7,7	7	14
Tail reaches middle of rear edge of eye. Hatching glandulae have appeared											

Table 56 (cont'd)

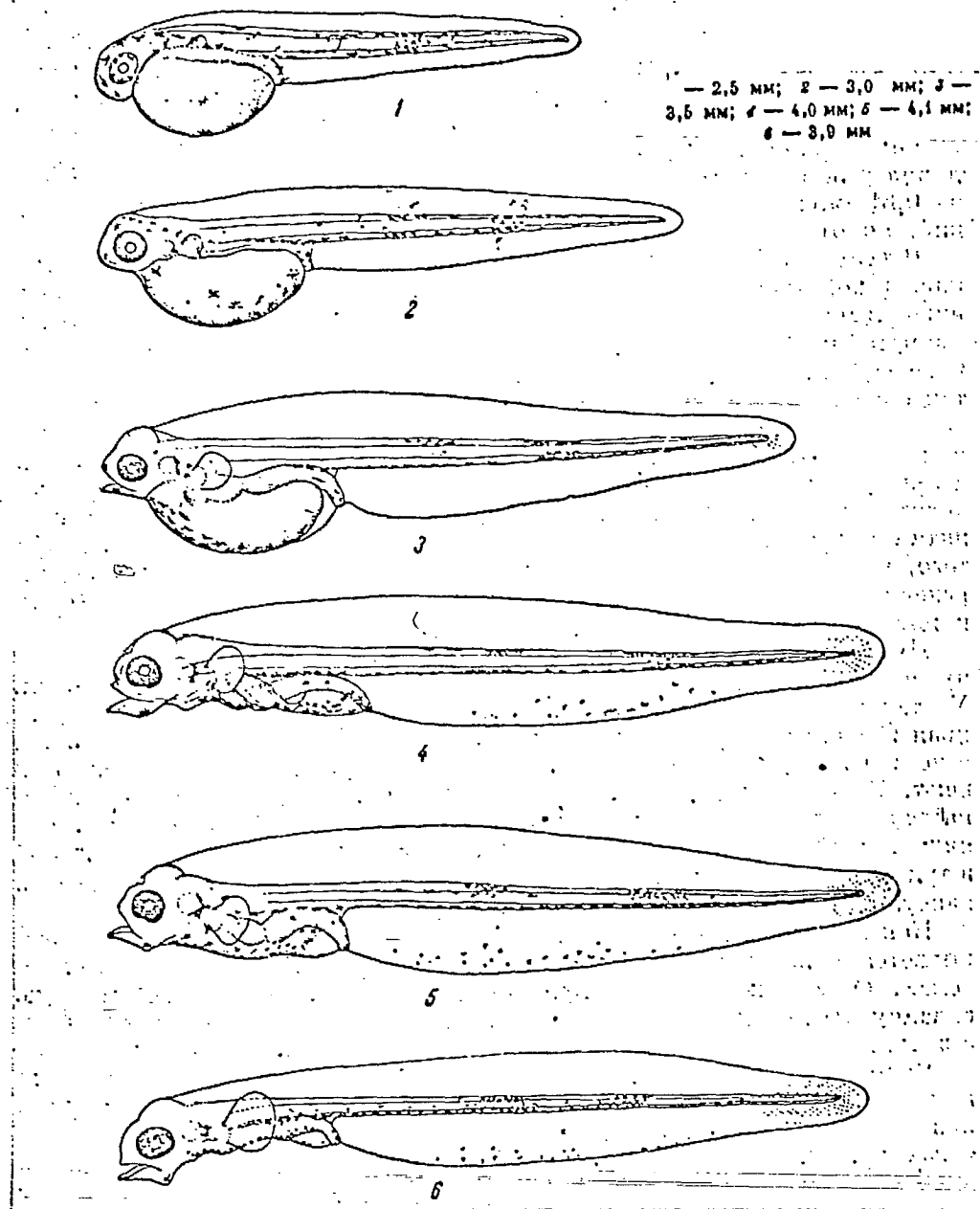
Stage of development	Temperature, in °C			Age		Temperature			Age	
	from	to	aver- age	days	hours	from	to	average	days	hours
	Beginning of hatching									
Mass hatching										
Yolk sac has been absorbed										
	+3,8	+10,0	+5,9	13	15	+13,3	+16,0	+10,1	11	21
	+12,0	+16,2	+15,3	7 суток после выклева	—	+14,0	+16,4	+15,2	6 суток после выклева	—

were situated on the upper edge of the tail and two on the lower edge. These rows were not always distinct, and their isolation was occasionally broken by individual cells located between the rows. There were a few melanophores on the intestine and the rectum. Neither the yolk nor the eyes were pigmented. Prior to hatching, the branched yellow chromatophores and dark melanophores formed an accumulation /361 in the shape of a band on the middle of the tail. Neither the yolk nor the eyes were pigmented. At the end of embryonic development there appeared on the head of the embryo a large number of hatching glandulae, of which there were noticeably more than at the same stage in the banded flounder, which resulted from the greater thickness of the egg membrane.

Black flounder prolarvae that had just hatched were smaller than corresponding banded flounder prolarvae (see Table 58 and Figure 53), and at first stayed on the bottom. Only a few hours after hatching did they begin to rise to the upper layers of the water. When the prolarvae rose up, they performed oscillating movements with their tails and spiraled, corkscrew-like, around their own axes, from right /362 to left, i.e., counterclockwise. Remaining for a time at the surface of the water, the prolarvae turned head downwards and, under the weight of the yolk sac, with the tail fully at rest, sank passively to the bottom.

The length of the first live prolarvae that had just hatched, in various series obtained from different brood stock, ranged from 2.55 to 3.4 mm and averaged 3.10 mm. According to Kurata's data (1956) the length of prolarvae that had just hatched was 3.5 mm. Their heads were inclined slightly

Figure 53- Prolarvae
and larvae
of L.
obscura



downwards, and the forward ends of the heads were free. There was no mouth. The yolk sac was as transparent as glass, and in the shape of an elongated oval. In live prolarvae its length varied from 0.69 to 0.87 mm and averaged 0.81 mm; the height range was from 0.41 to 0.46 mm, averaging 0.45 mm. The tail was short, but was relatively longer than in the banded flounder.

There were 10 to 11 myotomes in the trunk and 29 to 30 in the tail. The rectum was short and comparatively wide. The eyes were colourless or slightly pigmented. The body was heavily pigmented. Lemon-yellow chromatophores and dark melanophores were scattered on the head and back and on the upper edge of the tail. On the middle of the tail (on the 17th to the 20th myotomes) a group of such cells formed a sharply striking band-spot. The upper stripe bounding it was located on the 18th to the 22nd myotomes, while the lower corresponding stripe was on the 18th to the 25th myotomes, i.e., it went somewhat further towards the end of the tail than the upper stripe. A few chromatophores entered the dorsal fin fold from the upper stripe. An indistinct spot was outlined on the middle of the forward half of the tail (on the 8th to the 11th myotomes). In addition, a discontinuous double row of cells passed along the lower edge of the forward half of the tail, and there were cells above the intestine, on the rectum and on the lower half of the yolk (see fig. 53, 1).

Prolarvae two days old (see fig. 53, 2) and those that had just hatched were at this moment at the same stage of development. In both, the head separated from the yolk to the level of the rear edge of the eye. The oral cavity was outlined. The pectoral fins increased in size and moved slightly forward. They were still immobile. The eyes became slightly dark. Yellow pigmentation changed little in comparison with that in the preceding stage. There was a noticeably greater change in the melanin pigmentation. An

accumulation of melanophores appeared on the head, above the brain and oral cavity; three to four cells appeared along the sides of the head behind the eyes, and between the auditory capsule and the pectoral fins.

As before, the band on the tail was distinct, and a forward band that had previously been only outlined on the 8th to the 11th myotomes stood out more sharply. Starry melanophores, extended in a lateral direction, branched out from both forward bands into the dorsal fin fold, and a rear band extended similar outgrowths into the anal fold.

A double row was clearly visible above the rear portion of the intestine; a similar row was outlined on the lower edge of the tail. There was a group of cells on the rectum and around the anus. A few scattered cells were retained on the sides of the trunk and on the tail. A large number of starry melanophores was visible on the lower and forward half of the yolk. Three days after hatching, at water temperatures of 6 to 9.4°, averaging 8.1°, the total length of the prolarvae ranged from 3.20 to 3.70 mm (see Table 57).

After five days the total length of live prolarvae varied from 4.07 to 4.19 mm, and averaged 4.12 mm (see fig. 53, 3). Their heads were freed from the yolk sac to the level of the rear edge of the auditory capsule or to the pectoral fins. The mouth and the intestine opened and intercommunicated. The pectoral fins grew to 0.24 mm and became mobile. The rudiments of two pairs of gill arches were noticeable. The tail lengthened, so that the distance from 364

the end of the snout to the insertion of the anal fin now represented on the average 35.5% of the length of the body instead of the 40% [in prolarvae] that had just hatched. A radiance appeared in the ^{fin}fold around the anus. The prolarvae became noticeably more mobile; more and more frequently they rose from the bottom to the surface and moved progressively in a horizontal direction. The eyes darkened and took on a greenish, metallic hue. Yellow chromatophores, as before, were located on the head, around the eyes and below the head, above the oral cavity. A row of chromatophores was visible on the back, above the intestine, and on the lower edge of the tail, as well as on the rectum. An accumulation of chromatophores was retained on the 8th to the 9th and the 17th to the 20th myotomes of the tail (see fig. 77, 7).

Melanin pigment was distributed in the same way as in the preceding stage, with the difference that scattered cells on the head, trunk and tail completely disappeared. Cells were clearly visible on the upper and lower jaws, and in front of the bases of the pectoral fins, as were bands on the tail.

After six days, only remnants were left of the yolk sac (see fig. 53, 4). Active feeding began. The prolarvae ingested small particles of raw or cooked chicken egg yolk placed in the aquarium. The intestine was curved. The pigmentation of the body, with the exception of the yolk sac, was similar to that in the preceding stage. The melanophores of the yolk sac, as a result of the reduction in the latter's volume, converged and on the lower surface of its remnants formed a dark, broad stripe.

Table 57

The Sizes and Correlation of the Body Parts of Prolarvae and Larvae of *L. obscura*

Age, in days	Length		Percentage of length of body					Percentage of length of head		
	total	body	aA	H	A	D	IC	O	aO	
Prolarvae that have just hatched										
Только что выклюнувшиеся предличинки	2,67	2,56	39,4	6,05	5,8	4,1	19,3	36,0	17,1	
1	(2,32—3,21)	(2,16—3,10)	(38,3—42,3)	(5,2—7,2)	(3,19—8,06)	(2,66—5,65)	(17,8—21,3)	(33,3—42,9)	(13,05—19,55)	
2	2,79	2,69	37,1	6,1	5,9	4,8	17,6	38,3	19,7	
	(2,62—3,17)	(2,53—3,06)	(36,0—36,3)	(4,9—7,3)	(5,0—6,6)	(3,1—5,7)	(17,3—18,95)	(34,8—42,0)	(17,4—21,0)	
3	3,14	3,03	36,7	5,4	6,6	5,6	16,6	39,5	19,1	
	(2,83—3,40)	(2,59—3,29)	(33,6—41,4)	(4,9—6,5)	(3,5—7,7)	(2,6—7,4)	(15,05—19,5)	(35,6—43,2)	(15,9—21,4)	
4	3,53	3,39	35,5	4,6	7,1	6,4	15,6	40,2	21,1	
	(3,20—3,70)	(3,08—3,54)	(34,2—36,6)	(4,5—5,8)	(6,1—9,4)	(4,8—8,3)	(14,3—16,2)	(37,8—43,2)	(18,2—23,8)	
5	3,22	3,34	37,2	5,2	8,5	7,2	16,9	42,9	16,6	
	(2,89—3,40)	(2,75—3,20)	(34,3—40,6)	(5,0—6,0)	(6,4—10,3)	(5,2—7,8)	(15,50—18,0)	(36,7—46,5)	(16,3—22,9)	
6	3,38	3,22	34,5	5,2	8,4	6,9	15,4	41,9	23,2	
	(3,20—3,41)	(3,04—3,27)	(32,8—35,7)	(4,3—5,3)	(7,9—11,0)	(6,4—8,1)	(15,0—15,7)	(40,9—43,2)	(15,9—23,8)	
7	3,26	3,10	34,5	4,8	—	—	16,0	—	—	
	(3,24—3,29)	(3,08—3,13)	(33,1—36,3)	(4,4—5,2)	(8,2—10,3)	(5,97—8,1)	(15,44—16,5)	(45,2—46,5)	(18,6—19,0)	
8	3,17	3,01	35,6	5,7	8,5	6,8	16,0	45,9	18,4	
	(3,13—3,55)	(2,97—3,38)	(33,3—33,0)	(4,0—5,2)	(8,1—8,8)	(6,2—7,4)	(14,29—16,65)	(45,2—45,4)	(18,2—19,0)	
9	3,29	2,6	34,0	4,5	8,0	6,2	14,7	46,0	16,1	
	(3,38—4,28)	(3,24—4,07)	(32,1—39,2)	(4,1—4,9)	(7,8—8,4)	(6,0—6,4)	(14,2—15,25)	(45,5—46,5)	(15,9—16,3)	
10	3,94	3,72	34,9	—	—	—	14,4	45,5	15,9	
	(3,54—4,23)	(3,36—4,01)	(32,0—36,2)							
11	4,16	3,94	34,4	3,5	8,9	8,9	15,79	41,2	15,1	
	(3,82—4,33)	(3,58—3,09)	(32,9—37,0)	(3,2—4,8)	(7,9—10,2)	(7,2—9,0)	(13,76—17,7)	(37,8—45,9)	(13,3—16,3)	
15	4,15	3,91	35,2	3,7	8,9	8,2	14,8	40,7	14,9	
	(3,92—4,33)	(3,71—4,10)	(32,7—37,4)	(3,5—3,9)	(7,9—9,7)	(7,3—8,8)	(14,20—15,75)	(38,4—43,7)	(13,0—17,3)	
	(8,23—8,67)	(7,97—8,16)	(32,6—36,1)	(26,8—27,0)	—	—	—	(26,0—25,7)	(21,1—21,4)	

After seven days only traces remained of the yolk sac. The length of live prolarvae averaged 4.37 mm. The curve in the intestine became more pronounced.

With the aid of their mobile pectoral fins and their long tails, the larvae swam rapidly in all directions and very vigorously devoured grains of chicken egg yolk. In many larvae the intestine was literally filled to the limit with food.

The larvae were phototropic: in vessels that were set out half in bright sunlight, they kept to the illuminated portion on the bottom.

There were no significant changes in the structure of the larvae in the course of eight to ten days.

After 11 days almost no trace remained of the yolk sac (see fig. 53, 5). The length of live larvae averaged 4.5 mm.

In spite of the fact that they were fed with chicken egg yolk, the prolarvae grew very slowly. In four days they grew 0.12 mm, whereas in the first days after hatching, their length in one day alone increased by 0.50 to 0.60 mm. It was evident that the yolk ingested by the larvae was not assimilated and, passing through the intestinal tract, was eliminated.

The gill apparatus was still not formed; five pairs of gill arches appeared, but there were still neither gill filaments nor rakers, and the breathing was of an embryonic nature. No formed blood elements were visible. Yellow

chromatophores were situated in the same way as in younger prolarvae, but the cells themselves had become less branched, and some had acquired the appearance of dots. It was because of this that the yellow pigment pattern lost the brightness that was peculiar to it in the early stages of development. As before, a small group of little yellow stars remained on the head, and a double row of sparsely scattered granules, on the back and on the forward portion of the head. The intervals between the cells of these rows were not uniform. A few starry yellow chromatophores were visible above the intestine, on the abdomen, on the rectum and on the bands of the tail. In addition, there were spots varying in size and form on the dorsal fin fold above the bands, and in some specimens there was also a spot on the ventral fin fold.

At this stage, the melanophores were more distinctly visible than previously, but as before, emerged most clearly 365 after fixation. Their distribution on the trunk and tail did not change. In connection with the disappearance of the yolk sac there appeared a short row of melanophores on the isthmus, and on the lower surface of the abdomen, as well as many scattered cells on the abdomen's lower lateral surface. In many specimens a row of melanophores was visible in the depth of the body above the chord.

Fifteen days after hatching, at an average water temperature of $+8.7^{\circ}$ the growth of the larvae in our experiments almost ceased (see fig. 53, 6).

In Kurata's experiments (1956) 45 days after hatching at a water temperature of about 6.8° the larvae reached a length of 6.6 mm. They were asymmetrical -- a third of the left eye rose above the profile of the head, and the corner of the mouth was located in front of the eye (see fig. 54). The rectum was bent and its end was directed towards the head, but the abdominal cavity was still not closed.

The height of the body represented about 20% of its length. The urostyle was sharply curved, and its end protruded outwards. The rays of the anal and dorsal fins were formed, with the exception of the last rays. The tail fin was homocercal and contained 17 rays.

The pigmentary pattern was of an entirely different character as compared with that in younger larvae. On the body and the fins pigment spots formed that were characteristic of flounder larvae. There were four well-developed forward spots, a fifth rear spot in the upper row, and three spots in the lower row. Differently outlined stripes corresponding to these formed on the rays of the fins. In addition, there were two accumulations (spots) on the middle line of the rear half of the tail, along with a few more or less distinctly formed upper lateral spots and two lower lateral spots. Moreover, a group of melanophores was visible at the base of the tail fin rays, on the head and on the rectum.

Highly characteristic were two groups of pigmentary cells on the lower jaw; of these, one, which was more compact, was located in the middle, and the other, wide-spaced, on the corner of the lower jaw.

A larva 8.23 (7.97) mm long was asymmetrical (see fig. 54, 2). Its left eye was much higher than its right and rose for $1/3$ [of its diameter] above the profile of the head. The larva was leaf-shaped, and the height of its body represented 26.7 [%] of its body length. The mouth was small, slanting, and slightly asymmetrical, and its corner was situated in front of the eye. The upper jaw was noticeably curved.

The urostyle was sharply curved, and its end, as in the preceding larva, protruded outwards. Under it was situated an almost symmetrical tail fin, in which there were 19 rays. The dorsal and anal fins were formed, and their rays, with the exception of the first two, were clearly visible. In the dorsal fin there were 66 rays together with those in front, and 46 to 47 rays in the anal fin. There were 37 to 38 vertebrae. Small ventral fins appeared. The pectoral fins were surrounded by a fin fold; they were small and their peaks extended somewhat beyond the middle of the abdominal cavity. The gill apparatus was not fully formed, and the gill filaments and rakers were rudimentary.

Pigmentation consisted of stripes and spots on the upper and lower edges of the tail and on the basal, and after a short interval, on the fin, rays of the dorsal and anal fins.

In the upper row there were five spots, of which the most distinct were the third and fourth (counting from the front); the second and fifth were less clearly defined, while the forward spot was represented by only one cell. In the lower

row there were only three fully developed spots. They corresponded to the middle three stripes of the upper row. The rear stripe above the last rays of the anal fin was indistinct and represented by only two cells. In addition, less developed intermediate spots were visible on the rays, between the third and fourth in the upper row and between 366 all three in the lower row. A row of sparsely scattered melanophores began at the level of the anus and passed above the vertebral column of the tail. There were a few smaller cells on the lower edge of the caudal peduncle.

Accumulations of melanophores were visible above the brain, in various areas of the gill cover, on the snout, in the corner of the mouth, and between the branches of the lower jaw; on each hyomandibular there was one large cell. A compact row of melanophores, accompanied in its rear portion by two short rows on each side, passed along the central line of the abdomen. Two short rows convergent in front were visible on the isthmus.

In addition, the following were visible on the surface of the trunk: surface melanophores behind the gill cover; a spot of the middle lateral row immediately behind the centre of the tail; the rudiments of the upper lateral 367 and lower lateral rows in the forward portion of the tail, and individual cells on the surface of the remaining part of the body. There was a clearly outlined spot in the proximal portion of the central rays of the tail fin.

A larva 8.67 (8.26) mm long (see fig. 54, 3) looked older in its degree of development. The height of its body

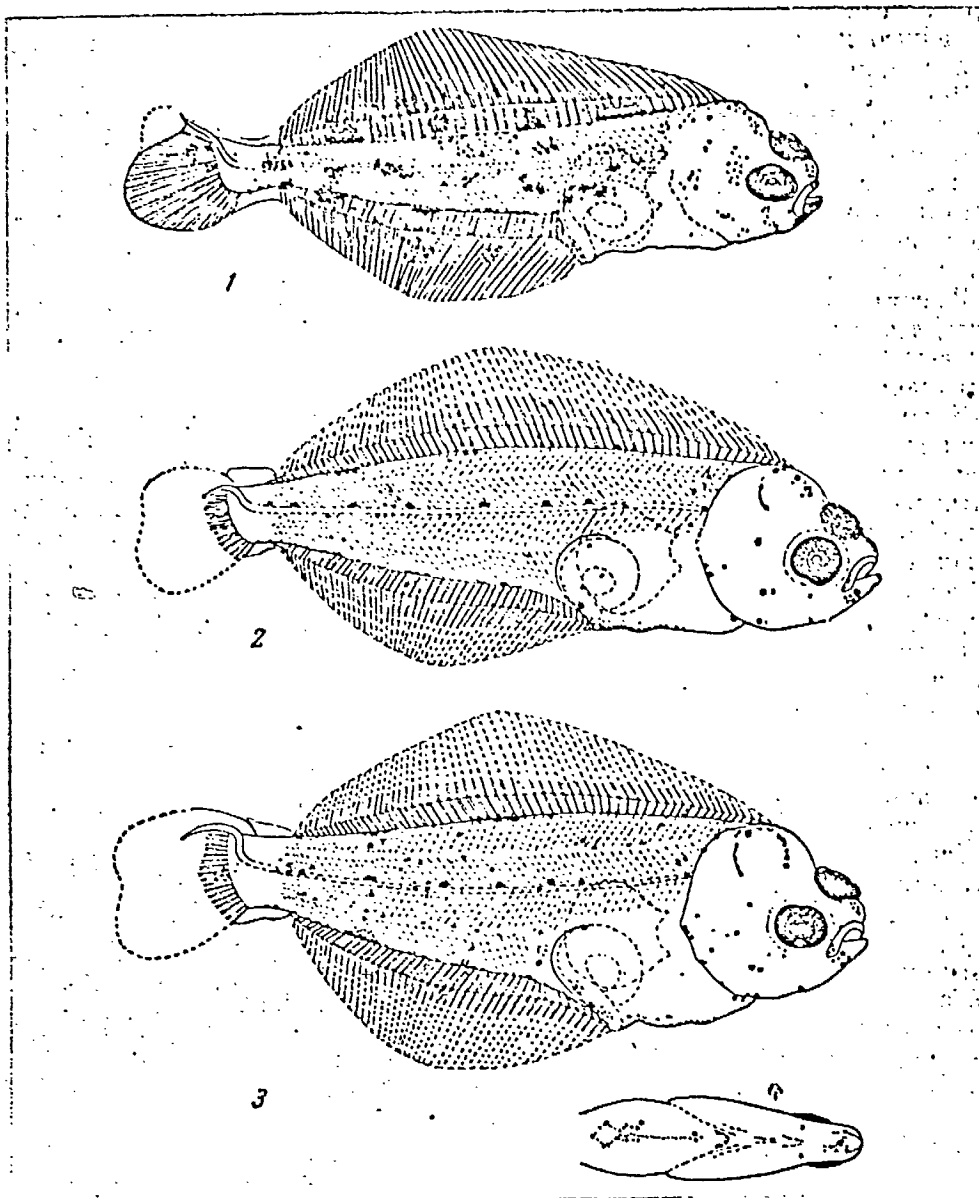


Figure 54- Larvae of *L. obscura*.

1- 6.6 (after Kurata); 2- 8.23 mm; 3- 8.67 mm (original)

represented 26.9% of its length. Half of the left eye had passed to the right side. As before, the urostyle protruded beyond the limits of the caudal peduncle. The dorsal fin began above the forward portion of the large brain and fell somewhat short of the eye. There were 61 to 62 rays in the dorsal fin and 47 in the anal fin. As previously, the remnants of the embryonic fold were visible on the edges of the caudal peduncle. There were no rays in the pectoral fins. There were 36 to 37 vertebrae with the urostyle (the first was not

entirely clear).

In spite of the fact that the larva that we are describing was caught in the upper layers of the water, its pigmentation was asymmetrical; the colour on the right side, as compared with that in the preceding stage, became noticeably more pronounced through the appearance of a large number of spots in staggered rows. The stripe-spots on the upper and lower rows of the tail were more distinct at this stage. The pigmentation of the head had the same appearance as in the preceding stage.

The left side became paler. The pigmentary cells on it, with the exception of three spots in the lower row and two in the upper, completely disappeared.

According to Kurata's data, the metamorphosis of larvae off the coast of Japan is completed in June at a length of 8 mm. In October juvenile fish reach 59 mm in length. In Soviet waters, as may be seen from the above, the metamorphosis of black flounder larvae is completed at larger sizes, evidently at about 9 mm.

The sizes and correlation of the individual body parts of the larvae that have been described are given in Table 59. The changes in the absolute sizes of individual body parts and in the proportions of growing black flounder prolarvae and larvae are subject to the same regular patterns as in other flounders and particularly in the banded flounder, i.e., the distance from the end of the snout to the insertion of the anal fin gradually decreases, while the tail increases in size; after absorption of the yolk sac the ratio of AA to the length of the

body decreases to 33 to 35%. The relative sizes of the head also decrease, and the eyes increase in size. Towards the moment of formation of the rays in the fins the head again increases in size, while the dimensions of the eyes greatly decrease.

It should be noted that the eggs of the black flounder are of the bottom type, and that their membrane is fairly thick and slightly sticky. The adhesive, mucous layer characteristic of Japanese flounder eggs is absent. The yolk is of a compact consistency and has an oily lustre. The blastodisc is large; according to this feature, black flounder eggs should be classed with the group of polyplasmatic eggs. Embryonic development at a water temperature of 2.4° lasts for about 21 to 22 days; at a water temperature of about 0° it continues for 42 days, and the prolarvae appear in plankton, evidently, at the end of April and beginning of May.

Eggs in various stages of embryonic development withstand, with no interruption in development, being frozen in ice and above-zero temperatures of up to 7° , in later stages up to 7° [sic], in still later stages up to 10° , and, prior to hatching, briefly even up to 16° .

The great plasticity of black flounder eggs, in comparison with those of the banded flounder, is fully in conformity with changing temperature conditions during the period of reproduction. Spawning begins at a below-zero temperature and ends when the temperature is above 0° .

As is the case with the banded flounder, the period most sensitive to an increase in temperature is that of cleavage.

Cleavage takes place according to the usual pattern. Segmentation of the embryo begins after the closing of the blastopore. The tail bud forms when there are 17 to 18 myotomes, and separation of the tail occurs when there are 25 myotomes.

Prior to hatching, the embryo makes almost a turn 368 and a half around the yolk. The prolarvae hatch with their heads slightly separated from the yolk, without a mouth, and with rudimentary pectoral fins, unpigmented or slightly pigmented eyes and a large yolk sac. Their length varies from 2.32 to 3.21 mm. There are 10 to 11 myotomes in the trunk and 29 to 30 in the tail. After hatching, the prolarvae at first usually lie on the bottom, and then, using the oscillations of their tails and by rotating the body around its own axis, they frequently rise up.

Absorption of the yolk sac at an average water temperature of 8.7° is completed in 15 days. The length of the larvae at this time varies from 3.92 to 4.33 (3.71 to 4.10) mm.

The passage of the left eye to the right side at a temperature of 6.8° begins 45 days after hatching, when the larvae are about 6.6 mm long; metamorphosis is completed off the coast of Japan at a length of 8 mm, and in Soviet waters, at a length of about 9 mm.

Yellow chromatophores and dark melanophores form two bands on the tail, which divide it into three almost equal portions.

A Comparison of Species of the Genus Liopsetta

As indicated above, the genus Liopsetta incorporates four species -- L. glacialis, L. pinnifasciata, L. putnami and L. obscura. The closest, morphologically and ecologically, are the first three species (they reproduce in winter at a water temperature of less than 0°). The black flounder -- L. obscura -- occupies a special place. Morphologically and ecologically, it deviates noticeably from the pattern of the first three species and reproduces in the early spring at a higher temperature (about 0°). L. glacialis and L. pinnifasciata, which are highly similar in their adult state, are also very similar in various stages of development.

The eggs of the arctic and banded flounder are pelagic and have a small perivitelline space. Their membrane is thin. The sizes of the eggs are similar (1.20 to 1.60 mm in L. glacialis and 1.43 to 1.61 mm in L. pinnifasciata).

In both species embryonic pigment consists of thickly scattered, comparatively large cells, which upon further development group into a single band located on the middle of the tail, and a row of cells above the intestine and on the lower edge of the tail (see figs. 48, 51 and 52).

Side by side with common features there are also the following differences: arctic flounder prolarvae and small larvae (up to the formation of rays in the dorsal and anal fins) are larger than banded flounder prolarvae and larvae; towards the moment of absorption of the yolk sac the distance from the end of the snout to the insertion of the anal fin is shorter in arctic than in banded flounder, and the tail is longer. Embryonic pigmentation is extremely similar in both

species; in arctic flounder prolarvae it is retained longer, and the larval pigmentation (a band) accordingly appears later. The band on the tails of arctic flounder larvae is less distinct and is shifted somewhat backwards.

A different picture is revealed when the eggs, prolarvae and larvae of the arctic, banded and black flounder are compared.

In contrast to those of the arctic and banded flounder, the eggs of the black flounder are comparatively small (0.78 to 0.94 mm); the membrane is thick and sticky. During their development, black flounder eggs remain near or on the bottom. The yolk is compact and of a light yellowish colour. The blastodisc is high and wide; its height represents about $\frac{1}{3}$ of the diameter of the yolk, whereas in the banded flounder the relative sizes of the blastodisc are noticeably smaller. The embryos of these species also differ in their structure. The black flounder embryo is comparatively fat; prior to hatching, because of the small size of the yolk, it makes 369 almost a turn and a half around the latter, whereas in the case of the banded flounder it is thinner and makes only one turn around the yolk before hatching.

Black flounder prolarvae that have just hatched are smaller than corresponding banded and arctic flounder prolarvae. A similar proportion is retained in all succeeding stages.

The yolk sac in black flounder prolarvae is smaller than in the species under comparison and is resorbed when the larvae's bodies are shorter: in the black flounder, when it is 3.71 to 4.10 mm, or an average of 3.91 mm, long; in the banded flounder, at a length of 5.27 to 5.57 mm, or an average

of 5.42 mm, and in the arctic flounder, when it is about 6.3 mm long.

Table 58

Correlation of Sizes of Body Parts of Prolarvae of
L. obscura and L. pinnifasciata (in mm)

Stage of development	Species	Length		% of Length of head				* LC		% of length of head
		total	body	aA	H	D	zh	LC		
Head separated to the level of the middle of the rear edge of the eye.....	1*	3,02	2,94	37,63	5,32	6,02	5,17	17,33	36,5	
	2**	4,89	4,69	41,77	4,62	7,82	7,00	17,17	37,8	
Head separated to the level of the rear edge of the auditory capsule and the pectoral fins...	1	3,59	3,39	35,5	4,58	7,15	6,41	15,29	40,5	
	2	5,11	4,89	40,5	4,67	7,85	7,74	13,54	30,83	
Larvae are approaching the moment when the absorption of the yolk sac is completed.....	1	4,15	3,91	35,2	3,73	8,98	8,28	14,94	40,76	
	2	5,74	5,42	39,01	4,69	7,60	6,9	14,3	31,7	

* 1 - L. obscura.
** 2 - L. pinnifasciata.

As may be seen from the data in Table 58, the relative sizes of the distance from the end of the snout to the insertion of the anal fin are less in the black than in the banded flounder, while the tail is correspondingly longer, which is in direct relation to the nature of movement.

The head of the black flounder, and especially its eyes, are relatively larger than in the banded flounder.

The prolarvae and larvae of the arctic and banded flounder also differ from black flounder larvae in their type of pigmentation: the former [i.e., the arctic and banded flounder] have only one band on the tail, and in both species.

* Translator's note: See Translator's note on p. 691.

it is located on the middle or almost on the middle. In the black flounder there are two such bands, and they divide the tail into three almost equal portions.

Thus the black flounder in all stages of its development differs sharply in its morphology from the arctic and the banded flounder. These differences, moreover, are so marked that it is difficult to class these species with one genus. It is evident that the genus Liopsetta artificially unites two groups of far, and perhaps even genetically, different species: L. glacialis, L. pinnifasciata and L. putnami on the one hand and L. obscura on the other. The question arises as to the possibility of segregating the latter species into another genus. Hubbs (1915, fide Norman, 1934) separates L. obscura into the genus Careus.

In the nature of the development of its eggs, prolarvae and larvae the black flounder is much closer to the Japanese flounder Pl. yokohamae, and even closer to the winter Ps. americanus, than to the banded or the arctic flounder.

The eggs of these species are of the bottom type and are comparatively small; in the black and winter flounder they are somewhat larger than in the Japanese flounder. The membrane of the eggs is thick and sticky. In Japanese flounder eggs 370 it is covered with an adhesive, mucous layer; this layer is absent in black and winter flounder eggs, and therefore the latter's adhesiveness, particularly towards the close of embryonic development, is much less evident.

In all of the [eggs] of the species under comparison the yolk is compact; in accordance with the sizes of the eggs, it is larger in the black flounder. Hence black flounder

prolarvae that have just hatched are longer than corresponding Japanese flounder, but shorter than winter flounder [at the same stage of development] (3.0 to 3.5 mm). The blastodisc is large, but in the black and winter flounders it is somewhat smaller than in the Japanese flounder. From their plasma content, the eggs of all three species may be classed with the group of polyplasmatic eggs.

The prolarvae of all species hatch with partially absorbed, but still large, yolk sacs; their heads are freed from the yolk to the level of the forward or rear edge of the eye. The smaller sizes of the Japanese flounder prolarvae are also retained in all succeeding stages. We unfortunately have no data on the proportions of the prolarvae of the American winter flounder, and are therefore compelled to compare only two of our own species (see Table 59).

In the black flounder the tail is relatively shorter than in the Japanese flounder; the head is smaller at the hatching stage, but subsequently adjusts, and towards the moment of resorption of the yolk sac appears to be even somewhat larger. In black flounder prolarvae that have just hatched the eyes are relatively smaller than in the Japanese flounder, and in larvae towards the moment of absorption of the yolk sac they become almost identical. The prolarvae and larvae of the black and Japanese flounders are similar in pigmentation, and in this respect differ from the winter flounder. In the first two species there are two bands on the tail which divide it into three portions, while in the winter flounder there is one such band.

Table 59

Correlation of the Sizes of Body Parts of Prolarvae and Larvae
of L. obscura and Ps. yokohamae (in mm)

Stage of development	Species	Length		% of length of body				% of length of head
		total	body	aA	lzh*	zh	lc	o
Prolarvae that have just hatched.....								
Larvae approaching the moment when absorption of the yolk sac is completed.....								
	1*	2,67	2,56	39,40	29,32	14,92	19,30	36,00
	2**	2,55	2,45	36,60	25,90	11,30	20,50	37,80
	1	4,15	3,91	35,20	—	—	14,80	40,70
	2	3,95	3,79	29,90	—	—	14,60	41,50

* 1 — L. obscura.
** 2 — Ps. yokohamae.

* Translator's note: See "Translator's note", p. 691.

Although the pigmentation of the black and Japanese flounders is generally similar, it nonetheless has features that are proper to each species: in the black flounder the rear band is continuous and is located almost on the middle of the tail, while in the Japanese flounder it consists of two stripes parted along the central line of the tail and shifted somewhat backwards. After the absorption of the yolk sac the number of melanophores on the lower half of the abdomen in black flounder larvae is much greater than in the Japanese flounder. The single band of the winter flounder is continuous, is situated on the middle of the tail, and corresponds to a similar band in the banded and arctic flounders and to the rear band in the black flounder.

To sum up, it may be noted that in egg diameter, membrane structure and size of blastodisc the closest resemblance exists between the black and winter flounders. 371 In its type of pigmentation, and the relative sizes of the head and eyes of its prolarvae and larvae, the black flounder resembles ~~the Japanese~~ the Japanese flounder; it differs somewhat from the latter, however, in the length of its tail (see Table 59).

In the ecology of its reproduction and development, as indicated above, the black flounder most resembles the winter flounder -- both species reproduce towards the end of winter and beginning of spring at a temperature close to 0°.

We are unfortunately unable to investigate and compare full series relating to further development of the species

under consideration. The data given above are insufficient to solve the complex problem of the interrelations of the black, Japanese, and winter flounders.

It is difficult to say whether the resemblance in the structure of the eggs and larvae of the foregoing species indicates kinship or is convergent. It is quite possible that these three species (as a result of adaptation to reproduction and development in similar ecological conditions) originated independently of each other, that is, parallelly. The following pairs of flounders had common ancestors: the black and the banded, the winter and the smooth, and the Japanese and the yellow-striped.

The only fact of which there is no doubt is the origin of bottom eggs from pelagic eggs. To judge from the presence of an additional adhesive layer and a large quantity of plasma on the membrane of Japanese flounder eggs, it may be assumed that the eggs of the Japanese flounder are the most specialized and probably the oldest, and that they have deviated the most from the original pelagic-type of egg.

Another species morphologically and ecologically close to the banded flounder is the smooth flounder L. putnami. This arctic-boreal form dwells off the Atlantic coast of North America (Bigelow and Schroeder, 1953). Its distribution is confined to offshore shallow areas with severe hydrological conditions. The geographical distribution of the smooth flounder appears to be a continuation of the geographical range of the arctic flounder, and in many features resembles that of the banded flounder. The geographical ranges of the smooth

and banded flounders, owing to the chilling action of the Labrador Current off the American coast and of the Kamchatka Current off the Pacific coast of Asia, are characterized by winter conditions that are no less severe than those in the geographical range of the arctic flounder. Information on L. putnami is even more meager than that on L. glacialis. In literature on the subject there is only an indication of finds of almost ripe females in December and of females, at the beginning of March, that had already laid their eggs. These data permit us to assume that it [presumably L. putnami] spawns at the end of December and in January and February, i.e., at the same time as the banded and arctic flounders. There are no data on the development of the eggs of L. putnami, and its eggs and larvae are unknown. Taking into consideration the morphological and ecological similarity of the species under comparison, it may be assumed that its [L. putnami's] eggs are also pelagic and not as large as those of the arctic flounder, but closer to the eggs of the banded flounder.

The great similarity of the eggs, prolarvae and larvae of the banded and arctic flounder indicate their undoubted genetic proximity.

Reproduction and development (in any case, the beginning) in all representatives of the genus Liopsetta, with the exception of L. obscura, are confined to the coldest time of the year. This indicates that this genus was probably formed under severe arctic conditions, possibly in the Polar Basin itself. Of the four species of the genus Liopsetta there

is only one that dwells in the High Arctic -- L. glacialis. Its geographical range is more extended than that of any of the other species of this genus. It is a euryhaline form, and spawns in December and January and partly in February, i.e., at the coldest time of the year¹, near coasts in slightly freshened water. It is possible that the 372 original form of this entire genus was one resembling L. glacialis, which evidently emerged at the beginning of the Quaternary Period. The periodic freshenings and salinifications that took place at this time could have led to the formation of a euryhaline form which became adapted to living and reproducing under the severe hydrological conditions of the freshened zone. Having occupied the offshore shallow zone and found there virtually no competitors among the other flounder, it spread widely along the entire arctic coast of Asia, Europe, and America and, finding favourable conditions, moved south along the Atlantic coast of North America as far as the southern area of Munn Bay, and along the Pacific coast of Asia as far as Peter the Great Bay inclusive. Having become adapted to the local ecological conditions of the Arctic as represented by the northwestern areas of the Atlantic and Pacific Oceans, it formed three separate species: L. glacialis, off the arctic coasts of Asia, Europe and America; L. pinnifasciata, off the eastern coast of Asia, and L. putnami off the eastern coast of America.

The capacity for reproducing at a below-zero temperature proved to be so persistent and conservative that L. pinnifasciata

¹
O.A. Avyagina (1953) disclosed sexually mature males in the Laptev Sea in July.

and L. putnami, entering other conditions, continued to retain this peculiarity. Reproduction under these conditions during the period of formation of a genus or species was a necessity and, when climatic conditions changed, it was biologically advantageous. Of the fish with pelagic eggs in Soviet Far Eastern waters, the only one to reproduce in winter is the walleye pollock, and it keeps to the more open areas of the sea. The conditions, however, under which L. glacialis and L. pinnifasciata dwell in Soviet Far Eastern waters evidently do not entirely answer the requirements of these species, since their numbers, in spite of their wide distribution, are relatively low. What we have stated permits us to assume that the geographical distribution of species of the genus Liopsetta is closely associated with the conditions under which they reproduce and develop.

This genus populates waters with a severe winter hydrological regime -- the Pacific coast of Asia, the Arctic coast of Asia and Europe, and the Atlantic coast of North America.

Off the Atlantic coast of Europe and the Pacific coast of North America, where the average temperature in February reaches $+2^{\circ}$, i.e., in places under the influence of warm currents, with a mild winter which is unfavourable for their reproduction and development, species of the genus Liopsetta are absent. Having become adapted to reproduction and development at a below-zero temperature, their eggs during the cleavage period sustain a limited temperature range of only 3 to 4° , while a water temperature of about 3° is

nearly lethal, and the optimum for the initial stages of development (cleavage) is lower than 0° . The winter temperature of the geographical range occupied by the species of the genus under consideration corresponds exactly to that which is necessary for the development of eggs off the Atlantic coast of North America. In winter this temperature extends to 42° north latitude, and off the Pacific coast of Asia, as far as 42.5° . There, where the winter temperature is close to 0° or above, the occurrence of representatives of this genus ceases.

The Genus Glyptocephalus Gotsche

The Long Flounder -- Glyptocephalus stelleri (Schmidt)

With the exception of the indications of P.V. Il'ina (1951) and P.A. Moiseev (1953) regarding the duration of the incubation period under experimental conditions at water temperatures of 15.1 to 16.1 , there is no information on the development of the long flounder. Data on the structure and sizes of eggs developing in the sea are available in studies by P.V. Il'ina (1951) and T.V. Dekhnik (1959). A very brief description of two larvae about 6 mm long is given in a work by T.S. Rass and M.V. Zheltenkova (1948). A more detailed description and illustrations of larvae 15.5 mm long and juvenile fish 53 mm long have been given by T.V. Dekhnik (1959). /373

We obtained material for artificial fertilization from sexually mature specimens caught with Danish seines during navigation in Ussuri Bay in the region of Askol'd Island on the

expeditionary ship Zoolog. In contrast to the other flounder species with which we were concerned, and because of intermittent spawning, usually very little sperm was obtained from one male; therefore to fertilize the eggs taken from one female we had to use the sex products from two or three males. A total of four series was obtained from 13 June to 9 July 1951.

The most successful development took place in the first two series, the results of observations of which have been used as a basis for the description of the development of this species. The eggs of the first series developed at water temperatures ranging from 11 to 16° and at an average temperature of 13.6°. In the second series the eggs developed at temperatures of 13 to 20°, averaging 16.6°. In the sea at this time the temperature of the surface water layers varied from 9.5 to 11.9°. The incubation period in the first series lasted for six to eight days, and in the second, for about five to seven days. According to the data of P. V. Il'ina (1951) and P. A. Moiseev (1953), the embryonic development of the long flounder at water temperatures of 15.1 to 16.1° lasts for about five days, and at an average temperature of 15.7°, about three days.

Ripe, live ovarian long flounder eggs are transparent and fairly large. Their sizes vary from 1.20 to 1.31 mm and average 1.27 mm. The membrane of the eggs is thick, with a large number of folds (see fig. 55) and fits the yolk closely. Eggs placed in water after fertilization floated to the upper layers, where they remained until the end of their development; when the water was slightly freshened they dropped to

the central layers, and some fell to the bottom of the vessel. In the water the eggs quickly swelled, after which their diameter increased to 1.23 to 1.47 mm and averaged as much as 1.36 mm. The yolks were large, from 0.92 to 1.16 mm, and their average size was 1.06 mm.

Long flounder eggs collected at sea had the same appearance and structure as those which had been artificially fertilized. Their diameter, from the measurement of 1,093 specimens collected in various long flounder spawning areas, varied from 1.20 to 1.61 mm and averaged 1.31 to 1.45 mm. The membranes of the eggs were thick, with a large number of folds. In contrast to those on Alaska plaice eggs, the folds of the membranes ran in various directions and caused it [the membrane] to have a reticulate, wavy structure.

The perivitelline space in live eggs represented a narrow aperture, which, after the egg was fixed, as a result of contraction of the yolk increased from 3 to 12%, and averaged 8.6%, of the diameter of the egg. There was no fat drop. The blastodisc was low; its height was 0.14 to 0.21 mm, which represented about 1/5 of the height of the yolk, while the diameter of the base was 0.56 to 0.62 mm, i.e., almost half of the diameter of the yolk. The blastomeres were considerably depressed, and rose only slightly above the surface of the yolk. The diameter of the embryonic disk was small; when viewed from above, it by no means covered the yolk.

The course of development of the eggs of the long flounder is given from the first series (see Table 60).

As may be seen from the data in Table 60, the first prolarvae hatched six days after fertilization. The hatching process did not take place at the same time, but continued for more than a day; the prolarvae that hatched last were, at the moment of hatching, more developed than the first and were 1374 almost at the same stage of development as larvae that had hatched two days previously.

The temperature "threshold" of development that we calculated was equal approximately to 4.9° , and the number of degree-days necessary for embryonic development amounted to about 55, or 1,320 degree-hours.

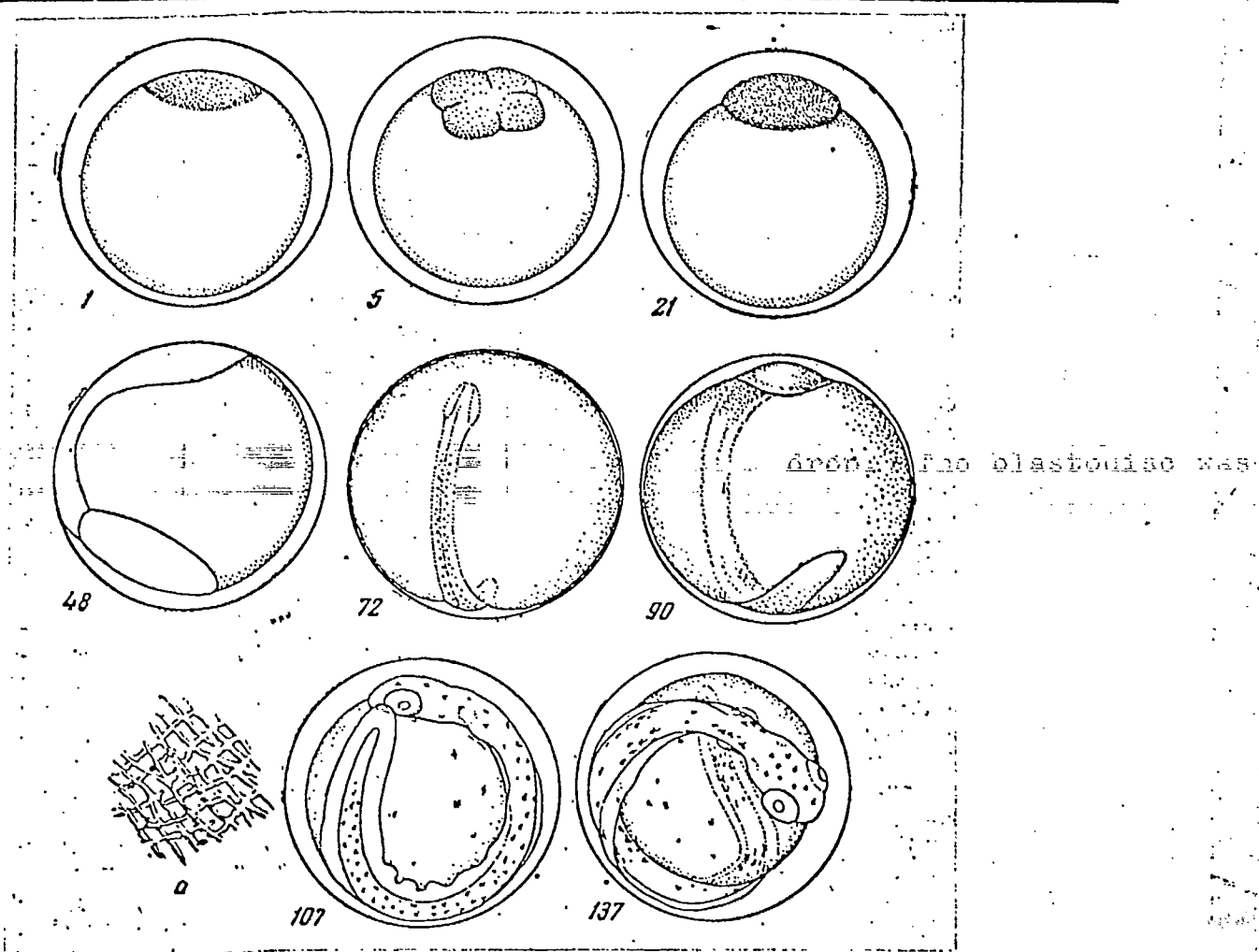


Figure 55 - The development of eggs of Gl. stelleri at a water temperature of 13.6° .

a - structure of membrane. The figures under the illustrations designate the hours of development

Pigmentary cells in the form of scattered dots appeared on the backs of the embryos; they subsequently increased in size, became branched and spread to the head and trunk and the upper and lower edges of the tail. Two rows were visible in outline among the scattered cells in the region of the auditory capsules and along the sides of the trunk. A small group of melanophores was visible on the rear end of the intestine. Prior to hatching, the melanophores that had been scattered previously, and the yellow chromatophores, regrouped in such a way that they formed five bands, of which one was located in the region of the pectoral fins, a second in the area of the anus and three at equal distances from each other on the tail. At all stages of developments, on the bodies of live embryos in the midst of the melanin pigment there emerged bright lemon-yellow chromatophores which disappeared after fixation. It is interesting to note that in contrast to the majority of other species of flounder the embryo of the long flounder lay on the surface of one side of the yolk and did not surround it. / 375

Long flounder prolarvae that had just hatched (see fig. 56) were comparatively large. Their length varied from 4.1 to 5.2 (3.50 to 5.10) mm and averaged 4.64 (4.51) mm. The yolk sac was in the shape of an elongated oval. Its length ranged from 1.22 to 1.38 mm and averaged 1.29 mm; its height varied from 0.49 to 0.57 mm, averaging 0.53 mm. The anus opened on the edge of the anal fin fold far in front of the middle of the body. The distance from the end of the snout to the insertion of the anal fin was short, shorter, in fact, than in all of the other species, and represented only

Table 60

Course of Development of the Eggs of *G1. stelleri* at
 Temperatures Ranging from 11 to 16.4° and Averaging 13.6°

Stage of development	Age in		Pigmentation
	days	hours	
Lastodisc accumulates.....	--	1	--
to 8 blastomeres.....	--	5	--
blastula.....	--	21	--
beginning of gastrula.....	1	6	--
blastoderm covers half of yolk.	1	17	--
embryo with rudiments of optic vesicles.....	2	--	--
blastopore closes.....	2	6	--
eyes have crystalline lenses. About 24 myotomes in body. Kupfer's vesicle.....	2	18	--
beginning of formation of tail bud.....	3	--	Scattered melanophores and yellow chromatophores have appeared on the back and the yolk of the embryo
beginning of separation of tail (beginning of third stage). Auditory capsules have two otoliths.....	3	18	Pigmentary cells on the trunk, head and tail
embryo envelops $\frac{3}{4}$ of yolk. Heart beats, movement appears.....	4	--	Pigmentary cells scattered
embryo completely envelops yolk	4	11	Same
rudiments of pectoral fins. Heart beats 59 to 60 times a minute. Hatching glandulae appear. End of embryo's tail goes beyond the head...	5	17	Pigmentary cells form five bands: one in the region of the pectoral fins, one in the area of the snus, and three on the tail
beginning of hatching.....	6	--	Same
end of hatching.....	8	--	"

31.2 to 36.3%, and an average of 33.9%, of the length of the body. The body was thin, its height representing only 4.1 to 4.9%, and an average of 4.4%, of its length. The eyes were not pigmented. The pigment on the trunk and the tail had the same appearance as in the embryo prior to hatching. It was represented by a faintly outlined accumulation of melanophores on the head, above the pectoral fins and above the anus, and by three more compact bands situated at equal distances from each other on the tail. The last band, which sent branches into the fin folds, fell somewhat short of 376 the end of the tail. Besides the accumulations, scattered melanophores (residual from the embryonic pigmentation) were visible in various places on the trunk and the tail. Large, starry, pigmentary cells were also scattered on the yolk. In live prolarvae, among the melanophores, particularly in the places where they accumulated on the trunk and tail and on the adjacent parts of the fin folds, bright, lemon-yellow chromatophores stood out sharply.

The prolarvae that hatched 12 hours later were larger and more developed than the first (see fig. 56, 2). Their heads straightened, and the volume of the yolk sac noticeably decreased. The length of such prolarvae ranged from 4.62 to 5.20 (4.46 to 5.06) mm and averaged 4.9 (4.74) mm. The yolk sac was 1.06 to 1.33 mm long and 0.53 to 0.57 mm high. The relative values of the distance from the end of the snout to the insertion of the anal fin were shorter than in the preceding [specimens] and represented 30.8 to 32.5%, and an average of 31.7%, of the length of the body.

A day after the beginning of hatching at an ~~average~~ average ^{water} temperature of 16.3°, the total length of the prolarvae

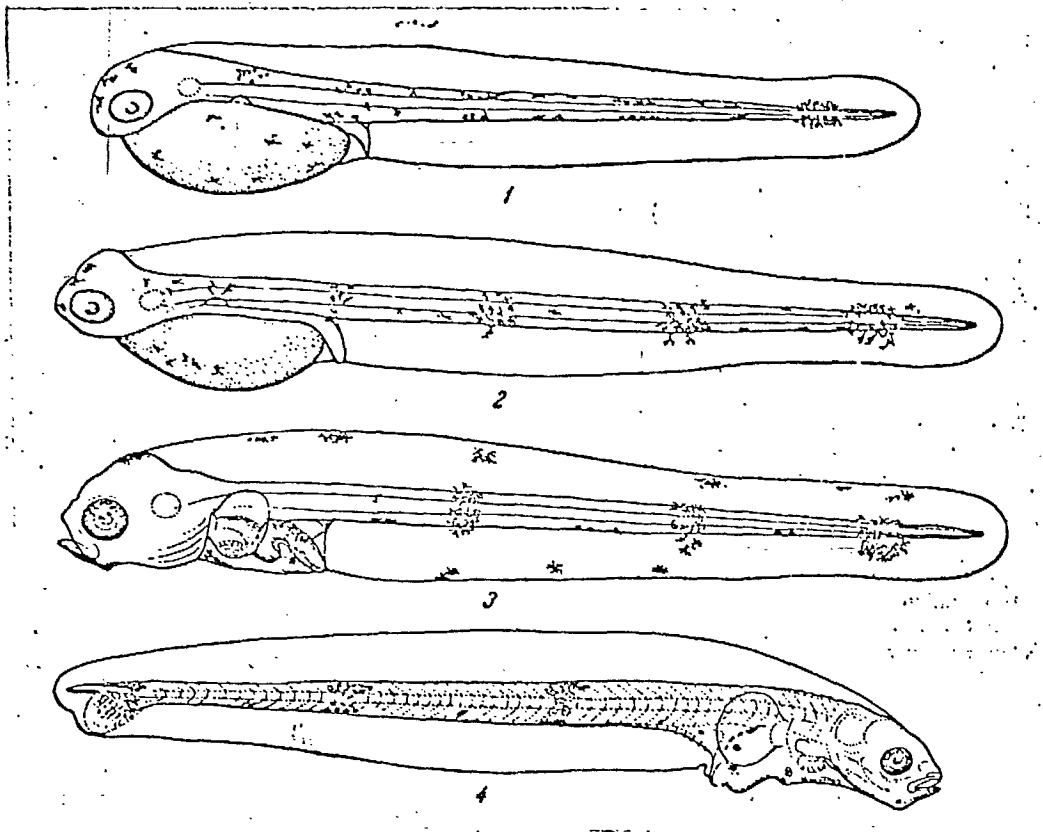


Figure 56 - Prolarvae and larvae of Gl. stelleri.

1 - 4.58 mm; 2 - 4.88 mm; 3 - 5.43 mm; 4 - 15.2 mm

reached 5.00 to 5.38 (4.83 to 5.22) mm and averaged 5.18 (5.01) mm. Their heads were freed from the yolk to the level of the rear edge of the eye and the forward end of the auditory capsule. There were no changes in pigmentation, with the exception of a reduction in the number of scattered melanophores.

After three days, almost all of the reserves of the yolk sac had been used (see fig. 56). A larva at this time was 5.43 (5.27) mm long. The trunk, as in the preceding stages, was short. The relative values of the distance from the end of the snout to the insertion of the anal fin became even smaller and at this stage represented only 29.2%.

The intestine curved even sooner than in the other 377 species, and formed a loop. Dark and yellow pigmentary cells were for the most part arranged in the same way as in the preceding stage, with the difference that their accumulations above the pectoral fins disappeared, the number of scattered cells decreased, and additional spots appeared on the lower edge of the tail, in the middle of the space between the anus and the first band, while the melanophores of the bands themselves as before sent branches in the direction of the fin folds.

A particularly large number of such formations branched out from the last band. The number of melanophores decreased on the head, but melanophores appeared on the lower jaw.

After four days, when the larvae reached a length of 5.4 to 5.5 (5.2 to 5.4) mm, there remained not a trace of the yolk sac. The pigmentation had the same appearance as in the preceding stage.

Larvae 6 to 7.5 mm long, like the preceding specimens, were long and thin, with a considerably drawn-in abdomen. The height of the body represented 4.5 to 5.8%, and the distance from the end of the snout to the insertion of the anal fin, 27.5 to 28.3%, of the length of the body. The head was rhomboid. The mouth was small and directed upwards, and the auditory capsule was larger than the eye. The pectoral fin was small; its tip reached only to the rectum, which opened at the level of the seventh myotome. The urostyle was straight. A compact thickening of a mesenchyme was visible under the last band, in the place of the future hypurals. The body was surrounded by a high fin fold.

The pigment had the same appearance as before, with the difference that there appeared additional spots between the bands, which, alternating, were located on the 6th, 21st to 22nd, and 38th to 39th myotomes.

A larva 15.2 (14.75) mm long (see fig. 56, 4) was symmetrical and as before was thin, with internal organs that were translucent. The body was surrounded by a high fin fold. The tail was long and the trunk was very short; the distance from the end of the snout to the insertion of the anal fin represented only 28% of the length of the body. There were 9 + 43 myotomes. The loops of the intestine were extremely constricted, and extended in the direction of the back and the abdomen. Behind the intestine was located a large urinary bladder, and behind it, in the form of a triangle, was visible a free space, in which gonads subsequently developed. The head was almost rhomboid. The mouth and the eyes were small. The auditory capsule as before, was larger than the eye. A binocular [literally, double-chambered] heart was translucent in front of the intestine, under the gullet. A thin-walled atrium cordis [auricle] was situated above and somewhat behind; under it was a small muscular stomach, from which there branched forward, in the direction of the gills, a clearly outlined aortic bulb. The gill chamber was covered with a thin gill cover. The gill apparatus was not fully formed. The gill filaments were short and were not equally represented on all of the arches; they were least developed on the first arch, better developed on the second and even better developed on the third and fourth arches. The branchlets of the pseudobranchiae were visible behind the eyes, on the inner side of the gill covers.

The pectoral fins retained their larval character; they were long and fan-shaped and covered almost the entire intestine, and [their] ends reached the level of the rear edge of the rectum.

The urostyle was slightly curved. Under it were visible hypurals which were still not fully formed and from which there branched out the rudiments of seven or eight rays.

The rudiments of pterygiophores were to be found at the bases of the forward portions of the dorsal and, to a large degree, the anal fin folds. There were 11 to 12 such rudiments in the dorsal fold and 17 to 18 in the anal fold.

The pigment that was characteristic of the preceding stages was also retained in this stage. The long flounder larvae kept to shallow depths and, since they were disclosed in surface fishing, led a pelagic mode of life.

Metamorphosis in the long flounder is completed very late, later than in other representatives of the group of slime [small-mouthed] flounder. Unfortunately, we have not traced the sequential course of metamorphosis because 378 of our lack of appropriate material. According to T. V. Dekhnik (1959), in a fingerling 53 mm long caught with a beam trawl on the bottom, the left eye was located on the profile of the head, while in a fingerling 64.2 mm long described by L. N. Musienko it had passed to the right side, and its metamorphosis had evidently been completed.

Among juvenile fish there were also smaller fingerlings only 50 mm long. It is evident that during the period of completion of metamorphosis body sizes vary considerably and range from 50 to 60 mm.

The change in the sizes of the body and of the plastic features of its individual parts in the course of development is shown in Table 61.

Table 61

Correlation of Body Parts of Prolarvae
and Larvae of *Gl. stelleri* (in mm)

Stage of development	Length		Percentage of length of head		
	total	body	aA	H	lc
Prolarva that has just hatched.....					
Prolarvae towards completion of absorption of yolk sac.....	4,1-5,2	3,5-5,1	33,9 (31,2-36,3)	4,4 (4,1-4,9)	15,8 (14,3-17,7)
Larvae. Urostyle straight.....	5,4-5,5	5,2-5,4	29,5 (28,5-29,8)	3,6 (3,4-4,0)	15,8 (15,3-16,1)
Urostyle slightly curved, 7 or 8 rays under it..	7,54	7,38	27,5	5,81	15,9.
	15,2	14,75	28,0	5,2	17,9

Table 61 (continuation)

Stage of development	Percentage of length of body		Percentage of length of head	
	D	A	O	aO
Prolarva that has just hatched.....				
Prolarvae towards completion of absorption of yolk sac.....	4,8 (3,1-6,3)	4,4 (3,1-6,3)	36,2 (28,5-36,1)	15,2 (13,6-18,1)
Larvae. Urostyle straight.....	6,2 (5,7-7,0)	5,9 (5,5-6,0)	28,4 (27,3-30,0)	15,5 (13,5-16)
Urostyle slightly curved, 7 or 8 rays under it..			28,8	23,1
			16,6	23,8

The change in the sizes of the body and of the plastic features of its individual parts in the course of development is shown in Table 61.

To sum up, it should be noted that the long flounder's eggs are pelagic and that their diameter varies from 1.20 to 1.61 mm. The perivitelline space represents from 3 to 12% of the diameter of the eggs. The membrane is thick and wavy.

At water temperatures ranging from 11 to 16.4° and averaging 13.6° the first stage of development lasts for approximately 1 day and 6 hours, the second stage, for two days, and the third stage, for 3 days. The prolarvae begin to hatch after six and eight days.

The lower "threshold" of development lies at about 4.9°.

Pigment in the form of dots scattered on the body appears in the middle of the second stage of development of the embryo. Up to the end of the third stage and the beginning of the fourth, the pigment on the body is scattered; 379 prior to hatching it changes into five accumulations of bands, of which one is located in the region of the pectoral fins, one above the anus, and three at equal distances from each other on the tail. The yolk is pigmented beginning from the second stage of development. In contrast to those of the Alaska plaice, the pigmentary cells are situated over the entire surface of the yolk. The prolarvae are large; their body length varies from 4.1 to 5.2 (3.50 to 5.10) mm and on the average amounts to 4.64 (4.51) mm. At a water temperature of 13.6° the yolk sac is absorbed in four days when [the prolarva] is 5.4 to 5.5 (5.2 to 5.4) mm long. The body

is thin and extended. The trunk is short and the tail is long. A cavity situated behind the rectum, and a large urinary bladder, are highly characteristic of the larvae.

Metamorphosis takes place very slowly. The appearance of the first seven or eight rays in the tail fin and the beginning of differentiation of the basal rays in the anal and dorsal fins is observed at a body length of about 15 mm. Metamorphosis is evidently completed at a length of 50 to 60 mm.

The pigmentation of the larvae is of the spotted-band type; it is represented by three main bands dividing the tail into equal portions, and by intermediate spots between these bands on the lower edge of the tail. In juvenile fish (Musienko, 1954) seven spots form on the upper edge, five on the lower, and four in the middle lateral rows. The vertical distributions of the spots of all of these rows correspond; hence the body of the fingerling appears interlaced with pigment bands. In addition, there are faintly marked, uncharacteristic spots in the upper lateral and lower lateral rows.

Comparison with Near Species

As indicated above, the genus Glyptocephalus is amphiboreally distributed and incorporates three species, of which two, Gl. stelleri and Gl. zachirus, live in the Pacific Ocean and one, Gl. cynoglossus, in the Atlantic. Gl. stelleri is distinguished from the two other species by smaller numbers of vertebrae and rays in the dorsal and anal fins.

There are no published data on the development and structure of the eggs or larvae of Gl. zachirus. The development of the Atlantic Gl. cynoglossus has been thoroughly studied (Cunningham, 1887; MacIntosh and Prince, 1890; Petersen, 1894 and 1904; Kyle, 1898; Ehrenbaum and others, 1905; Schnakenbeck, 1928; Nybelin, 1935, and others).

The reproduction of Gl. cynoglossus occurs at different times in the different regions of its geographical range. In the North Sea, it begins in May, and in the Irish Sea, in April.

Its eggs, as in the Pacific species, are pelagic, with a thick, wavy membrane; their size, however, is noticeably smaller and ranges from 1.07 to 1.3 mm. At a water temperature of 8 to 9° the incubation period lasts for seven to eight days. The larvae hatch about 4.9 mm long.

The data of different authors are at variance concerning the nature of the pigmentation of embryos and larvae. According to Cunningham and Ehrenbaum, the embryo is characterized by a slight pigmentation consisting only of delicate scattered melanophores and yellow chromatophores. Pigment is retained in this form in prolarvae that have hatched; only after two days, when the prolarvae are 5.1 mm long, is it converted into five groups, of which one is situated at the pectoral fins, a second at the anus, and three on the tail.

According to Nybelin's data (1935) individual scattered melanophores and chromatophores which appeared at the end of the second stage of development of the embryo regroup into the five pigmentary groups described above much sooner, as early as towards the close of the embryonic period. The

discrepancies noted in the descriptions of pigmentation by Nybelin on the one hand and Ehrenbaum on the other probably resulted from different incubation temperatures. It is 380 possible that Cunningham and Ehrenbaum were concerned with eggs and prolarvae developing at a higher temperature than was the case with the material studied by Nybelin. It is well known from experiments that a reduced temperature (specific for each species) lengthens the embryonic period, and that the prolarvae hatch more developed both in structure and pigmentation.

Gl. cynoglossus and Gl. stelleri have much in common in the structure and pigmentation of their prolarvae and larvae. Both species have a very long tail and a correspondingly short distance from the end of the snout to the insertion of the anal fin; at the moment of hatching, this distance is almost equal to the length of the body, and in older prolarvae and larvae represents less than $1/3$ of this length. A large urinary bladder and a free space behind it are characteristic of the larvae of both species. There is also the difference that the prolarvae of Gl. cynoglossus hatch smaller than those of Gl. stelleri, this lag in body length being retained in subsequent development as well. The larvae of Gl. cynoglossus, which are equally large, are always more developed than those of Gl. stelleri.

The pigmentation in the embryonic, prolarval and larval stages of the species under comparison is extremely similar, with the difference that the pigment group on the heads of Gl. cynoglossus larvae is retained throughout the entire pelagic period, while in Gl. stelleri it disappears early (prior to the establishment of rays in the dorsal and

anal fins). In addition, in Gl. cynoglossus there are melanophores on the gill cover that are absent in Gl. stelleri, and the pigmentation of the lower jaw is more strongly developed.

All of the above indicates that at all stages of embryonic and postembryonic development the species under comparison are extremely similar, which points to their genetic proximity. The differences between them are unimportant and are expressed in a slight deviation in pigmentation and body sizes.

The Genus *Pleuronectes* L.

The Starry Flounder -- *Pleuronectes stellatus* Pallas

The development of the starry flounder off the coast of America has been studied by Orcutt (1950), and off the coast of Northern Japan, by Yusa (1957). On the basis of material obtained by artificial fertilization and incubation, Orcutt and Yusa give a description and detailed series of drawings on embryonic development, along with several illustrations of prolarvae and younger larvae.

The above authors give no description whatever of the structure of older larvae. Information on the structure and morphological features of individual stages of development of the eggs of the starry flounder is available in keys that we have published to pelagic eggs of Peter the Great Bay (Pertseva-Ostroumova, 1955).

We have studied the development and structure of the eggs, prolarvae and larvae of the starry flounder living in Soviet waters partly from eggs caught on 29 April 1951 in

Avacha Bay, which we incubated; from the prolarvae and larvae hatched from them, and partly from material collected at sea.

Both our own data and those of Orcutt (1950) and Yusa (1957) are used in describing the course of development and the structure of the eggs, prolarvae, larvae and juveniles of the starry flounder.

The embryonic development (see figs. 57 and 58) of the starry flounder in our experiments took place at a water temperature of 7 to 8° and lasted for about seven days. The water temperature in the sea during the spawning period ranged from 0.58 to 5.54°.

In Orcutt's experiments, the incubation period at a water temperature of 10.5° lasted 4 days and 14 hours; at a temperature of 12.5°, 2 days and 18 hours, and in Yusa's experiments at water temperatures of 2.0 to 5.4°, 14 days / 381 and 17 hours. The speed with which individual stages elapsed at different temperatures is shown in Table 62.

In comparing our data on development with those of Yusa, we made an attempt to calculate the temperature threshold and the quantity of degree-hours required for the embryonic development of the starry flounder. It was ascertained that the temperature threshold was approximately equal to 0.2°, while the number of degree-hours amounted to 1,231, or 51 degree-days.

In comparing the results of the development of the eggs of two series off the coast of California at water temperatures of 10.5 and 12.5°, we obtained a temperature threshold of 7.2°, while the number of degree-hours required for completing embryonic development equalled 15 degree-days.

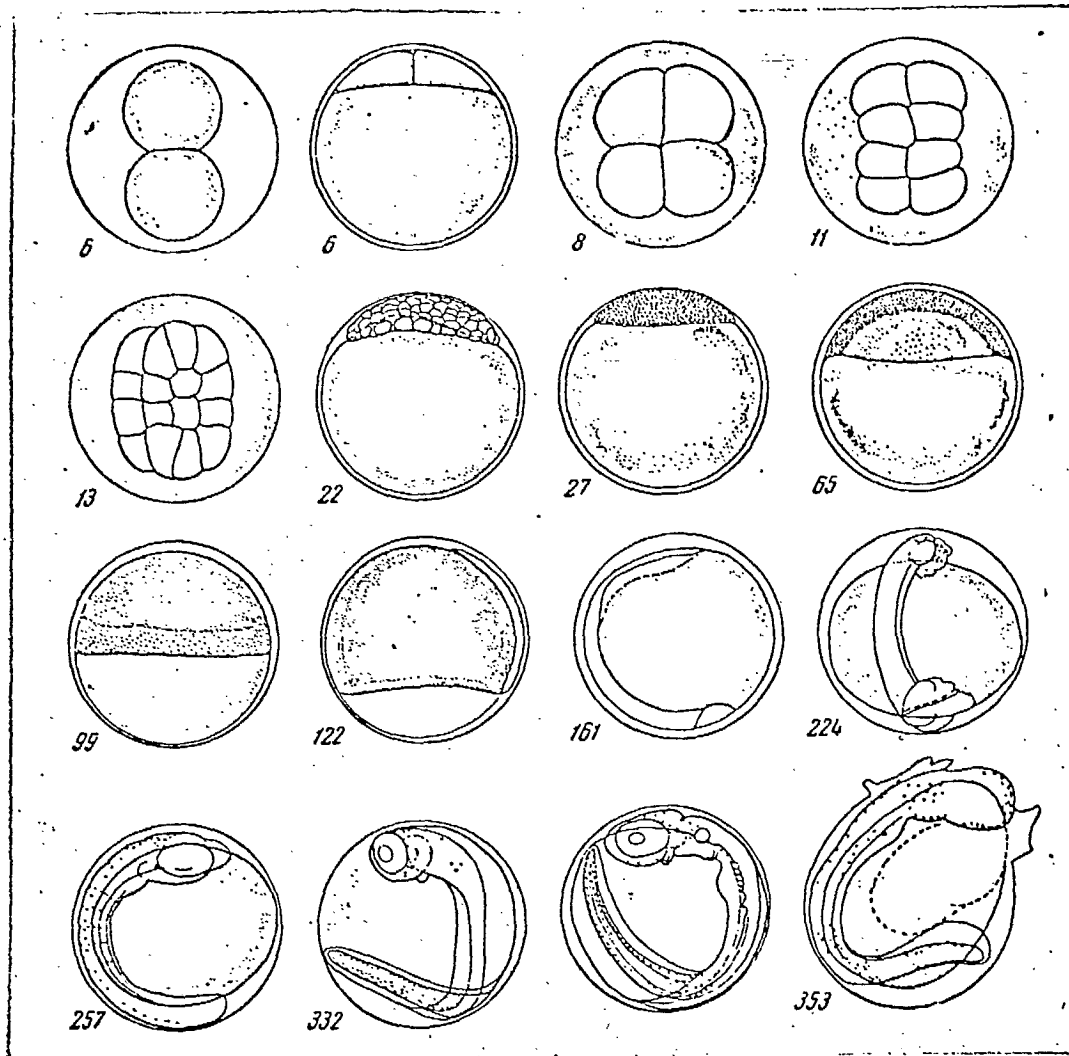


Figure 57 - The development of the eggs of Pl. stellatus
at water temperatures of
2.0 to 5.4° (after Yusa)

The figures under the illustrations designate the
hours of development

The temperature threshold that we calculated for the starry flounder reproducing off the coast of Asia was evidently close to the real threshold, since the mass spawning and development of the eggs of the starry flounder off the Soviet coast takes place at a water temperature on the bottom of about 1° , and, off the coast of Hokkaido, at about 2° . Also, it is evident that the temperature threshold (7.2°) was nearly real that we calculated for a special stock of starry flounder, living off the coast of California, which 382 has a preference for warmth and whose reproduction and development, in accordance with the climatic conditions of its geographical range, take place at a high water temperature -- about 11° .

The diameter of ripe ovarian eggs ranges from 0.89 to 0.94 mm. The eggs, according to our data and Orcutt and Yusa, are round and pelagic. The membrane is very thin, and in fully swollen eggs it is completely smooth. In fixed eggs it has a rosy-lilac colour. The diameter of starry flounder eggs in Soviet waters, from the measurement of 1,678 specimens, ranges from ~~(0.92)~~ 1.00 to 1.28 mm and averages 1.04 to 1.22 mm. The diameter of eggs off the coast of Hokkaido (after Yusa) ranges from 0.97 to 1.01 mm. The perivitelline space represents (5.7) 7.4 to 14.6% of the diameter of the egg and averages 9.8 to 11.8%. In their quantity of plasma, the eggs of the starry flounder most resemble eggs of the oligoplasmatic type.

Cleavage and further development take place in the same way as in flounder that have pelagic eggs (see fig. 57). Kupfer's vesicle and the embryos of the eyes appear prior to

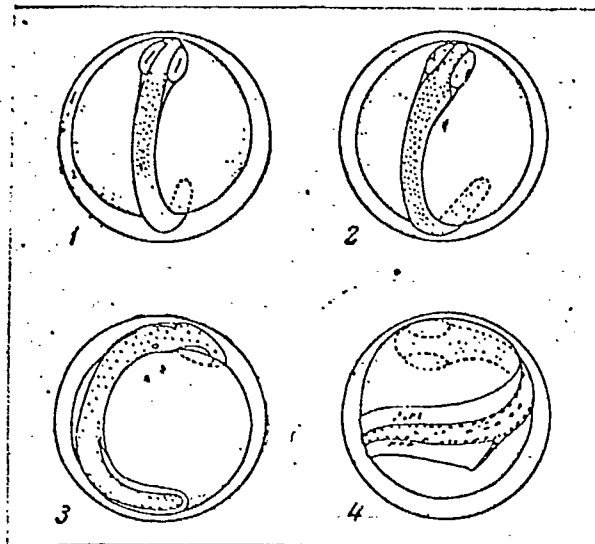


Figure 58 - Eggs of Pl. stellatus after fixation. The figures under the illustrations are ordinal numerals (original)

the closing of the blastopore, and segmentation and crystalline lenses, after this process. Pigment in the form of scattered dots is disclosed simultaneously with the beginning of the establishment of the tail bud; at the same time, Kupfer's vesicle shrinks and subsequently disappears. The embryo at this time envelops more than half of the yolk.

Pigment that has appeared in the form of scattered dots in the forward half of the trunk is thick, and in the rear half is sparser and oriented in two rows situated parallel to the chord. Neither the head of the embryo in the region of the eyes nor the end of the body is pigmented at this time. At the end of the second stage and the beginning of the third the pigmentary cells spread to the region of the eyes and the rear half of the body, which proves to be just as thickly pigmented as the forward half (see fig. 58).

In the third stage (see fig. 58, 2 and 3) the pigmentation on the trunk retains the same thickly scattered

character as in the second stage, with the difference that the pigmentary cells become larger and branched. The head, the eyes, the tail and trunk are intensively pigmented, the pigmentary cells being distributed on the tail in such a way that when it is examined from the side, on the upper edge their aggregate has the appearance of a regular compact row, and on the lower edge they are sparsely scattered in some places and connivent in others.

There are a few pigmentary cells on the rear end of the intestine, on the anal pipe and in the region of the pectoral fins, on the yolk. Large, branched melanophores are visible on the fin folds, on the level of the middle of the tail.

At the end of the third and fourth stages of the embryo (see fig, 58, 4) the pigmentation has the same appearance as in the preceding stage, with the difference that the pigmentation on the fins, the rear end of the intestine and the anal pipe becomes more pronounced. As in preceding stages, individual scattered cells go beyond to the eyes.

In comparing the sizes of the eggs collected in 383 different regions (see Table 63) it may be seen that in the Sea of Okhotsk, off the western coast of Kamchatka, the eggs and especially their yolks are somewhat larger than in 384 Peter the Great Bay or in the Bering Sea.

The larger sizes of starry flounder eggs off the western coast of Kamchatka fully conform to the sizes of the specimens inhabiting this region. According to the data of P. A. Moiseev (1953) and our own material, the starry flounder is noticeably larger (37.2 mm) off Western than off Eastern (30.4 mm) Kamchatka.

Table 62

The Speed of Development of *Pl. stellatus* at Water Temperatures
of 2.0 to 5.4° (after Yusa), ^{and} 10.5° and 12.5° (after Orcutt)

Stage of development	Duration of development in						Stage of development	Duration of development in						
	days	hours	days	hours	days	hours		days	hours	days	hours			
2 blastomeres							Prior to closing of blastopore							
4 blastomeres							Blastopore closed							
8 blastomeres							10 to 16 somites							
16 blastomeres							18 to 20 somites							
32 blastomeres							25 somites							
Morula							Embryo envelops about $\frac{3}{4}$ of yolk; 30 to 32 somites							
Blastula and periblast							Notochord has appeared							
Gastrula (beginning)							Heart has appeared							
Embryonic ring has reached $\frac{1}{2}$ of yolk							First movement							
Embryonic ring has reached $\frac{3}{4}$ of yolk							Hatching							
Optic vesicles have appeared														

765.

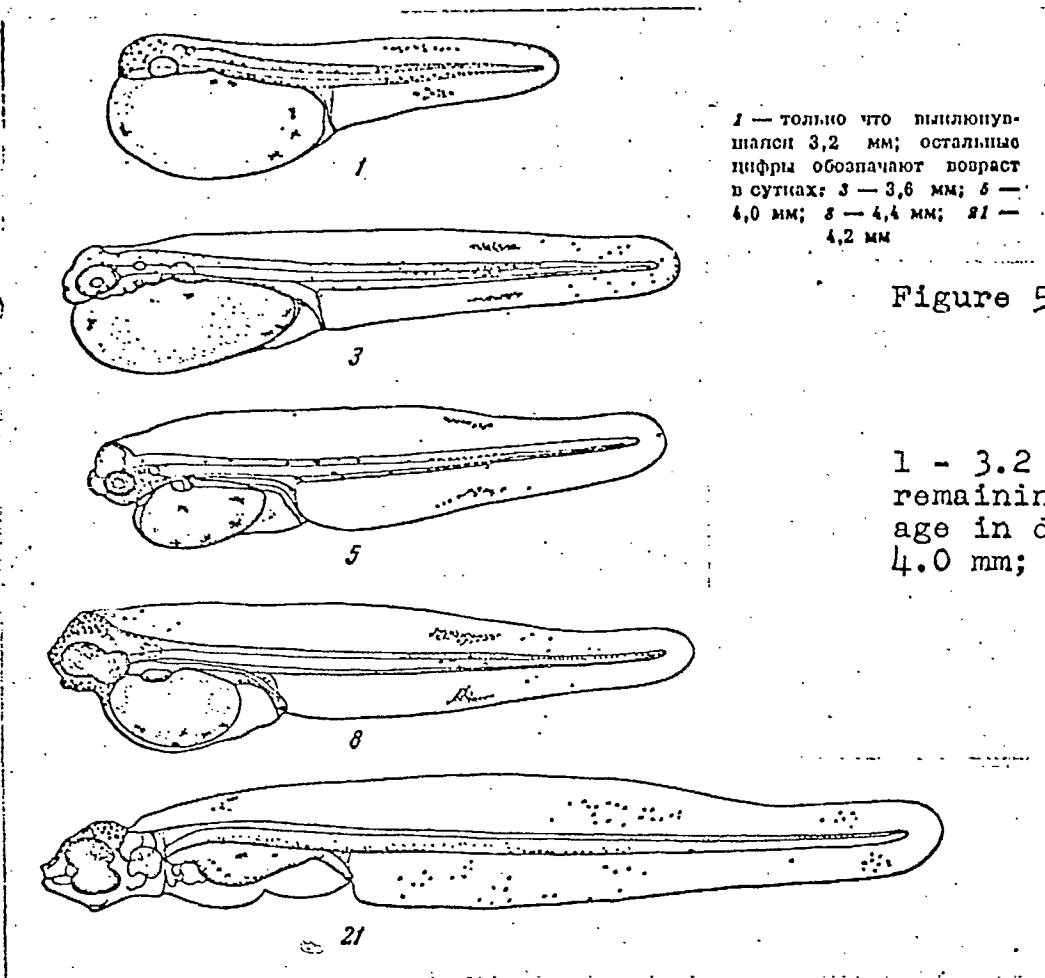
Table 63

Size of Eggs of *Pl. stellatus* (in mm) in Various Regions

Region where collected	Month of collection	Egg sizes		Yolk sizes	
		average	range	average	range
Anadyr Gulf	June				
From Cape Navarin to Cape Olyutorskii	Same				
Kamchatka Gulf	May	1,04	1,00-1,17	0,78(1-2)	0,75-0,82
Kronotskii Gulf	Same	1,07	0,92-1,13	0,83(0,81) (1-4)	0,76-0,94 (0,78-0,85)
Eastern coast of Kamchatka	April	1,05-1,08 1,09-1,12	1,01-1,22 1,00-1,17	0,86 0,84-0,86	0,78-0,94 0,71-0,97
Western coast of Kamchatka south of 52° north latitude	May	1,07-1,20	1,03-1,28	—	0,85-1,01
Northern Kurile Islands (on Pacific side)	June	1,22	1,22	1,03(2)	1,08(0,99)
Off southern tip of Sakhalin	May	1,1 1,09	1,01-1,13 1,01-1,20	— 0,80-0,81	— 0,71-0,90
Peter the Great Bay	April				

Starry flounder prolarvae that have just hatched (see fig. 59, 1, and 60, 1) are small and transparent, and keep to the surface layers of the water. Their activity is low, they swim with their yolk sac up, and the head in such a position is lower than the tail.

The total length of live prolarvae varies from 2.25 to 2.35 mm in Soviet waters, from 2.58 to 3.36 mm off the coast of Hokkaido and from 1.93 to 2.08 mm off the American coast. The yolk sac is in the shape of an elongated oval; it is from 1.10 to 1.15 mm long, and in Yusa's experiments its length was approximately 1.51 mm. The height of the yolk sac



1 — только что выклюнувшийся 3,2 мм; остальные цифры обозначают возраст в сутках: 3 — 3,6 мм; 5 — 4,0 мм; 8 — 4,4 мм; 21 — 4,2 мм

767.

Figure 59 - Prolarvae and larvae of Pl. stellatus (after Yusa).

1 - 3.2 mm; has just hatched; remaining figures indicate age in days; 3 - 3.6 mm; 5 - 4.0 mm; 8 - 4.4 mm; 21 - 4.2 mm

accordingly ranges from 0.50 to 0.65 (0.67) mm. The tail is very short, and the distance from the end of the snout to the insertion of the anal fin represents 49.3% of the length of the body. There are about 40 myotomes in the body, which is heavily pigmented. Yellow chromatophores and dark melanophores are thickly scattered on the back and on the rear part of the intestine. On the middle of the tail they form a noticeable accumulation, recalling a similar formation in banded flounder larvae, with the difference that in [the latter] this band consists of large, branched melanophores and is more distinctly marked. On the same level a group of large melanophores is visible on the fin fold, and a few others that are shifted to the rear, closer to the end of the tail, may be seen on the anal fin fold.

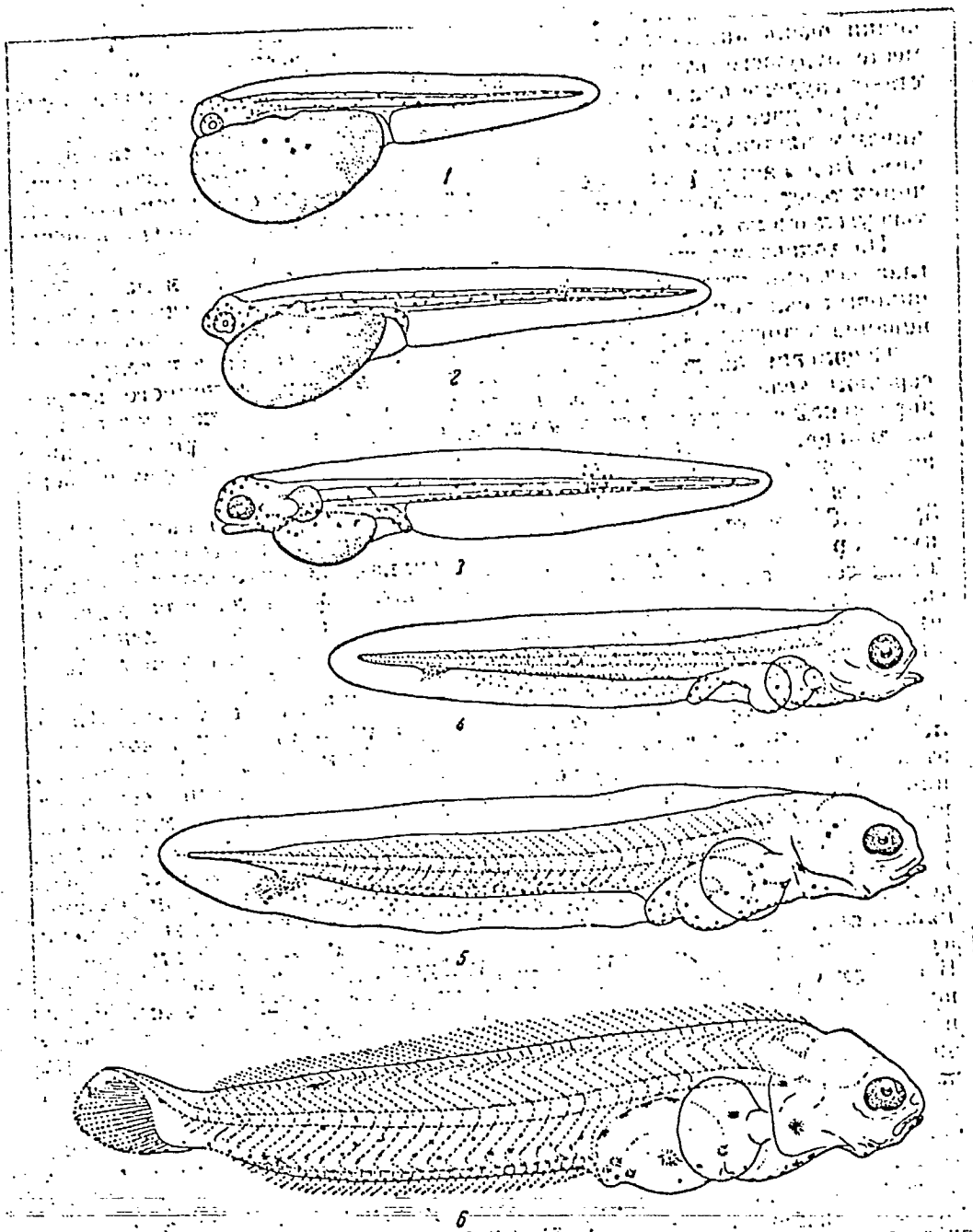


Figure 60 - Prolarvae and larvae of Pl. stellatus (after fixed material)

1 - 2.4 mm; 2 - 3.0 mm; 3 - 3.22 mm; 4 - 4.6 mm; 5 - 5.9 mm;
6 - 6.6 mm (original)

In the pigmentation of their tails and fin folds starry flounder prolarvae resemble Eopsetta grigorjewi, but the chromatophore zone on the fins of prolarvae of the latter species has an arch-like shape open in front (see fig. 20).

Twelve hours after hatching, the prolarvae in Orcutt's experiments reached a length of 2.58 mm, while the yolk sac decreased in size to 0.88 mm. The pigmentation did not change.

After 24 hours the length of a larva reached 2.99 mm. At this stage the larvae were very active and swam vigorously in all directions. In the place of the future mouth there appeared a small depression; the pectoral fins grew noticeably and were 0.22 mm long (see fig. 60, 2).

After two days the length of the larvae reached 3.15 mm. The external appearance of the larvae changed. The yolk sac became lower and more oblong. The mouth opening appeared, but it still did not function. The larvae now swam, so that their bodies formed an angle of about 75° with a horizontal plane.

A bright green pigment appeared on the head between the eyes. The edges of the eyes were amber-green in front and amber in the rear. The chromatophores of the fin folds formed triangular accumulations whose wide base was directed towards the edge of the fin, and peak, towards the body.

The accumulation on the dorsal fin was situated somewhat in front of the middle of the body, and on the anal fin, somewhat behind. A row of melanophores on the edge of the dorsal fold was directed forwards and extended to the level of the pectoral fins. In addition, individual rows of melanophores ran along the upper and lower edges of the body.

After three days, the larvae reached 3.20 mm in length, and in Yusa's experiments, 3.40 to 3.84 mm, (see fig. 59, 3), and the pigment on the eyes took on a bluish-green tint. Melanophores were visible on the upper part of the head and on

the occiput. Dark green pigmentary cells appeared behind the eyes and on the end of the intestine. One large, greenish cell was situated near the tip of the lower jaw. After three and a half days peristalsis appeared in the intestine.

After four days the larvae were 3.50 mm long and their bodies 0.19 mm high. The mouth and the jaws functioned. The yolk sac became quite small, its size ranging from 0.24 to 0.29 mm. In Yusa's experiments, the larvae reached this stage on the 16th day at a length of 4.55 mm. A fin fold appeared in the pectoral fin. It [the fin] was 0.29 mm long. The greenish pigmentation retained the same appearance as in the preceding stage. The eyes took on something of a dark blue hue. The pupil became darker. Large starry melanophores were visible on the body at the base of the fin folds. A few such cells were also situated at the end of the intestine. The head took on angular contours. In Orcutt's experiments the yolk sac was absorbed on the fourth day, and in Yusa's experiments, on the 20th day. On Orcutt's experiments the prolarvae were fed with copepod nauplii that had just hatched, sea urchin blastulas, diatoms and other small plankton collected with a plankton net. The larvae began to ingest food only on the fifth day after the yolk sac had been fully absorbed.

On the seventh day of development, the heads of the larvae became high, with a very sharp snout and a terminal mouth, while the jaws were lengthened and bent.

In spite of their ingestion of plankton, the larvae at this stage revealed signs of starvation. The overall length of their bodies was only 3.4 mm and was less than that of four-day-old larvae.

On the tenth day in Yusa's experiments, out of 466 hatched prolarvae only 14 remained alive. The bodies of the larvae became still shorter and their length totalled only 3.0 mm; the larvae themselves appeared extremely emaciated.

Corresponding larvae in Yusa's experiments were 4.2 mm long (see fig. 59, 21). On the eleventh day in Orcutt's experiments all of the larvae died.

The description of the following pelagic stages, in / 387 the course of which there took place both metamorphosis and the preparation for a bottom mode of life, is given after material collected in Soviet waters in various starry flounder spawning areas. (see Table 64).

Table 64

Conditions under which Larvae of Pl. stellatus were Caught.

Region	Date	Depth of catch, in m	Level of catch	Length, in mm	
				total	body
Olyutorskii Gulf...	June	35	Surface		
Same	26	46	41 to 0		
"	26	96	Surface	3,62-4,33 4,35-5,47	3,46-4,29 4,18-5,17
Northeastern tip of Sakhalin...	July	135	Same		6,59
Same	22	135	Same	4,26-8,00 6,30-6,87	4,40-8,32 6,65-7,21

Larvae from 3.6 to 4.3 mm long were thin and delicate, and had evidently lost their yolk sacs quite recently. The intestine was straight and considerably dilated in front. The corner of the mouth was on the level of the forward edge of the eye. The urostyle was straight, and a small mesenchymal thickening was noticeable in the place of the future hypurals.

Larvae 4.5 to 4.6 mm long looked somewhat older (see fig. 60, 4). The height of the body represented 6.1% of its length. A curve appeared in the intestine; in younger larvae it was only outlined, while in older specimens (4.6 mm) it formed almost a full loop. The urostyle was still straight, and the mesenchymal thickening under it became more compact. The pectoral fins occupied three myotomes. There were 8 to 9 myotomes in the body and 26 to 27 in the tail.

Pigment was represented by a group of scattered punctate cells on the middle of the tail, and by two parallel rows of such cells on the lower edge of the tail. An irregular row of melanophores was visible in the depth of the body, above the chord of the tail. A fairly compact row of melanophores passed along the middle of the lower half of the abdomen, and a few scattered, starry melanophores were visible along the sides of the abdomen, above the rear portion of the intestine. There were two or three fairly large, starry cells in front of the pectoral fin and on the lower jaw.

In larvae 5.3 mm long the intestine formed a small loop. The height of the body represented 8% of its length. The urostyle was curved slightly upwards, and under it were visible the outlines of hypurals, from which the rudiments of four fin rays branched out.

In larvae 5.3 to 5.9 mm long (see fig. 60, 5), the intestine grew to such an extent that its loop occupied the entire abdominal cavity and in some specimens was adjacent to the excretory intestine. The pectoral fin was situated over the extent of six myotomes, and its end almost reached the rear edge of the intestinal loop. The height of the body represented about 11.4% of its length. Four or five rays were

outlined in the tail fin. At the bases of the dorsal and anal fin folds there appeared the thickened stripes of future pterygiophores that had still not been differentiated.

Larvae whose length varied from 6.7 to 8.32 (from 6.6 to 8.0) mm (see fig. 60, 6) appeared as flat, externally symmetrical small fish whose body height represented from 11.0 to 18.4% of their length. The head was slightly angular, and the snout was short. The mouth was small, and its corner was situated in front of the eye. In spite of the small difference in their sizes, the development of the larvae that are being described progressed considerably in comparison with 388 the preceding larvae. Vertebrae were noticeable at this stage; there was a total of 35 to 36, of which 26 were in the tail and 9 to 10 in the trunk. Pterygiophores formed at the bases of the dorsal and anal [fins], and the rudiments of fin rays appeared. The development of the latter was not uniform; in the forward part of the fins they were more or less distinct, and in the rear part they were either hardly noticeable or entirely absent. Thirty rays were outlined in the anal fin, and in the dorsal fin, because of injury to the latter, they were difficult to count. Eight or nine rays were noticeable in the tail fin. The pectoral fin occupied six or seven myotomes. The gill cover did not entirely screen the gill chamber.

It should be noted that less developed larvae that were of equal or even larger size were found in the same places among the larvae described. The bodies of these less well developed larvae were noticeably lower and their urostyles less curved; although the pterygiophores were differentiated, there were still no rudiments of fin rays.

The pigmentation in the younger larvae did not change; in older specimens there was a clear tendency towards a reduction in the number of melanophores scattered on the surface of the tail and the abdomen, and a large pigmentary cell (the rudiments of the future rear spot of the upper row) appeared on the upper edge of the rear half of the tail (fig. 60, 6).

Comparison with the fluke -- *Pl. flesus*

The eggs, prolarvae and larvae of *Pl. flesus* and its individual subspecies are described in the works of several authors (Malm, 1868; Cunningham, 1887; Holt, 1891 and 1893; MacIntosh and Masterman, 1897; Heincke and Ehrenbaum, 1900; Petersen, 1906; Ehrenbaum, 1905-1909; Schnakenbeck, 1929; T. A. Pertseva, 1936; Kosyakina, 1938; Kazanova, 1952 and 1953; Vodyanitskii and Kazanova, 1955; Mukhacheva, 1957 and others).

The eggs of *Pl. flesus*, like those of *Pl. stellatus*, are pelagic, but their diameter varies sharply in different subspecies in different regions (see Table 65). The structure and pigmentation of the embryos of all subspecies of *Pl. flesus* and *Pl. stellatus* are quite similar. Characteristic of all are the comparatively large diameter of the embryo, which is only one-sixth to one-eighth that of the egg, and intensive pigmentation. Considerable similarity is also found among their prolarvae and larvae. All have a characteristic ac- / 389 cumulation of pigmentary cells on the middle of the tail and a diffuse, fine-celled pigmentation, which is added later, on its lower half and a smaller quantity on its upper half. A thickly scattered pigment on the fin folds is also characteristic of all larvae of this genus.

Table 65

The Sizes of Eggs of Pl. flesus and Pl. stellatus in Different Regions

Species	Region	Egg sizes, in mm	Author
<u>Pl. fl. septentrionalis</u>	Pechora.....	0.96 to 1.05	Alekseeva, 1949
<u>Pl. flesus</u>	Barents Sea. Chesha Bay....	0.78 to 1.03	Pertseva, 1936 Kazanova, 1949
<u>Pl. fl. bogdanovi</u>	White Sea.....	0.74 to 1.05	Mukhacheva, 1957
	North Sea.....	0.82 to 1.13	Ehrenbaum, 1905
<u>Pl. fl. trachurus</u>	Baltic Sea.....	0.83 to 1.43	Kazanova, 1952
<u>Pl. fl. luscus</u>	Black Sea.....	1.10 to 1.25	Kosyakina, 1938
<u>Pl. stellatus</u>	Sea of Okhotsk.....	1.03 to 1.28	Ourselves
	Bering Sea.....	0.92 to 1.22	Same
"	Eastern coast of Kamchatka.	1.01 to 1.24	"
"	Peter the Great Bay.....	1.01 to 1.20	"
"	Off the coast of Hokkaido..	0.97 to 1.01	Yusa, 1957

The formation of rays in the larvae of both species and subspecies of the fluke begins at different lengths in different regions (see Table-66).

It may be seen from Table 66 that with the same body differentiation the larvae of Pl. stellatus lag behind those of Pl. flesus in size, while the larval length at which fin rays appear increases from south to north. Pigmentation, however, to judge from the illustrations of the above authors, intensifies from north to south. Prolarvae are most pigmented in the Black Sea, and to a notably lesser extent in the Baltic Sea.

Table 66

Stage of Development and Body Length (in mm) of Prolarvae and Larvae
of Pl. flesus and Pl. stellatus Collected in Different Regions

Region	Prolarvae towards moment of absorption of yolk sac	Stripes of pterygiophores have appeared	Rays have appeared, but forward and rear rays are underdeveloped. Urostyle protrudes outwards	All rays formed	Author
Off the coast of eastern Kamchatka	3.5 to 4.0	5.30 to 5.90	6.70 to 8.32	--	Ourselves
Coast of Hokkaido..	4.55	--	--	--	Same
American coast.....	3.5	--	--	10	Orcutt, 1950.
Black Sea.....	2.9	7.37	8.39		
North Sea.....	4.0	7.20	6.9	10.3	Ehrenbaum, 1905-1909
Baltic Sea.....	3.0 to 4.0	7.39	8.59	--	Kazanova, 1952
Barents Sea.....	--	6.1	9.0	--	Rass, 1949
Chesha Bay.....	--	--	9.5	--	Kazanova, 1949
Pechora Bay.....	ca 5.0	--	8.9	--	Alekseeva, 1949
White Sea.....	--	6.6	--	--	Mukhacheva, 1957

Larvae collected in the White Sea and in Chesha Bay in Pechora Bay are of the same colour. According to Kazanova and Alekseeva (1949), there are fewer melanophores on their tails, but these melanophores are much larger than in many flukes from the southern regions.

In summing up the above, it should be noted that starry flounder eggs are pelagic. Their diameter ranges from (0.92) 1.00 to 1.28 mm, and their membrane is thin and of a

lilac hue. At water temperatures of 2.0 to 5.4° the first stage of development lasts for about 2 days and 12 hours; the second stage is completed in 10 days and 17 hours, and the third, in 13 days and 20 hours. At water temperatures of 2.0 to 5.4°, the larvae hatch in 14 days and 17 hours, and at a water temperature of 12.5° they hatch in 2 days and 20 hours.

In Soviet waters the length of prolarvae that have just hatched runs from 2.25 to 2.35 mm; off the coast of Hokkaido they are from 2.58 to 3.36 mm long. Off the American coast, in Monterey Bay, the corresponding size range is much smaller -- from 1.93 to 2.08 mm.

At water temperatures of 10.5 to 12.5° the yolk sac is absorbed on the 4th day, and at water temperatures of 2.0 to 5.4°, on the 20th day.

In the first case, towards the moment of absorption 390 of the yolk sac, the length of the larvae reaches 3.5 mm, and in the second case, 4.55 mm.

The rays in the dorsal and anal fins are outlined when the larvae are from 6.7 to 8.32 (from 6.6 to 8.0) mm long.

Pigment in the form of scattered cells appears on the back of the embryo at the end of the second stage and subsequently spreads to the head and tail.

In prolarvae that have hatched, the scattered cells on the middle of the tail group into an accumulation in the form of a band. On the same level there is a group of large melanophores on the dorsal fin fold, and a few melanophores that have been shifted to the rear (nearer the end of the tail),

on the anal fin fold. Towards the moment that formation of the rays is completed, the pigmentation on the tail is transformed into spots situated on its upper and lower edges.

The eggs and larvae of the starry flounder and the fluke are greatly similar at all stages of development, indicating the close kinship between these species.

The Genus *Kareius* Jordan et Snyder

Two-coloured (Korean) Flounder -- *Kareius bicoloratus*

(Basilevsky)

Information on the development of the two-coloured flounder is limited to indications by Kuragami (quoted from Moiseev, 1958) and Okada (1955) on egg sizes, the length of hatched prolarvae and the duration of the period of incubation. The diameter of two-coloured flounder eggs, according to Kuragami's data, is 1.10 mm, and according to Okada, 1.013 to 1.099 mm; at a water temperature of 13.5° the incubation period lasts for about 4 days and 40 minutes. We have unfortunately been unable to acquaint ourselves with Kuragami's work and therefore do not know the details of the structure or morphology of the eggs, prolarvae or larvae.

At the end of October and beginning of November 1951 in the southwestern and southern parts of Peter the Great Bay, at a depth of 62 m eggs were collected in the second to fourth stages of development that resembled starry flounder eggs, but differed from them in more abundant pigmentation and a lack of pigment on the embryonic fins.

The diameter of these eggs varied from 1.00 to 1.15 mm and averaged 1.08 mm, i.e., it corresponded to the egg diameter indicated by Kuragami for the two-coloured flounder.

The eggs were round, and the yolks were large, their sizes ranging from 0.89 to 1.01 mm and averaging 0.96 mm. The perivitelline space was narrow and represented from 3 to 7% of the diameter of the egg.

The embryo in the second stage of development was pigmented (see fig. 61, 2 and 3).

In the third and fourth stages (see fig. 61, 4 to 6) pigmentary cells were thickly scattered on the head, trunk and tail. Pigment appeared on the yolk at first in only a small quantity; the amount of pigment later increased gradually, and towards the close of embryonic development the entire yolk was dotted with a large number of melanophores.

According to Okada's data (1955) live, two-coloured flounder prolarvae that had just hatched were approximately 2.97 mm long. Their bodies were pigmented with yellow chromatophores and dark melanophores evenly scattered from the head to the tail.

In Korea Bay in the first half of December 1949 we collected eggs and fingerlings 4.0 to 12.3 mm long which, in the same way as their eggs, were extremely similar to starry flounder fingerlings that were of equal size, but differed from the latter in a large number of vertebrae and rays in unmatched fins, and in a more intensive pigmentation. On the basis of these features we classed these larvae with the two-coloured flounder.

Larvae 4 to 4.5 mm long were externally completely 391 symmetrical. The urostyle was slightly curved, and future hypurals were outlined under it. The head was short and

the snout smaller than the eye. The pectoral fins were of medium size, and their ends reached the middle of the trunk. Pigmentation consisted of small, slightly branched, almost punctate melanophores, most of which were located on the tail, with a smaller quantity in the remaining portion of the body. A regular double row of melanophores ran along the upper and lower edges of the tail, and a thinner row on the trunk, along both sides of the fin fold. In addition, a large quantity of melanophores was scattered on the lower lateral surface of the tail; in the central portion [of the tail] these melanophores also entered onto the upper lateral surface. Larger, branched melanophores were located above the intestine, a fairly compact pigment row passed along the middle line of the abdomen, and a few cells were scattered to the right and to the left of the latter. There were one or two cells on each side of the isthmus, and a small quantity scattered on the gill and auditory regions of the head.

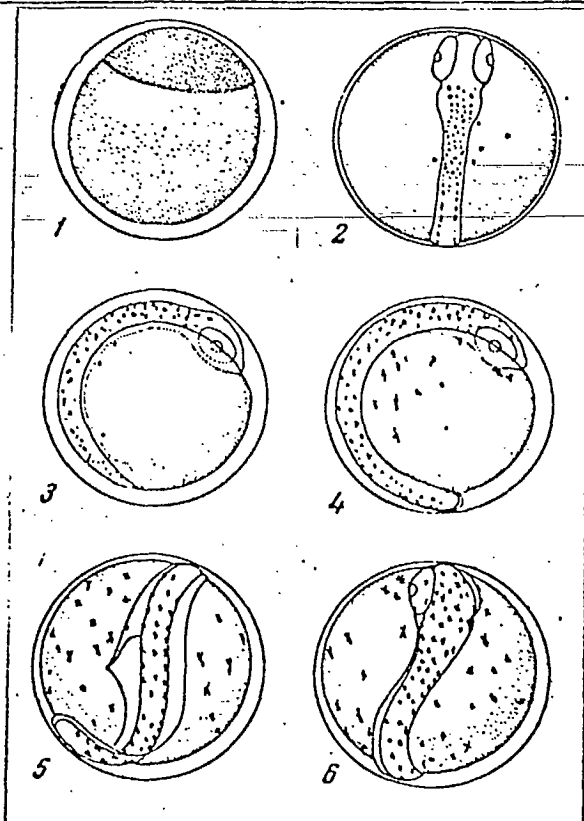


Figure 61 - Eggs of Kareius bicoloratus after fixation.
The figures indicate ordinal numerals

In larvae 5.15 (4.93) mm long the urostyle was almost straight (see fig. 62, 1). The height of the body represented 9.2% of its length. The myotomes were sigmoid, but their marginal branches were still very small. Thickened stripes with the rudiments of pterygiophores appeared at the base of the central portion of the future dorsal fin and in the forward portion of the anal fin.

Pigmentation had the same appearance as in the preceding stage, with the difference that the number of cells increased on the isthmus.

In larvae from 8.6 to 8.9 (8.4 to 8.50) mm long the height of the body represented 12.4 to 18.3% of its length. The urostyle was curved. Nine or ten rays were outlined in the tail fin. Pterygiophores were defined in the forward and middle portions of the anal fin, but in the dorsal fin they were noticeable only in the central portion.

The head was rounded and the snout was short. A gill cover in the form of a skin fold covered the entire gill chamber.

In larvae 9.08 mm long the height of the body represented 18.2% of its length. (see fig. 62, 2). Pterygiophores formed in the dorsal and anal fin folds, and very short fin rays were outlined in the greater part of the anal and dorsal fins. Vertebrae, numbering 38 (39), were clearly visible at this stage. Small ventral finlets appeared. The tail fin was nearly homocercal, and it contained nine to twelve rays. The 393 gill apparatus was not fully formed. The gill filaments were only slightly developed: they were best developed (and here not fully) on the third and fourth arches and most weakly

developed on the first arch. The gill rakers were rudimentary, and had the appearance of tubercles.

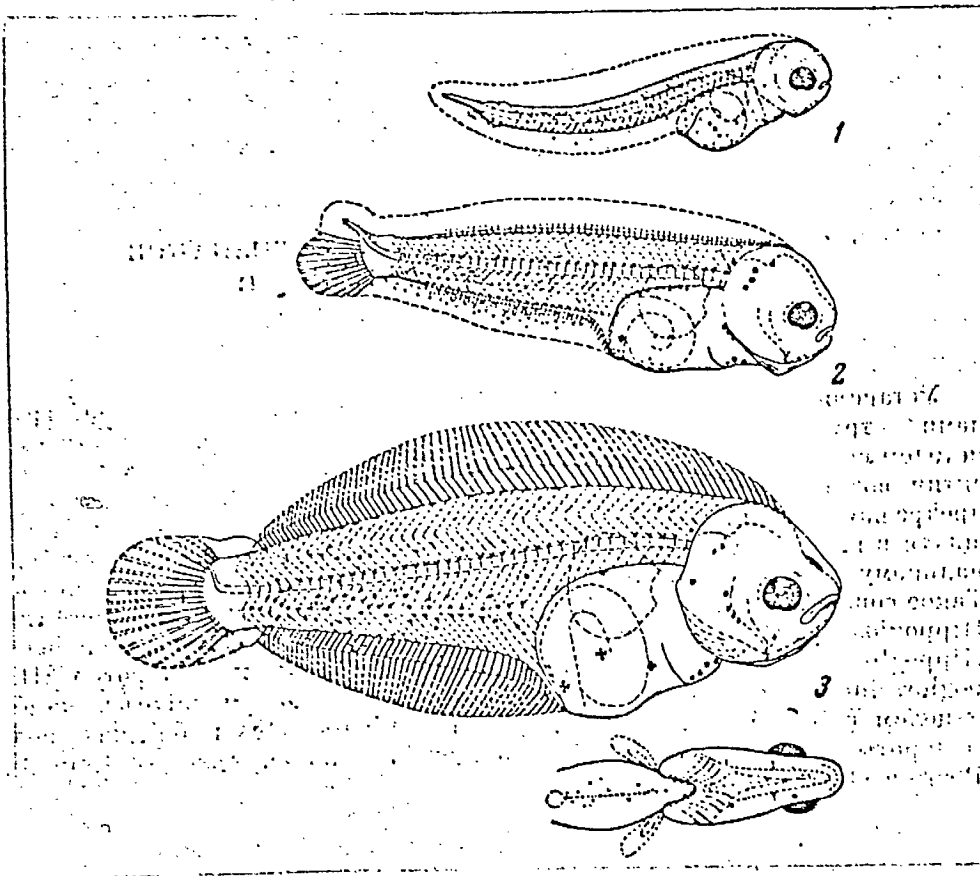


Figure 62 - Larvae of Kareius bicoloratus.

1 - 5.15 mm; 2 - 9.00 mm; 3 - 14.0 mm

To the pigment that existed in the younger larvae there was added a series of compact melanophores -- one for each segment, at the base of the neural arch, above the backbone (which facilitated the vertebral count); a large quantity of punctate melanophores was scattered on the anal fin fold, and a few less, on the fin rays of the tail. Pigment was completely absent at the end of the caudal peduncle.

In larvae 14.17 (12.34) mm long (see fig. 62, 3) the height of the body represented 31.6% of its length. The rays of the anal and dorsal fins were fully formed. There were 18 rays in the tail fin and 38 vertebrae in the body. The left

eye was noticeably higher than the right. Five rays formed in the ventral fin, but none were as yet visible in the pectoral fin.

The head was short and rounded. The olfactory capsules were large. The pigment retained its larval character. The sizes and proportions of individual parts of the bodies of the larvae that have been described are given in Table 67.

Table 67

The Sizes and Correlations of Body Parts of Larvae of *K. bicoloratus*

Dimension	Sizes of larvae, in mm	In per cent of l						In per cent of Cl					
Total length (L).....													
Standard length (l)..													
Distance from end of snout to insertion of anal fin.....	7,23 8,00 8,95 9,50 10,26 14,17	—	—	—	—	—	—	—	—	—	—	—	—
	7,01 7,80 8,50 9,08 9,67 12,34	—	—	—	—	—	—	—	—	—	—	—	—
Distance from end of snout to insertion of dorsal fin.....	2,69 3,06 3,44 3,93 3,72 4,54	36,0	39,2	40,5	43,2	38,4	36,8	—	—	—	—	—	—
	— — — — — 1,10	—	—	—	—	—	8,9	—	—	—	—	—	—
	0,65 1,07 1,56 1,65 1,59 —	9,0	13,7	18,3	18,2	16,4	—	—	—	—	—	—	—
Height of body behind anus.....	0,46 0,44 0,53 0,58 0,55 0,66	—	—	—	—	—	—	35,4	31,1	29,1	26,9	24,4	22,0
	0,21 0,26 0,46 0,39 0,38 0,44	—	—	—	—	—	—	15,5	17,2	14,3	18,1	17,2	14,7
Diameter of eye.....													
Length of snout.....	1,35 — 1,90 2,15 2,25 3,00	18,3	19,3	21,4	23,7	23,3	24,3	—	—	—	—	—	—
	— — — — — 2,80	—	—	—	—	—	22,6	—	—	—	—	—	93,3
Length of head to pectoral fin.....	— — — — — 1,47	—	—	—	—	—	8,5	—	—	—	—	—	—
	— — — — — 1,05	—	—	—	—	—	11,9	—	—	—	—	—	—
Height of head.....													
Length of caudal peduncle.....													
Height of caudal peduncle.....													

Chapter II.

A COMPARISON OF THE TAXONOMIC FEATURES AND THE
INTERRELATION OF GENERA OF FAR EASTERN FLOUNDER

/ 394

To establish kinship among taxonomic groups is a difficult problem which may be solved by only one method -- that of comparison. At the same time, it is necessary to cover, at various stages of development, as large a quantity as possible of the features of the groups being studied. Without predetermining the result, we attempted to compare data at our disposal on the embryonic and postembryonic development of certain of the flounder forms examined above. Such a comparison was expedient for halibut (Atheresthes, Hippoglossus, and Reinhardtius); small large-mouthed flounder (Cleisthenes, and Hippoglossoides); small large-mouthed, medium-mouthed and small-mouthed [genera] (Hippoglossides, Acanthopsetta, Limanda); the most important small-mouthed flounder as a whole (Limanda, Platessa, Liopsetta and Pleuronectes), and near genera of small-mouthed flounder in pairs (Limanda, Pseudopleuronectes, Liopsetta, and Pleuronectes).

The Genera Atheresthes, Hippoglossus and Reinhardtius

.There is much in common in the reproduction of species of these three genera of halibut. All reproduce at considerable depths, in the drop-off zone. Spawning occurs mainly in winter, in December and January, and probably in February, at a low, above-zero temperature of 2 to 3°.

There is reason to assume that the eggs, prolarvae and larvae of the halibut under comparison are larger than in all the remaining flounder that we have studied.

Their eggs are bathypelagic and develop in the deep levels of the open water. The prolarvae and larvae gradually float up to higher layers of water and simultaneously shift to the shore in such a way that the juvenile fish originating from them in the end approach the offshore shallow zone.

The halibut under comparison, in the structure and pigmentation of their prolarvae and larvae, fall into two sharply isolated groups, of which one embraces the species of arrowtoothed halibut, and the other, the true and Greenland halibuts. The heads of the larvae of arrow-toothed halibut are covered with spines; the pigmentary cells on the tail form two accumulations. The heads of true and Greenland halibut larvae have no spines; the pigmentary cells on the tail are scattered and form no accumulations.

The features of arrow-toothed halibut prolarvae and larvae that we have indicated are highly significant and without doubt reflect the genetic remoteness of this genus from the true and Greenland halibuts.

The Greenland and true halibuts also differ in all stages of development. To begin with, the eggs of the Greenland halibut are noticeably larger than those of the true halibut (4.0 to 4.5 mm as against 3.0 to 3.8 mm), while prolarvae that have just hatched are accordingly larger. This correlation is also retained in all succeeding stages. Rays form in unmatched fins in the Greenland halibut, and the latter itself lies on the bottom, at larger sizes than is the case with the true halibut (see Table 68). /395

Table 68

The Sizes of Halibut Larvae towards the Moment of Differentiation
of Pterygiophores and Rays in Unmatched Fins (in mm)

Stage of development	Greenland	True	Arrow-toothed
Urostyle slightly curved, 8 to 10 rays outlined in the tail fin.....	20.0	13.0 to 17.8	11.6 to 12.8
Urostyle sharply curved, 14 to 16 rays in tail fin. Pterygiophores have appeared.....	19.0 to 24.2	15.0 to 17.0	16
First rays have appeared in the dorsal and anal fins.....	22.7 to 27.0	14.1 to 17.3	--
All rays have been established. First pigmentary spots have appeared on the dorsal and anal fins.....	32	17.9 to 22	About 20

The bodies of Greenland halibut are longer than those of true halibut. Their pectoral fins are small, their tips scarcely going beyond the middle of the abdomen, whereas in the true halibut the pectoral fins are large and cover the entire abdomen as far as the anus itself. In addition, the true halibut's snout is pug-like, while that of the Greenland halibut is extended. Finally, the establishment and development of pterygiophores and rays in the fins of ^{the} Greenland halibut proceeds from back to front, whereas in the true halibut these processes take place forwards and backwards from the middle.

Both halibut genera differ also in the proportions of their bodies. The relative sizes of the head and of the distance from the end of the snout to the insertion of the anal fin, as well as body height, are at all stages of development noticeably smaller in the Greenland than in the true halibut.

The pigmentation of true and Greenland halibut larvae at the prolarval and larval stages is comparatively weakly developed. Finely punctate, scattered melanophores appear at first only on the surface and the distal edges of the rear portion of the dorsal and anal fins, and then spread forward. In addition, the lower and lower lateral rows in their tails consist in both cases of obliquely situated, intermyomeric melanophores. Although there is a general similarity in the character of pigmentation, there are also noticeable differences. The pigmentation of the fin folds in the true halibut is more intensive than is the case with the Greenland halibut. At the same time, the marginal melanophores of the fin folds in Greenland halibut larvae are concentrated only in the rear half, while in true halibut larvae they extend far forward (see figs. 3-6).

The conversion of larval to fingerling pigmentation in Greenland halibut larvae coincides with the initial appearance of rays in the dorsal and anal fins, while in the true halibut it occurs later, after the formation of rays.

The differences indicated between the prolarvae and larvae of the Greenland, true, and arrow-toothed halibut are extremely significant and evidently reflect the genetic separation of these genera.

The Genera *Acanthopsetta*, *Hippoglossoides* and *Limanda*

/396

It has been assumed that the genus *Acanthopsetta* is very close to the flathead flounder (Norman, 1934; Moiseev, 1953, and others). A study, however, of the individual development of the above flounder does not confirm this assumption.

The larvae of Acanthopsetta and of the flathead flounders differ sharply in all stages of development both in plastic features and in pigmentation. Nor are there less significant differences in pigmentation. In Hippoglossoides embryonic diffuse pigmentation is replaced by a sharply marked band-spot pigmentation, whereas in Acanthopsetta it is replaced by a linear-row type of pigmentation. Similar features are a row of cells bordering the end of the urostyle. and, in older larvae, a lower lateral row of intermyomeric cells. The linear distribution of the pigment and particularly the lower lateral and lateral rows of cells in Acanthopsetta larvae bring the latter somewhat closer to halibut larvae, which evidently represents convergence.

Acanthopsetta larvae are, in the character of their pigmentation, outwardly similar to L. aspera larvae, and there are cases where, when material is being sorted, they are incorporated into one group. Upon attentive examination Acanthopsetta larvae can be found to be distinct both in morphological and plastic features, and primarily in pigmentation.

In the first place, the lower row of cells in Acanthopsetta larvae differs sharply in its structure from an analogous row in Limanda larvae. In the former it consists of alternating single and double melanophores, whereas in the latter it is composed of two almost parallel rows. Then, too, the end of the urostyle in Acanthopsetta larvae is bordered by a row of cells, and the upper lateral row passes along almost the entire tail, while in Limanda the end of the urostyle is not pigmented, and the upper lateral row by no means reaches the level of the anus. Finally, the pectoral fins in Acanthopsetta

are not pigmented and the ventral row has no additional cells.

Acanthopsetta larvae, as compared with Limanda larvae of equal size, have a lower body, a long tail, an extended snout and larger eyes.

The Genera Cleisthenes and Hippoglossoides

The genera [sic] Cleisthenes are compared to the genus Hippoglossoides (Norman, 1934); a comparison, therefore, of the structure of their eggs and larvae at all stages of development is of considerable interest.

The species of both of the genera under comparison have pelagic eggs that differ substantially in their structure.

Cleisthenes eggs are minute, with a small perivitelline space. The eggs of all species of the genus Hippoglossoides are large, with a large perivitelline space (see Table 69).

Table 69

A Comparison of the Sizes (in mm) of the Eggs of Cleisthenes with those of Hippoglossoides

Species	Diameter of eggs	Yolk sizes		Sizes of perivitelline space	
		range	average	range	average
Sohachi flounder....	0,90-1,03	0,64-0,87	0,71-0,80	3,0-18,0	7,0-11,0
Flathead flounder...	2,00-3,67	0,82-1,53	0,90-1,33	20,0-33,0	27,0-32,0

Smaller sohachi flounder (Cleisthenes) prolarvae and /398 larvae lag behind in size at the moment of hatching and in all subsequent stages.

Towards the moment of absorption of the yolk sac sohachi flounder larvae are shorter than 4 mm, while flathead flounder are longer. Rays begin to be established in the sohachi flounder at a length of 9.4 (8.4) mm, and in the flat-head flounder, much later.

These two genera also differ in the proportions of their bodies. The distance from the end of the snout to the insertion of the anal fin, the height of the body, and the length of the head of the larvae are, towards the moment of absorption of the yolk sac and the establishment of the rays in the fins, greater in the sohachi than in the flathead flounder, and the eyes are smaller (see Table 70).

The prolarvae and larvae of the genera under comparison also differ to a very great extent in pigmentation. In Cleisthenes the embryonic pigment on the tail changes into two broad bands interrupted along the middle line, while in Hippoglossoides it changes into three or four such bands. Thus a comparison of the structure of the eggs and larvae of these genera shows that in early stages of development they differ sharply, which confirms the dissociation of the genera Cleisthenes and Hippoglossoides.

The Genera Limanda, Platessa, Liopsetta and Pleuronectes

P. Yu. Schmidt (1950) considered the three independent genera of small-mouthed flounders -- Platessa (according to Norman, Pleuronectes), Pleuronectes (according to Norman and Schmidt, Platichthys) and Liopsetta -- to be closely related, and incorporated them into the one genus Pleuronectes in the class of subgenera on the basis of the structure of jaw and pharyngeal teeth. P. A. Moiseev (1953), too, follows the

Table 70

The Sizes and Proportions of the Body Parts of Prolarvae and Larvae of

Cl. herzensteini and H. dubius

Species	Stage of development	Length, in mm		Percentage of length of body		Percentage of length of head
		of body	total	a ^A	lc	0
Sohachi	Prolarvae that have just hatched					
Flathead	Same					
Sohachi	Larvae towards moment of absorption of yolk sac					
Flathead	Same	2,10—2,51	2,17—2,59	43,50—52,50	19,10—23,5	26,40—35,50
Sohachi	Establishment of rays in unmatched fins	2,53—3,04	2,60—3,13	46,40—51,00	19,10—25,40	30,00—32,70
Flathead	Same	3,34—3,63	3,56—3,76	35,6—38,00	15,00—15,50	31,40—41,30
		4,97—5,40	5,10—5,60	33,3—36,4	12,0—13,5	36,60—41,00
		8,40	9,40	40,00	29,00	21,00
		9,50	10,30	39,5	20,8	23,9

system of P. Yu. Schmidt. According to A. P. Andriyashev (1954), the genus Platessa is close to the genera Limanda and Liopsetta, occupying, in several features, an intermediary position between them, while the genus Liopsetta also resembles the genus Pleuronectes. The genera Platessa and Liopsetta are closest in the quantity of myotomes in the trunk section. The same degree of resemblance is observed when bodily length and the proportions of individual body parts are compared.*

Towards the moment of absorption of the yolk sac Platessa differs sharply from Limanda in the length of its body and the distance from the end of the snout to the insertion of the anal fin, and is much closer to Liopsetta. In the size of its eyes Platessa occupies an intermediate position between the above genera (see Table 71).

Approximately the same correlations are retained / 399 in the comparison of larvae that closely resemble each other in size (see Table 72).

The eggs of all of the species of flounder under comparison are pelagic (not counting the divergent form Liopsetta obscura), and attain their greatest size in Platessa, a somewhat smaller size in Liopsetta, and a still smaller size in Pleuronectes, while Limanda has the smallest eggs. The membrane of Platessa eggs is thick, reticulate and wavy, and in the eggs of the remaining forms it is thin and almost smooth. After fixation with a 2% formalin solution the membrane of Platessa eggs becomes a dark, brownish-lilac colour, and in Pleuronectes, a rose-tinted lilac colour.

* In view of the absence of data on the body proportions of Atlantic species, plastic features are compared only on the basis of Far Eastern flounder.

Table 71

Sizes (in mm) and Plastic Features of Larvae of Representatives of
the Flounder Genera Limanda, Platessa, Liopsetta, Pleuronectes
towards the Moment of Absorption of the Yolk Sac

Species	Length		Percentage of length of body		Percentage of length of head
	total	body	distance from end of snout to insertion of anal fin	length of head	diameter of eye
<i>L. aspera</i>	2,96—3,52	2,80—3,36	32,4—36,4	13,5—14,5	39,0—48,7
<i>Pl. quadrituberculata</i>	6,34—7,16	5,58—6,94	37,0—39,0	13,5—16,4	31,4—41,8
<i>L. pinnifasciata</i>	5,58—5,86	5,27—5,57	37,6—40,0	14,4—14,8	29,4—33,2
<i>Pl. stellatus</i>	3,50—4,55	3,25—4,29	38,4—39,2	16,8—18,1	28,6—37,1

Table 72

Sizes (in mm) and Plastic Features of Larvae of *L. aspera*,
Pl. quadrituberculata, *L. pinnifasciata* and *Pl. stellatus*.

Species	Length		Percentage of length of body		Percentage of length of head
	total	body	distance from end of snout to insertion of anal fin	length of head	diameter of eye
<i>L. aspera</i>	—	5,6—6,9	—	27,6—36,8	13,4—22,7
<i>Pl. quadrituberculata</i>	6,34—7,16	5,58—6,94	37,0—39,0	13,5—16,4	31,4—41,8
<i>L. pinnifasciata</i>	5,07—5,83	4,84—5,55	36,8—38,2	13,0—15,3	28,2—36,8
<i>Pl. stellatus</i>	5,26—5,90	5,02—5,60	38,2—41,7	16,0—20,0	26,9—35,7

In the nature and distribution of pigmentary cells on the body of the Platessa embryo there is revealed a similarity to Liopsetta and, to a lesser degree, to Pleuronectes.

The Platessa prolarvae hatch with pigmented eyes, and are only slightly larger than Liopsetta prolarvae, much larger than those of Pleuronectes, and still larger than those of Limanda. They strongly resemble the latter in pigmentation. Features common to these species include a row distribution of melanophores and the lack of accumulations of pigmentary cells on the tail, with, however, the difference that in Platessa the middle lateral row is longer, and begins at the level of the anus and not from the second third of the tail. In addition, Platessa larvae differ from those of Limanda in a short row on the upper edge of the end of the tail, and in the absence of melanophores on the pectoral fins.

The pigmentation of prolarvae and larvae of Liopsetta and Pleuronectes, as we saw above, has a completely different character, and is in sharp contrast to that of Platessa and Limanda.

After rays have been established in the fins, the pigmentation of Platessa occupies an intermediate position between that of Limanda and Liopsetta.

The increase in length and the form development of the larvae of the groups under comparison take place in such a way that the larger sizes of Platessa larvae towards the moment of absorption of the yolk sac are retained only to the initial formation of the rays in the anal and dorsal fins. Subsequently, the lengths of Platessa and Liopsetta larvae become almost equal and Platessa larvae lag in length behind Limanda larvae. The smallest Limanda larvae, towards the moment of absorption of the yolk sac and the moment of formation of unmatched fins, outstrip, in length, the larvae of the species

under comparison. The larvae that lag most in length at this stage of development are those of Pleuronectes. Their metamorphosis ends earlier than in the forms listed and at the shortest length. Liopsetta comes second in the speed with $\angle 400$ which its metamorphosis is completed; Platessa is in third place, and Limanda, last.

The history of development shows that Platessa, in several features in the embryonic and later stages, is closer to Liopsetta than to Limanda.

The Genera Liopsetta and Pleuronectes

Eggs of species of the genus Liopsetta are larger than those of species of the genus Pleuronectes, and prolarvae that have hatched are accordingly larger. The smaller sizes of the prolarvae and larvae of Pleuronectes are also retained in succeeding stages, so that the length of their bodies at each stage of development is less than \angle corresponding \angle body lengths in Liopsetta, and at the same sizes, Pleuronectes larvae are shorter in the body than those of Liopsetta. The character of the melanophores and their distribution on the embryos of both species are similar. The pigmentary cells are fairly large and slightly branched, and thickly cover the body of the embryo. After hatching, a more or less compact accumulation of melanophores (a band) forms in like manner on the middle of the tail in prolarvae of both genera.

The pigmentation of the larvae of the banded and starry flounders is especially similar.

The larvae of the banded and starry flounders at ^{similar} ~~same~~ stages of development differ in body length, but are similarly

pigmented, and bear a close resemblance in the relative sizes of the distance from the end of the snout to the insertion of the anal fin, and of their eyes (see Tables 73 and 74).

Table 73

The Sizes and Correlation of the Body Parts of Larvae of L. pinnifasciata and Pl. stellatus towards the Moment that Absorption of the Yolk Sac is Completed (in mm)

Species	Length		Percentage of length of body			Percentage of length of head
	total ^s	body	aA	H	lc	O
L. pinnifasciata	5,58—5,86	5,27—5,57	37,6—40,0	4,65—4,8	14,0—14,8	29,4—33,2
Pl. stellatus	3,50—4,55	3,25—4,29	38,4—39,2	5,9—7,4	16,8—18,1	28,6—37,1

Table 74

The Sizes and Correlation of the Body Parts of Larvae of L. pinnifasciata and Pl. stellatus Flounders (in mm)

Species	Length		Percentage of length of body			Percentage of length of head
	total	body	aA	H	lc	O
L. pinnifasciata	5,07—5,83	4,84—5,55	36,8—39,5	4,8 (4,3—5,8)	14,05 (13,0—18,2)	28,2—36,8
Pl. stellatus	5,26—5,90	5,02—5,60	38,2—41,7	10,23 (7,8—13,3)	18,01 (16,0—20,0)	26,4—35,3

In banded and starry flounder larvae that are equal in length but different in degree of development, body proportions differ in that banded flounder larvae have a lower and more elongated body and that the distance from the end of the snout to the insertion of the anal fin, and the sizes

of the eyes, disclose no sharp differences. The similarity of the pigmentation and the plastic features of the larvae indicates the proximity of the genera Pleuronectes and Liopsetta (without L. obscura).

The Genera Limanda, Pseudopleuronectes and Lepidopsetta 401

As is known, the species of the genus Pseudopleuronectes up to 1934 were not segregated from the genus Limanda, and up to the present time are considered as taxonomically close. Hence their comparison is of great interest in the light of embryological data.

As indicated above, in their reproduction and development the species of the genus Pseudopleuronectes fall into two ecological groups -- the early spring, including Ps. yokohamae and Ps. americanus, and the spring-summer, with the single species Ps. herzensteini.

Ecologically, the genus Limanda resembles only the latter species. The reproduction and development of the species of Limanda and Ps. herzensteini take place at the same time under the same conditions: in the spring and summer, at a comparatively high surface water temperature. No resemblance, however, is disclosed in the structure of the eggs, or particularly of the prolarvae or larvae.

The eggs of all of the species of the genera Limanda and Ps. herzensteini are small and pelagic and are similar in the first stages of development. Identifying features at this stage are the somewhat larger diameter of the eggs and the size and structure of the yolk in Ps. herzensteini. With the appearance of the embryo and particularly the pigmentary cells

on the latter, the differences between the eggs of the species under comparison become more noticeable, and in the course of further development increase still more. The embryos of L. aspera and L. punctatissima are less pigmented; the lower edge of the tail is either not pigmented at all or has only one to three melanophores, whereas in Ps. herzensteini there are many more melanophores, and prior to hatching they group into two or three accumulations. The differences in the pigmentation of the tail which have appeared in the embryonic stage after hatching intensify still further.

The pigmentary cells on the tails of the prolarvae and larvae of L. aspera are at first scattered, and then form longitudinal rows; the pigmentary cells in all species of Pleuronectes form accumulations in the shape of bands. In Ps. herzensteini there are three such bands, in Ps. yokohamae, two, and Ps. americanus, one.

No such difference is observed in the pigmentation of the trunk, or particularly the lower surface of the abdomen or the head. The lower surface of the abdomen and head of all these species is heavily pigmented but, in contrast to L. aspera, in Ps. herzensteini the melanophores situated along the sides from the middle abdominal row separate into two groups -- forward and rear (see fig. 39). These differences are retained in later stages of development.

Towards the moment that rays appear in the unmatched fins, the difference noted in the pigmentation of the tail begins to be obliterated. As indicated previously, in formed larvae, accumulations in the form of spots on the upper and lower edges of the tail also appear in species of Limanda,

but at this time new identifying features are added which are related to the number of vertebrae and rays in unmatched fins.

The prolarvae and larvae of the subgenus Myzopsetta (L. punctatissima punctatissima and L. proboscidea) and L. ferruginea in the nature of their pigmentation are somewhat closer to species of the genus Pseudopleuronectes in that the pigmentary cells on their tails form accumulations which in comparison with those of Pseudopleuronectes are much less clearly marked and are represented by a short upper stripe (L. punctatissima proboscidea) or a small group of cells (L. punctatissima punctatissima).

Larvae of L. punctatissima punctatissima and L. punctatissima proboscidea, which have a slight similarity in the pigmentation of the tail, are noticeably larger than those of L. aspera, and differ from Ps. herzensteini in the pigmentation of the lower surface of the abdomen.

In contrast to Ps. herzensteini and L. aspera, the lower surface of the abdomen in L. punctatissima larvae is only slightly pigmented, and aside from a middle row of 402 melanophores, there either are no additional pigmentary cells along the sides from the abdomen, or there are only one to three cells. The species of the early spring ecological group -- Ps. americanus and Ps. yokohamae -- differ to an even greater extent from Limanda. Their eggs are of the bottom type and sticky; the yolk is compact and has a glassy lustre. Limanda eggs are pelagic. The melanophores on the tails of prolarvae of all species of Pseudopleuronectes form accumulations in the shape of bands and stripes which are absent in Limanda.

The above important morphological distinctions between identical stages of development of species of the genera Limanda and Pseudopleuronectes indicate their undoubted generic independence. At the same time, as indicated above, it is evident that the taxonomic system of the genus Pseudopleuronectes itself needs revision.

The genus Lepidopsetta (Norman, 1934) is also taxonomically close to the genus Limanda, and differs from it in the nature of its reproduction and in the structure of its eggs in the same way as Ps. yokohamae and Ps. americanus differ from Limanda. Like Ps. yokohamae and Ps. americanus, species of the genus Lepidopsetta reproduce in winter and spring at a low temperature close to 0°. Species of Lepidopsetta, Ps. yokohamae and Ps. americanus, which are similar in the ecology of their reproduction, have many similar features in the structure of their eggs and larvae. A common characteristic feature of species of Lepidopsetta, Ps. yokohamae and Ps. americanus is represented by bottom eggs with an extremely compact yolk structure, atypical for flounders. A no less important similarity between them is disclosed in the pigmentation of their prolarvae and larvae. The pigmentary cells on the bodies of the latter are grouped alike into two accumulations, of which the rear has the appearance of a band, while the forward accumulation is represented by an upper stripe. It should be noted that the larvae of Ps. americanus deviate somewhat from this type: in contrast to Ps. yokohamae and Lepidopsetta they develop only one band, situated on the middle of the tail.

The eggs, prolarvae and larvae of Lepidopsetta and of two species of the genus Pseudopleuronectes, however, which are generally similar, are at the same time specifically different.

To begin with, the membrane of the eggs of the former does not have the adhesive layer that exists in the eggs of Ps. yokohamae, and in this respect is closer to that of Ps. americanus. The prolarvae and larvae of Lepidopsetta are more heavily pigmented than are the species of Pseudopleuronectes in general and Ps. americanus in particular. They have many thickly scattered melanophores on the lower half of the abdomen and the head, a unique accumulation of these melanophores on the anal and dorsal fin folds, and a few cells, occasionally blending into a solid stripe, on the lower edge of the pectoral fins.

In subsequent development the initial similarity gradually decreases, and towards the moment of completion of metamorphosis, juveniles of Ps. yokohamae differ from Lepidopsetta in several plastic and meristic features. L. aspera, which in its initial larval stages has a more primitive pigmentation, occupies an intermediate position between the two foregoing species in the number of its vertebrae and rays.

It is quite possible that Limanda aspera is closest to the common initial form for all of these genera. The ancestors of the genera Lepidopsetta and Pseudopleuronectes, which had disjoined from the latter [presumably Limanda aspera] in the process of adapting to conditions of habitation, reproduction and development in various environments, proceeded by different routes in their evolutionary development and formed not only independent species, but genera as well.

The Genera Glyptocephalus, Tanakius, Microstomus and
Hippoglossoides

The genus Glyptocephalus is close to the genera Tanakius and Microstomus, whose species have long intermingled. After the investigations of Hubbs (1932), however, / 403 and especially after the thorough analysis of the identifying features of these flounders carried out by T. S. Rass (1950), there is now no difficulty in determining the species to which the flounder of these genera belong.

Hence it is expedient to compare the history of development of the species of these genera. Unfortunately, the necessary information on this problem relating to all of the species that interest us has not been published, and we can make a comparison only with an Atlantic species -- M. kitt, the history of whose development has been thoroughly studied (Cunningham, 1889; McIntosh, 1891; Kyle, 1898 and 1923; Petersen, 1904; Ehrenbaum, 1905 and 1909; Schnakenbeck, 1928; Nybelin, 1935; Pertseva, 1936, and others).

The eggs of Microstomus kitt, like those of the genus Glyptocephalus, are pelagic and comparatively large (their diameter ranges from 1.13 to 1.46 mm), and in their size are closer to Gl. Stelleri than to Gl. cynoglossus. Their membrane, in contrast to those of other species of eggs, is thin and reticulate.

According to Ehrenbaum's data, larvae that have just hatched are usually fairly large, their length ranging from 4.7 to 5.5 mm; smaller larvae from 3.5 to 4.0 mm long are, however, also found.

In their structure and pigmentation the larvae of the species under comparison appear similar, but upon close examination important deviations are disclosed. To begin with, in larvae of M. kitt the distance from the end of the snout to the anus represents more than 1/3 of the length of the body (in both species of the genus Glyptocephalus it is less than 1/3), and the body of the M. kitt larva is much higher; the older the larva, the greater is this difference. In older M. kitt larvae there are four transverse bands on the tail, while in Glyptocephalus there are three. In M. kitt these bands are discontinuous and consist of stripes and spots situated on the upper and lower edges; in Glyptocephalus they are continuous and occupy the entire width of the tail. Moreover, in Glyptocephalus, in addition to the main bands, the same quantity of lower spots and stripes exists in the space between them: in M. kitt there are also spots on the edges of the fin folds that correspond to the transverse bands of the tail; in Gl. stelleri and Gl. cynoglossus there are no such spots on the fins.

The above differences increase more and more in proportion to further development, and in late stages they are so great that they are immediately evident.

Glyptocephalus larvae are thin and long, while M. kitt larvae at a similar stage are short and wide. Hypurals begin to be established in M. kitt when [the larvae] are 6 mm long, whereas in Glyptocephalus this process takes place at lengths of 12 to 15.5 mm. Metamorphosis is completed in M. kitt at a length of 18 mm, and in Glyptocephalus at lengths of 50 to 60 mm.

In a comparison of the history of development of M. kitt and of species of the genus Glyptocephalus more or less similar features are visible only in the most initial stages of development. In prolarvae this similarity is disrupted, and the divergence in features subsequently increases to an ever greater extent.

It may hence be assumed that the ancestors of the genera Microstomus and Glyptocephalus, which we are comparing, were at one time very close but that their ancestors lost this proximity in the process of evolution and withdrew comparatively far from each other.

In conclusion, we shall compare the larvae of the long flounder with prolarvae and larvae of flathead flounder (Hippoglossoides) that are found simultaneously.

In long flounder prolarvae there are three main continuous bands on the tail; the melanophores of the last of these do not go as far as the very end of the tail. In flathead flounder prolarvae, four bands form on the tail, and the melanophores of the last band surround the end of the tail. In addition, the rectum of long flounder prolarvae is immediately adjacent to the yolk sac, and in larvae, to the loop of the intestine; in flathead flounder there is a space between these organs that is filled with fin fold. /404

The larvae of small-mouthed [slime] flounder are also characterized by the smaller sizes of their mouths and by a shorter trunk, whose size usually represents less than 1/3 of the length of the body.

The Genera *Kareius* and *Pleuronectes*

As is known, Norman (1934) incorporates the genera *Pleuronectes* (*Platichthys*) and *Kareius* into one genus.

V.K. Soldatov and G.U. Lindberg (1930), P.Yu. Schmidt (1931) and L.S. Berg (1949) consider them to be independent. A comparison, therefore, of the histories of development of *Kareius* and *Platichthys* is of considerable interest.

The eggs of the starry and Korean flounders are very similar in their external appearance and size. Both are pelagic, with a small perivitelline space, and are larger in comparison with eggs of species of the genus *Limanda*. Differences between them appear from the moment of formation of pigment.

In the starry flounder the yolk, with the exception of a small section at the pectoral fins, is not pigmented; in the two-coloured flounder it is dotted with a large quantity of melanophores. The fin folds of the embryos, prolarvae and younger larvae of the starry flounder have accumulations of melanophores on the level of the middle of the tail; these accumulations are absent in the two-coloured flounder. The pigmentary cells of Korean flounder prolarvae that have just hatched are scattered evenly, and in the starry flounder form an accumulation in the shape of a band on the middle of the tail.

Starry flounder larvae appear similar to two-coloured flounder larvae, but upon careful examination they, like the prolarvae, are distinguished by certain features (see figs. 61 - 63).

The pigmentation of the tail of both species is diffuse and finely punctate, but in the Korean flounder it is more strongly marked than in the starry flounder. An important distinction in the larvae of the starry flounder is a double row of melanophores on the upper edge of the trunk and the tail, and a more regular row of deep cells (one for each segment) along the middle line of the body at the base of the neural arches of the backbone. In addition, two-coloured flounder larvae are distinguished by a larger number of myotomes, vertebrae, and rays in unmatched fins.

Thus the starry flounder differs from the two-coloured flounder at all stages of its development.

The degree of difference between Pl. stellatus and K. bicoloratus is much more marked than that between Pl. stellatus and Pl. flesus.

The correctness, then, of separating the two-coloured and starry flounders into different genera is confirmed by material on their ontogenetic development.

The foregoing permits us to isolate the taxonomic features of the individual genera and species of flounder in the attached keys.

THE INFLUENCE OF WATER TEMPERATURE AND SALINITY
ON THE DEVELOPMENT OF CERTAIN SPECIES OF FLOUNDER

Of the entire complex of factors influencing the development of eggs and larvae we were able to concern ourselves only with temperature and, to a much lesser extent, salinity. A great deal of attention has been directed, both in the Soviet Union and abroad, to studying the effect of reduced and increased temperature. A vast number of experiments has been set up and analyzed, and many articles have been written, most of which have originated from Soviet, and mainly Leningrad, investigators (Vernidub, 1940 and 1941; Detlaf and Ginzburg, 1945; Korovina, 1952 and 1953; Nikiforov, 1939; Lozino-Lozinskii and Lyubitskaya, 1940; Olifan, 1940 and 1945; Morozova and Karakash, 1939; Privol'nev, 1935, 1939, 1941, 1949 and 1953; Privol'nev and Razumovskii, 1939; Trifonova and Popov, 1937; Trifonov, Vernidub and Filippov, 1939; Stroganov, 1939; Trofonov, 1949, and others).

These investigations have reached an especially high level of development in the last 15 to 20 years because of the demands of fish culture practice caused by the construction of hydroelectric power stations, the necessity for artificial reproduction of many species of valuable commercial fish -- perch, bream, pike-perch, and certain species of whitefish, salmon, smelts, herring, sturgeon etc.

Placing individual portions of eggs from one series, developing under optimum conditions from the moment of fertilization, for the same length of time into conditions of high or low temperature, a shortage or complete absence of

oxygen, and into solutions of poisons that suppressed breathing, the investigators established that the survival and physical condition of the embryo vary in different stages. The term "susceptibility" has been adopted for designating the stage or period of greatest mortality or deepest disruption of normal development resulting from the action of various factors on the developing eggs of fish. This conception is not related to the acceleration in development that occurs when the temperature increases.

An idea was at first obtained as to the non-specificity of the response reaction of the embryo to various external influences.

V. M. Korovina (1952 and 1953), however, established that fish embryos at various stages of development have different resistance to all of the influences that were tested.

The above investigators have established the boundary values of the fluctuations of various conditions [as they affect] the development of embryos; we, however, have been interested in the possibility of development only under the fluctuations of natural conditions.

The Effect of Fluctuations in Salinity on Egg
Development
Development in Fresh Water.

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Banded and black flounder. As indicated above, the banded flounder keeps to the shallow offshore-zone, where it prefers freshened water and even enters the lower courses of rivers, i.e., completely fresh water (Berg, 1948-1949); Schmidt, 1950; Moiseev, 1953). It was hence necessary to solve the problem of whether or not the development and

reproduction of the eggs of this flounder were possible in fresh or freshened water. In order to clear up this problem, two experiments were set up involving artificial fertilization in fresh water. Artificial fertilization, however, did not take place, since the sperm that was released into the fresh water coagulated into flakes that dropped to the bottom. The eggs, too, dropped to the bottom in the same way. A blastodisc formed parthogenetically in the course of 24 hours in the eggs that remained in the fresh water, but no cleavage occurred in either the first or the succeeding periods of 24 hours.

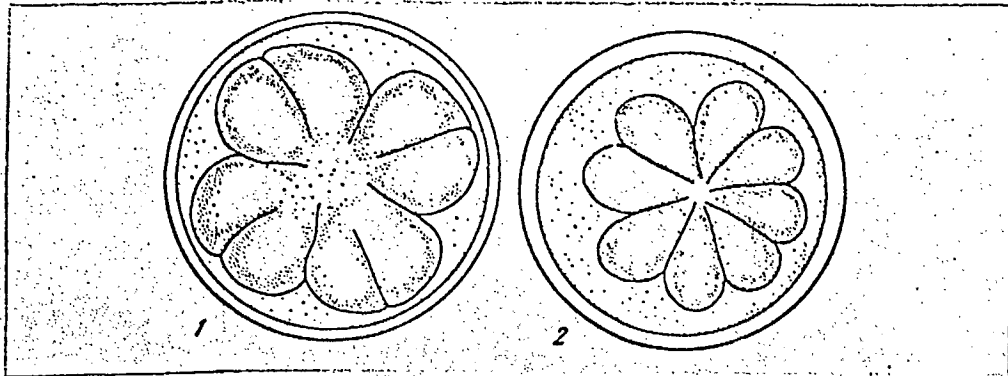


Figure 63 - Cleavage in an egg of L. pinnifasciata.
1 - in fresh water; 2 - in semi-salt water

Experiments were then set up on the effect of fresh water on eggs in various stages of development that had previously developed in salt water.

The results of the experiments showed that the development of banded flounder eggs in fresh water is impossible, since under these conditions cleavage takes place improperly (fig. 63). Twenty-four hours after the beginning of the experiment all of the eggs died.

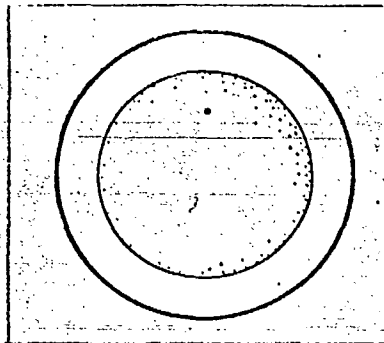


Figure 64 - Egg of *L. obscura* in fresh water

Experiments to ascertain the possibility of developing black flounder eggs in fresh water also yielded negative results. Black flounder eggs that had just been fertilized swelled greatly after being transferred to fresh water; consequently, a large perivitelline space formed between the egg membrane and the yolk, and the eggs themselves took on an appearance that was not characteristic of this flounder (see fig. 64). The swollen eggs stayed on the bottom, and their diameter in our experiments varied from 1.1 to 1.20 mm, averaging 1.15 mm, whereas the size of the control eggs did not exceed 0.94 mm. No cleavage was disclosed in eggs that had been placed in fresh water, and the eggs quickly died.

It follows from our experiments that not only the fertilization, but the development of already fertilized banded flounder eggs is impossible in fresh water, and that black flounder eggs cannot develop in fresh water either.

Development in Brackish Water

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(seawater of less than full salinity)

Banded flounder. Two experiments were carried out to investigate the possibility of the development of flounder eggs in brackish water.

Developing banded flounder eggs, fertilized in normal sea water, were transferred to seawater that had been half diluted with fresh water (S was about 16‰). The eggs immediately dropped to the bottom and lay there until the end of embryonic development. Most of the eggs developed abnormally; hence we disclosed many malformed specimens which had no eyes. The hatching of both normal and deformed larvae took place very sluggishly, and some embryos which did not free themselves from the membrane, died. The prolarvae that hatched were, in their general appearance and pigmentation, similar to prolarvae that had developed in normal seawater, but many of them lay on the bottom, and moved very languidly or were entirely motionless.

The state of the prolarvae did not improve subsequently; they continued to lie on the bottom, their tails were bent and their appearance was clearly nonviable. In spite of the fact that the larvae were transferred to salt water, they died in a few days. From the control eggs, which developed under the same temperature conditions in brackish water, there hatched fully viable, normally developing prolarvae, which kept to the upper layers of the water and swam well. The experiment demonstrated that a salinity reduced to half the normal level inhibits embryonic development, as a result of which many deformed specimens appear, and nonviable prolarvae hatch.

Black flounder. Similar experiments conducted with black flounder eggs showed that fertilized eggs in freshened water at first developed normally. In certain eggs, however, after the formation of 32 blastomeres, the middle blastomeres were observed to fuse into one solid mass, and at the blastula stage there began a mass breakdown of the blastomeres. Nonetheless some eggs, which safely passed this stage, continued to develop further.

The further development of the eggs was complicated by the formation on their membranes of a thick bacterial coating, which caused a slowing in rates of development, mass mortality and delay in hatching. After the eggs were immersed for a few minutes in a weak solution of potassium permanganate, development improved, and on the whole the prolarvae hatched, but as compared with that in other series, the hatching process began with some delay and was extremely lengthy, which indicated poor development conditions. The prolarvae in the series that we are describing hatched, at an average temperature of 3.4° , after only 23 days, whereas in another series at a lower temperature of 2.4° , the prolarvae hatched after 21 days.

Our experiment indicates (admittedly only very approximately) the possibility of developing only the most plastic eggs in freshened water, while the bulk of eggs dies at the very beginning of development in the cleavage stage (morulae - blastulas).

The sohachi flounder. Experiments were also arranged on the effect of salinity fluctuations on the development of the eggs and larvae of the sohachi flounder. A group of eggs obtained from one female was divided into three parts, of

which one was placed in fresh water, another, in sea water, and the third, in a mixture of equal parts of fresh and sea water (S about 16%). The eggs placed in fresh water, as was to be expected, died very rapidly. Development in undiluted [sea] water took place normally and thus served as a control. In semisalt water all of the eggs also developed normally; moreover, the prolarvae that hatched from /408 them did not, at any of the stages that we traced, differ morphologically in any way from the larvae that were in sea water.

Since the control group in pure sea water developed at the same speed, and the prolarvae that hatched were of the same appearance and size, it may be stated that a certain freshening does not harm sohachi flounder larvae in the stages of development that we have traced.

The Japanese flounder. According to Yamamoto's experiments (1939), Japanese flounder eggs develop normally at salinities of 20.90 to 40.11‰, and larvae, at salinities of 14.34 to 33.74‰. A salinity lower than 7.83‰ leads to the deformation of the larvae.

To judge from our observations, the different reaction of eggs of the above species to semisalt water is closely related to the conditions under which the eggs of these fish are naturally spawned and develop.

The banded and black flounders lay their eggs at a stable salinity. The weak reaction of Japanese and sohachi flounder eggs and larvae to reduced salinity may be explained by the reproduction and development of their eggs during the spring and summer period under conditions of intermittent

fluctuations in salinity.

The results that we have obtained are only very approximate and need further investigation.

Development in Slightly Freshened Water

The banded flounder. Some of the developing eggs (of series XI) were transferred to slightly freshened water taken from an ice hole during the melting period. The eggs were lowered into the main body of the water, and some fell to the bottom. Placed under the same temperature conditions as were the eggs of the initial series, they developed normally, and from them there hatched fully viable prolarvae, which did not differ either morphologically or in their behaviour from larvae that had developed in normally salt water. It is an interesting fact that the hatching process took place more harmoniously in the experiment than in the control. The prolarvae that hatched in slightly freshened water kept to the surface layers and swam animatedly. This experiment indicated the possibility of the development and, probably, the spawning, of banded flounder in a slightly freshened zone, near the outflow of rivers, which evidently does take place under natural conditions. Thus at the time of our studies, sexually mature specimens of banded flounder were caught at shallow depths of 10 to 15 m at various places in Amur Bay. The capacity of banded flounder eggs to develop in somewhat freshened water is of immense biological significance. The duration of incubation of eggs of this species at temperatures in the sea in February and March (-1.8 to 1.0°) is about one and one-half to two months. Consequently, during the ice-melting period the eggs are under conditions of fairly heavy freshening and drop to pelagic depths. Here they

continue to develop safely, having avoided harmful mechanical action from ice breaking up and shifting in the upper layers of the water.

The Effect of Different Temperatures
on the Development of Eggs

The rock sole. As indicated above, rock sole eggs have developed successfully in series where the water temperature at the beginning of cleavage did not exceed 4.2°C . A temperature increase to 7.2 to 10.2° caused abnormal cleavage, breakdown of the blastomeres and the subsequent death of the eggs.

The Japanese flounder. Yamamoto's experiments (1939) /409 on the effect of temperature on the development of Japanese flounder eggs and larvae showed that the eggs developed normally at water temperatures of 6 to 16° . The optimum temperature was about 9° .

A temperature range of 7.7 to 19.7° is favourable for the normal development of larvae.

In our experiments, which were conducted at the end of April and the beginning of May 1952, artificially fertilized eggs developed normally at temperatures of 4 to 12° (an average of 8.4°). At 20 to 25° the eggs died rapidly.

In 1953, in eggs obtained on 6 April in Anna Bay also through artificial fertilization, cleavage began at water temperatures of 14.8 to 18° and went as far as the blastula stage. The cells subsequently slipped from the blastodiscs and the eggs died.

The effect of temperature on the course of development of the banded flounder has been studied in more detail.

The banded flounder. As indicated above, temperatures of -2.0 to $+2.6^{\circ}$ are favourable for the embryonic development of this flounder during the cleavage period, as are those of -2.0 to $+3.6^{\circ}$ (5) during the period of formation and growth of the embryo. Development in the last two periods can also take place at higher temperatures of up to $+6.2^{\circ}$ (8), but this temperature may be considered as being close to lethal, since it causes mass mortality among the embryos, and the premature hatching of underdeveloped and clearly nonviable pro-larvae.

The course of development of banded flounder eggs in experiments at different water temperatures is shown in Table 75 and in fig. 65, whence it may be seen that in our experiments the eggs were subjected to the effect of above-normal¹ temperature at various stages of development, beginning with the moment of fertilization and ending with the last stage before hatching.

In analyzing the nature of development of the eggs in individual stages under various temperature conditions, the following conclusions may be made. Water temperatures ranging from -2 to $+2.3^{\circ}$ are favourable for the period immediately following fertilization and the beginning of cleavage. Cleavage takes place at a temperature of $+3^{\circ}$, but the disposition of the blastomeres that have formed deviates a little from the norm. Under subsequent favourable conditions, many

¹ We considered the norm to be the demersal temperature of -1.7 to -2.0° existing during the spawning period.

eggs develop normally. At a water temperature in excess of 3.0° cleavage takes place abnormally, and the egg quickly dies.

The period from 16 to 128 blastomeres progresses normally at water temperatures ranging from -2 to $+2.3^{\circ}$. At water temperatures from $+2.4$ to 3.0° cleavage proceeds normally, but shortly after the formation of 128 blastomeres, signs of the disintegration and slipping of blastomeres appear, and at the blastula stage the eggs die.

The period of the blastula and the beginning of the epithelial blastula progresses normally at water temperatures of -2.2 to $+3.2^{\circ}$, and no injurious effect is noticeable from this temperature.

Because of the absence of precise data, nothing definite can be stated regarding the period of gastrulation. A temperature of $+3.6^{\circ}$ in Series XI (see Table 54) appeared to have no inhibitory effect. Lower temperatures of 3.2 to 3.5° during the period of formation of the embryo caused the development of deformed specimens and nonviable embryos, most of which died after the establishment of optic vesicles. Mass mortality in these stages was also observed in other series.

The death of some embryos and the very sluggish hatching of others was also observed in the stage preceding hatching. It may be seen from the above that the blastula stage of formation of the embryo, at 16 to 128 blastomeres, and immediately prior to hatching, is the most susceptible. /410

As indicated above, the banded flounder begins to reproduce in winter, under the ice, at a water temperature of about -2° . As may be seen from our experiments, the eggs can

also develop at a higher temperature. The range, however, of temperature fluctuations at which the development of

Table 75

The Effect of Temperature Fluctuations on the Development of Eggs
of L. pinnifasciata

Temperature, in °C	Stage of development	Age		Condition of eggs
		days	hours	
Series II				
+4.0	Preparation for cleavage	--	1	--
+4.0	Prior to beginning of cleavage,	--	6	--
0	4 to 16 (8) blastomeres	--	20	Cleavage irregular, blastomeres different
+2.4	8 to 16 blastomeres.....	--	24	Same
+4.4	8 to 16 and 32 blastomeres	1	6	"
+6.0	32 to 64 "	7	7	"
+7.0	Morula.....	1	18	Disintegration of morula begins
+4.6	Same.....	2		Same
+5.7	"	2	6	Morula has disintegrated
4.2	Transition to blastula..	--	18	Eggs have died
Series III				
+5.4	Preparation for cleavage	--	1	--
+4.0	Prior to beginning of cleavage	--	6	--
+1.4	8 to 16 blastomeres.....	--	20	Cleavage irregular, blastomeres different
+8.2	16 to 32 "	1	22	Same
+5.4	32 to 64 "	1	6	"
10.2	Morula.....	1	18	Disintegration, mass mortality
+5.0	Same.....	2	--	Mass mortality

Table 75 (cont'd)

+0.9	Transition to epithelial blastula	2	6	All have died
	Series IIIa			
-1.0	Preparation for cleavage	--	1	Normal
0	Same.....	--	6	Same
-2.0	2 to 4 blastomeres.....	--	18	On the night of 10 February water was covered with ice. Normal
+0.2	More than 4 blastomeres	--	24	Normal
+2.0	More than 8 "	1	2	Same
+2.3	16 "	1	6	"
+3.0	About 64 "	1	18	"
+2.7	Morula.....	2		Blastomeres begin to slip and morula, to disintegrate
+0.6	Transition to blastula..	2	6	Slipping of blastomeres and disintegration of blastodisc (see fig.66)
-2.4	Gastrulation.....	3	--	Mass disintegration
-3.0	Overgrowing.....	10	--	Mass mortality

banded flounder eggs is possible is, at the cleavage stage, 411 extremely limited and varies from -2.5 to +3.0°, the latter temperature being essentially close to lethal. The reaction of the eggs in later stages towards increased temperature is different. After gastrulation, banded flounder eggs become less sensitive to an increase in temperature; the farther the development of the eggs has gone, the wider are the temperature fluctuations they withstand. The period of development from the beginning of overgrowing to the closing of the blastopore

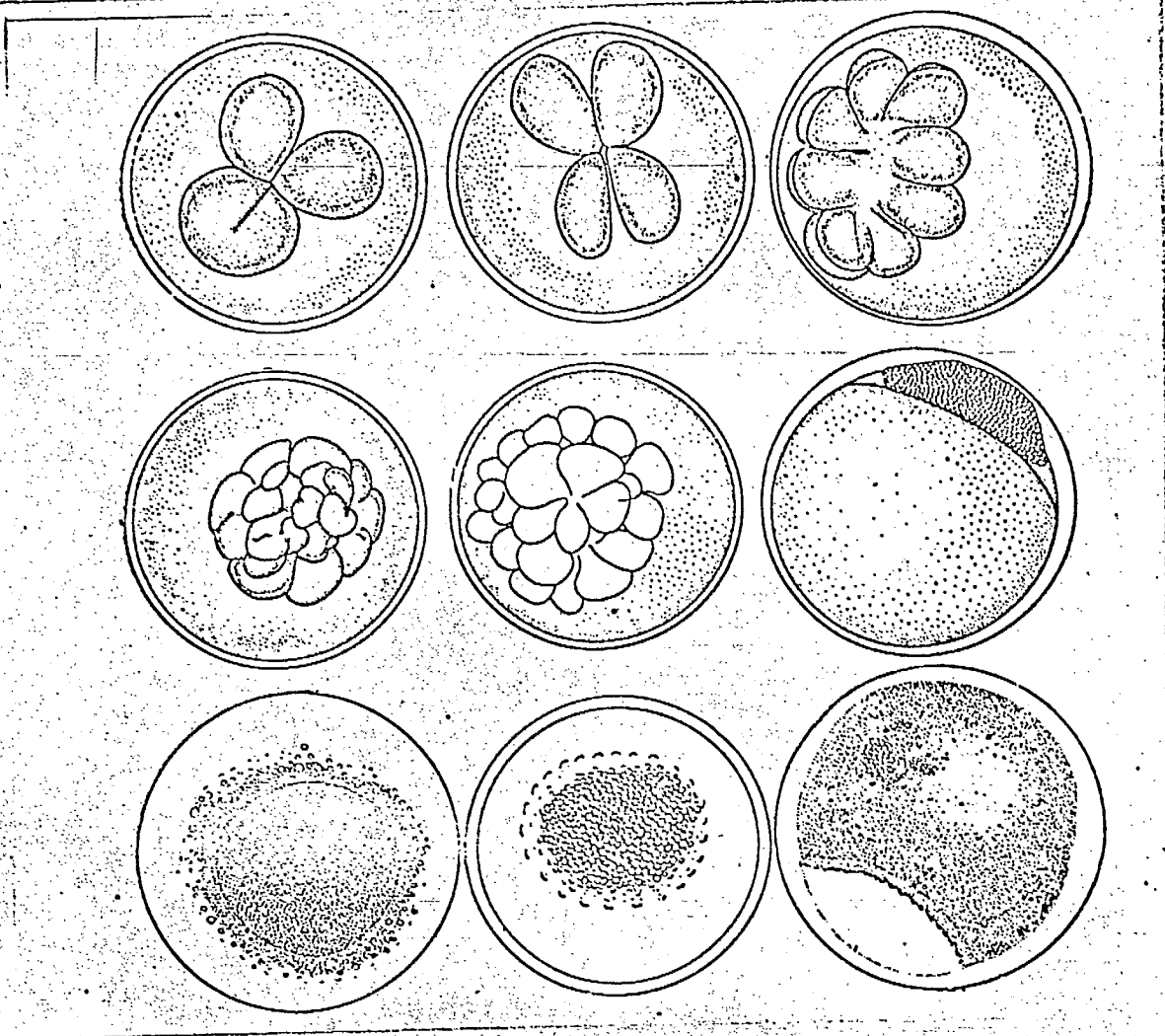


Figure 65 - Development of eggs of L. pinnifasciata at an increased temperature

in some series took place normally even at a temperature such as $+3.6^{\circ}$. The embryos were least sensitive to increased temperature in the period of growth, withstanding at this time an increase in temperature to $+5^{\circ}$ (see Table 54). Prolarvae that had hatched, and particularly larvae, endured an increase in temperature of up to 7 and 10° .

The capacity of eggs in the cleavage stages to withstand only negligible fluctuations in temperature (stenothermy) corresponded to the natural conditions at the places where they were spawned. As has already been mentioned more than once,

the spawning of the banded flounder is confined to the coldest season and takes place under the ice, at an almost constant, steady temperature; during the ice-melting period the temperature is either very low or rises only very negligibly. Thus for example, on 13 February in Amur Bay at a depth of about 10 m we noted a temperature of -2° , and after 21 days during the ice-melting season the temperature rose to only -1.7° . Consequently, eggs that had been laid were, at the beginning of their development, at an almost constant temperature that ranged from -2 to -1° and did not undergo daily fluctuations.

Matters were different with respect to eggs in late stages, and particularly prolarvae and larvae, which appeared coincidentally with the spring period, when the water was being freed from ice, and the spring sun considerably warmed the surface layers of the water, increasing its temperature to $+5^{\circ}$. Because of the diurnal warming of the surface layers of the water and their cooling at night, there appeared fairly perceptible daily fluctuations in temperature, to which were subjected the eggs in late stages of development and the prolarvae, both located in the upper layers; for both eggs and larvae these fluctuations became the norm. Sharp fluctuations in temperature during the early embryonic stages (cleavage and gastrulation) do not take place under natural conditions, and the species is not adapted to them.

Thus in the development of the banded flounder we disclosed sharply outlined stages characterized by different demands made of the environment.

The sharp fluctuations in temperature, which could not be avoided in our experiments, had a very important effect on

the course and results of development. This went counter to natural conditions under the ice, where, as indicated above, the temperature for a long time remained almost constant, and, if it rose in the spring, did so very slowly and gradually.

It is interesting to compare the experimental conditions of development of the eggs with circumstances observed under natural conditions. As may be seen from fig. 66, each species developing in nature has a latent (potential) possibility of developing within wider temperature fluctuations, the range of these fluctuations corresponding directly to the fluctuation of the natural conditions of development of the eggs of a given species. Thus, for example, the banded flounder, which develops in winter in a stable environment, is almost stenothermic. The development of its eggs in the cleavage stage, as we saw above, takes place normally within very narrow limits of temperature fluctuation, from -2 to $+2.6^{\circ}$; at later stages, the upper limit of development shifts to $+6$ to 8° . The following species are less sensitive in the cleavage stage and are capable of developing within the limits of temperature fluctuations as given: the rock sole, from -1 to $+4.2^{\circ}$, the black flounder, to $+8^{\circ}$, and the Alaska plaice, to $+10^{\circ}$. The Japanese and starry flounders, which develop in the readily warmed offshore zone, subject to daily fluctuations, withstand an even wider range -- from 0 to 12° , and up to $+16^{\circ}$ off the coast of Japan. The optimum temperature for development lies at about $+8.4$ to 9.0° . A highly marked plasticity in respect to temperature is displayed in the development of spring- and summer-spawning forms -- the Japanese flathead flounder, the yellowfin sole and the yellow-striped and longsnout flounders, which are capable of developing at temperatures from 0° .

Unfortunately, we do not have at our disposal any experimental data on the development of northern populations of yellowfin sole, or starry or other flounders. To judge, however, from the conditions of development of the starry flounder off the Asiatic coast and the coast of America, in the region of Monterey Bay, it may be assumed that the temperature boundaries and the "threshold" of development in the North are lower, and the amplitude of temperature fluctuations, much smaller, than in the south. Thus, for example, the "threshold" of development of the starry flounder off the American coast, in Monterey Bay, is $+7.2^{\circ}$, while off the Asiatic coast, in the region of Hokkaido and southeastern Kamchatka, it is much lower 414 and is equal approximately to 0.2° . It is quite possible that at the same temperature the rates of development of northern populations are different (probably faster) than those of southern populations. This problem is of great practical and theoretical interest, and special research is needed to solve it.

The Development of Deformities

In connection with the effect of temperature on egg development, it is interesting to note that among banded flounder eggs developing under laboratory conditions there originated, at various stages of their development, a large number (from 32 to 62%)¹ of deformities, expressed in the absence of differentiation in the forward part of the neural tube and its uneven growth, and in the underdevelopment or absence of eyes. In some deformed specimens the eyes were smaller than normal, and in others, only one eye had developed; there were many in which the eyes were entirely absent (see fig. 67). In the trunk and tail

¹ Among eggs that we immersed in the sea for development the number of deformed specimens represented only 6% of the total.

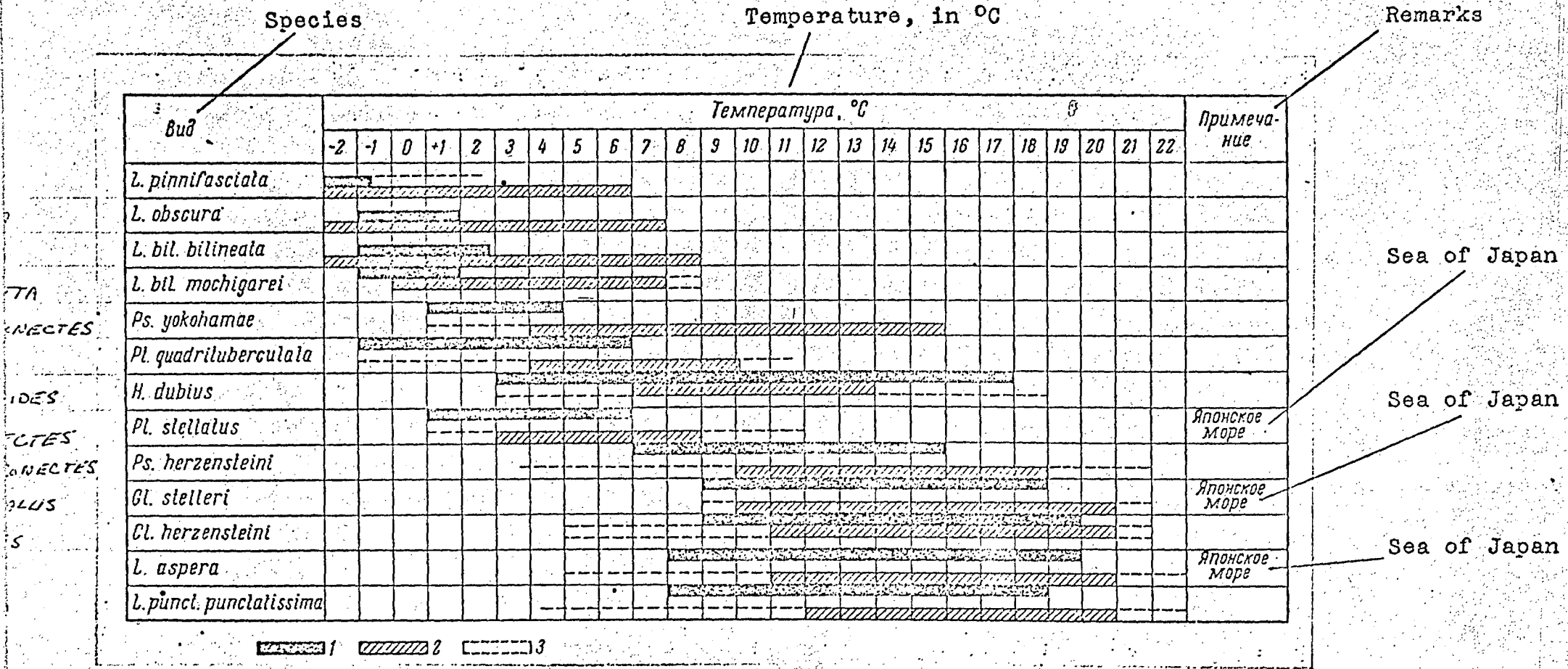


Figure 66 - Temperature conditions under which flounder eggs develop

1 - under natural conditions; 2 - in experiments; 3 - assumed in nature

sections differentiation still took place, and in most cases fairly distinctly. Deformed prolarvae that had hatched kept to the surface of the water, like normal specimens, and subsequently developed at almost equal rates. The resorption of the yolk sac occurred normally, the mouth opening appeared on time, the tail lengthened and pectoral fins grew. The two groups were also similar in the character of their pigmentation. Deformed prolarvae, however, were at once distinguished from normal specimens by a crooked or simply curved tail and abnormally distended mouth and gill cavities (see fig. 68). They also differed in the nature of their movement, this difference being particularly sharply manifested in late larval stages. Whereas normal prolarvae and larvae moved freely in all directions, eyeless or one-eyed specimens as a rule revolved around their own axis, most frequently in a spiral, and their forward motions were extremely faint. In general, they had no reaction to light. Deformed larvae, placed together with normal larvae in a vessel of water darkened on one side, remained in the same place as at the beginning of the experiment; normal larvae, as indicated above, left the darkened portion of the vessel and collected in its illuminated part. Subsequently, after the yolk sac had been absorbed, the deformed larvae usually died more rapidly than normal larvae.

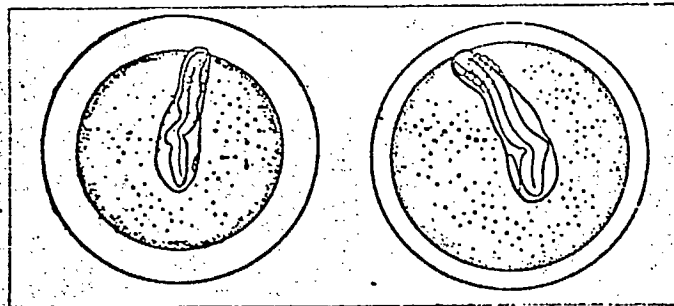


Figure 67 - Abnormal embryos of L. pinnifasciata

The deformed development of fish has been noted by both Soviet and foreign researchers; different deformities have emerged upon the action of the most diverse factors on the eggs. Thus Stocchard (1921) obtained deformities through the action of chemical irritants; Hata (1929) and Stroganov (1939b), by the influence of mechanical effects, and Kellicot (1916), through the action of low temperature and increased salinity, while N.P. Nikolyukin and A. Longinov (1930), S.G. Kryzhanovskii, N.N. Disler and Smirnova (1953) obtained deformities under the influence of low temperature and in hybridization. T.I. Privol'nev (1935), M.F. Vernidub (1940, 415 1941 and 1949), A.N. Trifonova and others caused abnormal development through the action of high temperatures. Günther and Hertwig noted the formation of deformed specimens in hybridization. G.A. Detlaf and A.S. Ginzburg observed a large number of deformed embryos when they incubated sturgeon eggs (1954). I.S. Vasil'ev (1957) noted that differentiation of the pink salmon embryo was disrupted when there was a reduced oxygen content (3 to 4 milligrams per litre).

The experiments of M.F. Vernidub (1940 and 1941) showed that high temperature and reduced oxygen content cause the most profound disruptions in the organism in early stages of development -- at the time of cleavage.

Cases are also known where deformities have developed even under natural conditions (Kryzhanovskii and others, 1953). In material [collected in] 1947 we found a two-headed sohachi flounder embryo (see fig. 69), while in 1952 an eyeless and a one-eyed rock sole larva were disclosed.

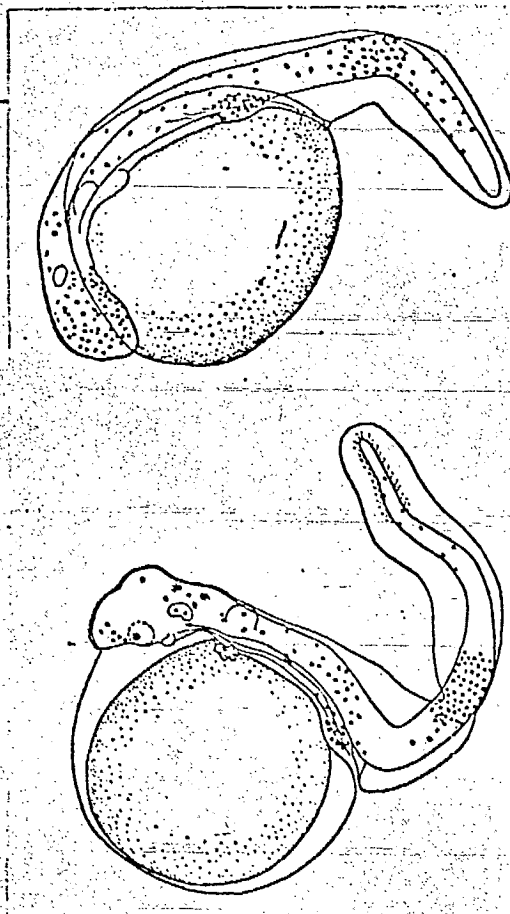


Figure 68 - Abnormal prolarvae of L. pinnifasciata.

The deformities in our experiments could have been caused by increased temperature, by sharp temperature fluctuations and by a reduced oxygen content (asphyxia), since the character of these deformities was for the most part the same as that resulting from the action of high temperature and asphyxia in the experiments by the above authors. As may be seen from Table 54, in the experiments with Series XI the temperature was increased three times: first, up to $+3^{\circ}$ immediately after fertilization, during the period of preparation of the embryo for cleavage; next, up to $+2.6^{\circ}$, at the stage of 16 to 32 blastomeres; on the third occasion, an increased temperature ($+3.6^{\circ}$) was maintained for more than two days at the stages of the epithelial blastula and the beginning of the gastrula. After the first increase in temperature, the appearance of many eggs was not quite normal. The second temperature increase

caused disruption of the blastodisc and the subsequent death of the eggs, while the third and most prolonged increase in temperature caused the process of differentiation of the embryos to be suppressed, resulting in the formation of a large number of deformed specimens. In our experiments on Series XI another factor had an important effect -- lack of oxygen (asphyxia), which could develop with increased temperature on the one hand and as a result of crowding of the eggs, on the other.

It is possible that under natural conditions deformities may have resulted from the action of heavy swells in stormy weather.

Various authors offer different explanations for the development of deformed specimens. Many (Privol'nev, 1935; Trifonova and others, 1939; Svetlov, 1934) believe that under the action of high temperature and other harmful factors 416 there is a disruption in the coordination of the speeds of development of individual rudiments of the embryo, which causes a disproportion in the growth speed of various tissues.

To sum up, it should be noted that the eggs and larvae of the flounder that we have investigated develop well in sea water of normal salinity. The eggs of the banded flounder develop most successfully in water that has been slightly freshened.

Our observations of the development of the eggs of the sohachi, Japanese, banded and black flounders in fresh, semisalt and slightly freshened water indicate the sharply expressed negative reaction of the eggs of these flounder species to fresh water, the near-negative reaction of banded and black

flounder eggs to semisalt water, and the high resistance of sohachi flounder eggs.

Flounder eggs and larvae are adapted to development in certain temperatures that differ for different species. This is closely related to the geographical distribution of and the temperature conditions prevailing in the areas in which the eggs of each species are laid and develop.

Within certain limits for each species an increase in temperature accelerates development, while a reduction in temperature produces the opposite effect. When temperature fluctuations exceed the boundaries of the upper and lower thresholds of development, they inhibit development and cause the formation of deformed specimens and the death of eggs and larvae.

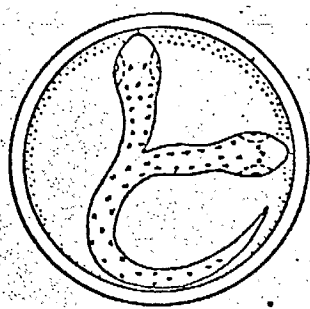


Figure 69 - Two-headed embryo of Cl. herzensteini

The eggs of flounder that reproduce in the cold season of the year (the banded and black flounders and the rock sole) easily endure a reduction in temperature to -2° , and even being frozen into the ice, and withstand a temperature higher than 3 to 4° very poorly. The eggs of flounder that reproduce in the spring and summer (the yellowfin sole and the yellow-striped, flathead, long and longsnout flounders), under conditions of periodic fluctuations in temperature, sustain temperatures of 3 to 4 to 21° .

The relationship of the various stages of development to the environment differs. In each species the most sensitive stage is that of cleavage. Numerous experimental investigations have shown that this phenomenon is common in biology and is widespread not only among fish, but also among invertebrate animals (Thorson, 1946). Under the influence of unfavourable conditions, during the period of cleavage the regularity of the latter is disrupted, the blastodisc which has formed disintegrates and the eggs subsequently die prior to gastrulation. All species display increased sensitivity at the stage that precedes hatching; unfavourable conditions delay hatching, which not infrequently leads to death. The larvae are more eurythermal and can exist under conditions in which the fertilization and cleavage of eggs is impossible. Thus, for example, starry flounder larvae enter fresh water and there develop normally.

A comparison of experimentally obtained data on the effect of temperature on development with data on the course of development at the temperatures prevailing under natural conditions shows that each species has a latent (potential) possibility of developing within wider temperature fluctuations than those that usually exist for it in nature. At the same time, the amplitudes of these fluctuations are specific for a species and in the final analysis are determined by the environment.

Chapter IVA GENERAL REVIEW AND THE REGULAR PATTERNS OF REPRODUCTION
AND DEVELOPMENT OF FLOUNDERReproduction

Our material permits an idea to be gained concerning 417 the individual regions of Soviet Far Eastern waters from the viewpoint of their value to the reproduction and development of flounder (see Table 76).

Sea of Japan. Peter the Great Bay. The bottom of Peter the Great Bay is a vast, slightly inclined continental plateau occupying, according to K. M. Deryugin (1939) an area of approximately 10,000 square kilometres. Beyond the 200-metre isobath there follows the slope of the continental plateau or bathyal region, in places with a steepness of up to 24° . Peter the Great Bay runs deep inland and has many inlets and small bays.

Hydrological conditions in the inlets are characterized by a considerable annual amplitude of fluctuations in temperature and salinity. During the winter the inlets are covered with solid ice, and the bays, with floating ice. The below-zero temperature at the surface of the water and at depths of 15 to 20 metres lasts from the end of December and the beginning of January almost to the end of March. The end of January and the month of February represent the coldest time of the year. At this time, the temperature of the surface layers of water drops to -2.5° , and at depths of 15 to 20 m, to -1.8° . Warming begins in April, the temperature of the water rises rapidly, and in summer the surface layers are warmed to more

than 20°. Summer thermal conditions are nearly subtropical, while those in winter suggest arctic conditions.

The water of Peter the Great Bay, both in pelagic areas and at the bottom, contains a fully sufficient amount of oxygen.

The area with the warmest water is Pos'et Bay. The winter monsoons, blowing from the mainland, early and quickly chill the offshore waters of the northern area. In the southern area their effect is softened by the streams of the warm Tsushima Current which extend to this region, and virtually no ice formation is observed in the winter.

The bottom fauna of Peter the Great Bay, particularly in its eastern area, is rich and varied. During the period of flounder development it yields vast quantities of larvae, which swim in the upper layers of the water and are excellent food for flounder larvae.

Because of the diverse conditions in different seasons of the year, the most widely diverse groups of flounders live and develop here.

In the eastern area of Peter the Great Bay, which we 419 investigated, out of 20 flounder species dwelling in the region we noted 14 reproducing (see Table 77).

The bulk (eight species) reproduces in summer, a much smaller number, (three species) in spring, two species in autumn, one in winter, and one in the winter-spring period (see Table 77).

Table 77

Spawning Seasons of Flounder in Peter the Great Bay*

Species	January	February	March	April	May	June	July	August	September	October	November	December
<i>H. hip. stenolepus</i>				+++								+++++
<i>L. pinnifasciata</i>				XXXXX+								
<i>L. obscura</i>				XXXXX+								
<i>L. bil. mochigarei</i>				XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>H. dubius</i>						XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>Pl. stellatus</i>					XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>Ps. yokohamae</i>					XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>Ps. herzensteini</i>					XXXXX+	XXXXX+	XXXXX+	XXXXX+	XXXXX+	XXXXX+	XXXXX+	XXXXX+
<i>Cl. herzensteini</i>					XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
<i>L. punct. punctatissima</i>						XXXX+	XXXX+	XXXX+	XXXX+	XXXX+	XXXX+	XXXX+
<i>L. aspera</i>						XXXX+	XXXX+	XXXX+	XXXX+	XXXX+	XXXX+	XXXX+
<i>A. nadeshnyi</i>						XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX
<i>Gl. stelleri</i>						XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX
<i>P. olivaceus</i>						XXXX	XXXX	XXXX	XXXX	XXXX	XXXX	XXXX
<i>K. bicoloratus</i>						XX+	XX+	XX+	XX+	XX+	XX+	XX+

* In this and succeeding tables x indicates spawning that has been noted, and +, assumed spawning.

Table 76 is on p 835

A temperate-boreal Sea of Japan species -- the banded flounder -- reproduces at the coldest time of the year (January and February) at below-zero surface and demersal temperatures of about -2.0° . Spawning takes place in the upper levels of the sublittoral, at depths of about 10 to 15 m. A southern-boreal Sea of Japan species, the black flounder, reproduces in the winter and spring period (from the end of February to the beginning of April in the upper layers of the sublittoral, at depths of about 10 to 15 m and at a temperature of about 0° . A temperate-boreal species -- the southern rock sole -- reproduces under the same conditions in the lower levels of the sublittoral. A southern-boreal Sea of Japan species -- the Japanese flounder -- reproduces in spring (from March to May) at a low above-zero temperature mostly of about $+2^{\circ}$ and

Table 76

The Reproduction Periods of Flounder in Different Regions

Species	Region										
	Peter the Great Bay	Tatar Strait	Aniva Gulf	South Kuriles, Hokkaido	Terpenie Gulf	Western coast of Kamchatka	Shelekhov Gulf	Eastern coast of Kamchatka	Korfo-kara-ginskii Bay	Olyutorskii Gulf	Anadyr Gulf
<i>P. olivaceus</i>	VI-VII	-	-	-	-	-	-	-	-	-	-
<i>A. evermanni</i>	-	-	-	-	-	XI-XII- II-III?	-	?XII-II-III XI-II-III?	XI-II-III?	-	-
<i>R. hip. matsural</i>	-	-	-	-	-	XI-XII- II-III	-	?XII-II-III	-	-	-
<i>H. hip. stenolepis</i>	X-?	-	-	-	-	XI-XII- II-III	-	?XII-II-III XI-II-III?	XI-II-III?	-	-
<i>H. elassodon</i>	V	-	-	-	-	IV-VI	-	IV-VI	IV-VI	VI	-
<i>H. dubius</i>	VI-VI	V-VI	-	-	-	-	-	-	-	-	VI
<i>H. robustus</i>	-	-	IV-V	-	-	-	V-VI	-	-	-	VI
<i>A. nadesnyi</i>	VI-VIII	VII-VIII	-	VII-VIII	VII-IX	-	-	VII-VIII?	VII-VIII?	VII-VIII?	-
<i>Cl. herzensteini</i>	V-VIII	VI-VIII	-	-	-	-	-	-	-	-	-
<i>E. grigorjewi</i>	-	-	-	-	-	-	-	-	-	-	-
<i>L. bil. bilineata</i>	-	-	-	-	-	III-IV	-	III-IV	III-IV-V?	III-IV-V?	-
<i>L. bil. mochigarei</i>	II-IV?	II-III	II-III	-	-	-	-	-	-	-	-
<i>L. aspera</i>	VI-VII	VI-VIII	VI-IX	VII-VIII	VI-IX	V-IX	-	V-IX	VI-IX	VI-IX	-
<i>L. punct. punctatissima</i>	V-VII	VI-VIII	VI-IX	-	VI-IX	-	?-VIII-	-	-	-	-
<i>L. punct. proboscidea</i>	-	-	VI-IX?	-	-	V-IX	-	V-IX	VI-IX	VI-IX	-
<i>Ps. herzensteini</i>	V-VII	VI-VIII	-	-	-	-	-	-	-	-	-
<i>Ps. yokobamae</i>	III-V	V-VI	V?	-	-	-	-	-	-	-	-
<i>Pl. quadrituberculata</i>	-	III-V	III-V?	-	III-VI	IV-V	V-VI	IV-VI	IV-VI?	IV-VI	IV-VI
<i>Gl. stelleri</i>	V-VIII	VI-VIII	VI-IX	VII-IX	VI-IX	?-VIII?	-	-	-	-	-
<i>L. obscura</i>	II-IV	II-IV?	II-III- IV?	-	-	-	-	-	-	-	-
<i>L. pinnifasciata</i>	I-II	I-II?	I-II?	-	-	-	-	-	-	-	-
<i>L. glacialis</i>	-	-	-	-	-	-	-	XII-II?	XII-II?	XII-II?	XII-II
<i>Pl. stellatus</i>	III-V	V-VI	V-VI	-	V-VI	IV-VI	V-VI	IV-VI	V-VI?	V-VI?	VI-VII
<i>K. bicoloratus</i>	VII-X	-	V-VI	-	-	-	-	-	-	-	-

at depths of approximately 5 to 10 m. A predominantly boreal species -- the starry flounder -- reproduces at a somewhat deeper level. A temperate-boreal Sea of Japan species -- the Japan Sea flathead flounder -- reproduces at depths of 20 to 70 m and at temperatures ranging mainly from +1 to +3°.

The group of summer spawning species is the richest and most diverse in respect to zoogeographical categories. The spawning of a temperate-boreal Sea of Japan species -- the yellow-striped flounder -- begins in the second half of May at depths of 10 to 25 m. At the end of May and beginning of June it is joined by the longsnout and sohachi flounders, as well as by a temperate-boreal Pacific species -- the yellowfin sole. The long flounder spawns somewhat later and further from the shore and at a considerable depth, for the most part in excess of 30 m, while the spiny flounder spawns in the open area of the Bay, at a depth mostly in excess of 50 m. The spawning of subtropical-boreal species -- the bastard flounder /420 and the two-coloured flounder -- has been noted in addition to that of the above mass forms. In Peter the Great Bay, to judge from the quantity of eggs, there form large spawning accumulations of flounder, in which the yellowfin sole forms the largest proportion.

The spawning stock concentrates mainly in Ussuri Bay, chiefly in the latter's eastern and western offshore areas.

In the central and outflowing zones of the Bay and around Askol'd Island only the Sea of Japan flathead flounder and long flounder engage in mass reproduction. Vostok and Amerika Bays are of less spawning importance for all species.

The duration of development of the eggs laid by different species fluctuates depending upon thermal conditions.

The most prolonged is the embryonic development of banded flounder eggs, which are laid in winter at below-zero water temperatures (about -1.7 to -2.0°). As our experimental observations have shown, the incubation period of eggs at this temperature lasts for about two months and, consequently, the prolarvae appear in plankton no earlier than the end of March and beginning of April; and the larvae, in the middle and at the end of April. Somewhat later, at the end of April, there appear the first black flounder larvae, and in May, the Japanese, starry flounder and flathead flounder larvae. The development of the eggs of summer-spawning species lasts from two to five and six days; therefore, a vast quantity of the prolarvae and larvae of all summer spawning forms appears in June. Towards this time, most of the larvae of the winter and early-spring-spawning flounders sink to the lower levels of the water or lie on the bottom. The mass appearance of larvae in plankton coincides with the peak of the spring development of plankton.

According to data from A. P. Kusmorskaya (1949), an abundance of phytoplankton is observed in Peter the Great Bay in March. Towards May its biomass is reduced, and the quantity of zooplankton increases. K. A. Brodskii (1937) noted two brief sharp increases, of uneven extent, in zooplankton in the northwestern Sea of Japan. The greater of the two was confined to May, and the lesser, to November. He did, however, note comparatively large biomass figures in June, during the period of mass appearance of flounder larvae.

On the basis of egg collections we have attempted to assess approximately the state of the flounder stock in Peter the Great Bay.

Intensive flounder fishing in Peter the Great Bay, which began from 1929 to 1930, has brought about a decrease in the flounder population and has been reflected in the latter's species composition. Yellowfin sole and sohachi flounder, which had previously predominated, forming up to 85% of the catch when fishing began, have begun to yield to other forms previously found only in the most negligible quantities. The slime and spiny flounders, which in the first years of fishing had been caught in insignificant amounts, towards 1939 began to acquire an independent value in the catches. Towards 1950 this process intensified even further (Moiseev, 1953).

Studies on a quantitative estimate of eggs in Peter the Great Bay in 1949, and particularly in 1951, 1952 and 1957, permit us to analyze the changes in the quantities of eggs both as a whole for all flounders and separately for each species (see Table 78).

The data given indicate that in 1952 the yellowfin sole population increased, while in 1957 a notable decrease again occurred¹. There is reason to fear that if fishing is irrationally organized, a further, and even greater, reduction in the population of this important commercial fish will take place in Peter the Great Bay.

Tatar Strait. This area is characterized by a large annual amplitude of temperature fluctuations. In the northern part of the Sea of Japan, off the Maritime Coast and in Tatar Strait there dwell 14 flounder species. /42

Investigations were conducted mainly in the southern part of Tatar Strait at the beginning of May, in July, and in August. In this region there reproduces the same complex of

¹ At the same time, there was an increase in the longsnout flounder population.

Table 78 /421

Average Catches and the Correlation of the Numbers of Eggs
of Different Flounder Species in Ussuri Bay at the
Time of Mass Spawning

Species	1949	1951			1952				1957	
	In surface fishing [*]	In surface fishing	%	In surface fishing	% [*]	Per square metre	%	In surface fishing	%	
Yellowfin sole										
Yellow-striped										
Longsnout	85,0	885	39,3	1737	42,6	73,0	29,0	1014	34,2	
Sohachi	—	330	14,8	1215	29,8	54,0	21,4	649	21,1	
Long	267	554	24,9	651	16,0	32,0	12,7	800	26,3	
	365	414	18,7	432	10,6	30,0	11,9	552	18,0	
	8	48	2,3	35	0,9	11,0	4,4	48	1,6	

* largest catch

species as in the eastern part of Peter the Great Bay, with the difference that here the subtropical-boreal species are absent and a subarctic-boreal species is added -- the Alaska plaice. For most of the flounders reproducing in abundance in Peter the Great Bay (the southern flathead, the sohachi, the Japanese, the yellow-striped and the longsnout), Tatar Strait is the northern boundary of the region of reproduction, and therefore the number of eggs of these flounders is here small.

The Alaska plaice spawns from the end of March to the beginning of May in the southern part of Tatar Strait. The largest quantity of eggs has been noted off the western coast of Sakhalin and in the region from Il'insk to Kholmsk. The Japanese flounder reproduces here in May and June, and the southern flathead flounder, probably from the beginning of May

to June. The yellowfin sole, and the yellow-striped sohachi, longsnout, spiny (Nadezhny's) and long (Korean) flounders have been noted spawning in June and August along the western coast of Sakhalin.

Since there have been no systematic collections during the period of mass spawning of the above flounders, it is difficult to evaluate the spawning grounds of the southern area of Tatar Strait, but to judge from the relief of the mainland shoal, the spawning significance of Tatar Strait is less than that of Peter the Great Bay. At the same time, the broad, slightly warmed shoal of the northern part of Tatar Strait is favourable for the mass spawning of the yellowfin sole, the Alaska plaice and the flathead flounder.

The spawning of flounder in Tatar Strait takes place within the limits of the 50-metre isobath; only the spiny flounder reproduces at a depth of about 100 m. The calendar periods of spawning are later than those in Peter the Great Bay (see Table 79).

Sea of Okhotsk. Aniva Gulf is comparatively shallow; the maximum depth does not exceed 100 m. The isobaths in the eastern part are contiguous, and in the western area they are extended fairly far apart. Thermal conditions are characterized by wide annual temperature fluctuations.

The fauna of Aniva Gulf, as is known, is transitional between the northern boreal and the southern boreal. The flounder group here is diverse (21 species) and consists of cold-water and warm-water species. In the period that we studied (May, and from July to the beginning of September) only five were noted spawning (see Table 84). /422

Table 79

The Spawning Seasons of Flounder in Tatar Strait

Species	January	February	March	April	May	June	July	August	September	October	November	December
<i>H. hip. stenolepis</i>				+++++							+++++	
<i>H. pinnifasciata</i>				+++++							+++	
<i>L. obscura</i> *				+++++								
<i>L. bil. mochigarei</i>				XX+++++								
<i>Pl. quadrituberculata</i>					XXXXXXX							
<i>H. dubius</i>							XX+++					
<i>Ps. yokohamae</i>							XXXXX					
<i>Pl. stellatus</i> *							+++++					
<i>Ps. herzensteini</i>								+++XXXX				
<i>Cl. herzensteini</i>								++XXXX				
<i>L. punct. punctatissima</i>								XXXXXXXXX				
<i>L. aspera</i>								XXXXXXXXXXX				
<i>A. nadeshnyi</i>								XXXXXXXXX				
<i>Gl. stelleri</i>								XXXXXXXXX				

* Spawning season not established

The northern flathead flounder reproduces at the end of April and in May, and the starry flounder, in May, and, probably, in June. There is reason to assume that the southern rock sole also reproduces here in the winter-spring period, and the Alaska plaice, in the spring. The yellowfin sole and the longsnout, long, and evidently, the sohachi, yellow-striped and spiny flounders reproduce from the end of June to the beginning of September in the northwestern and northeastern parts of the Gulf, on a slightly warmed shoal. Mass spawning by the yellowfin sole and the longsnout flounder is confined to the end of July and the beginning of August. The spawning accumulations of yellowfin sole are fairly large, since catches have yielded up to 1,659 eggs in surface fishing and up to 70 specimens per square metre. The quantity of longsnout flounder is much less than that of yellowfin sole: egg catches of the

former did not exceed 10 specimens per square meter and 262 specimens in surface fishing. The bulk of both species lays its eggs at bottom temperatures of about $+3^{\circ}$.

Terpenie Gulf. The southeastern coast of Sakhalin is the boundary region of cold-water northern-boreal and southern-boreal fauna. According to P.A. Moiseev, 16 species of flounder dwell in this region.

In Terpenie Gulf, which is characterized by a broad mainland shoal, the starry flounder spawns in May and June, and the yellowfin sole, from the end of July to the beginning of September. The largest accumulations of the latter species are concentrated in the northern part of Terpenie Gulf, where discoveries have been made of up to 1,878 eggs in surface fishing and as many as 1,000 eggs per square metre. The bulk of these flounder reproduces at depths of 20 to 50 m and at water temperatures ranging from 1.0 to 4.0° at the bottom and from 10.4 to 17.0° at the surface. The spiny flounder reproduces from July to September in the central zone of the sublittoral at depths of 100 m and more.

The South Kurile Islands are a region of broad shoals adjoining the northern coast of Hokkaido and the South Kurile Islands and populated by a diverse and, to a very great extent warm-water, flounder fauna consisting of 21 species in the first region and 20 in the second.

Here a small number of yellowfin sole and sohachi 423 flounder specimens have been noted spawning in July and August, as have a small number of long flounder from July to September.

The western coast of Kamchatka represents a broad shoal and is characterized by a high biomass of food

invertebrates which reaches particularly large proportions in the southern regions. The annual amplitude of temperature fluctuations is small.

During the winter the shoal is covered with ice. Warming begins in March and April. In the southern part of the coast towards the end of May the surface temperature reaches $+3^{\circ}$, and the demersal temperature, $+2^{\circ}$. In summer, from June to August the water warms at the surface to 5 and 10° , and, in places, to 13° , at the bottom to $+2$ and $+3^{\circ}$, in August to $+5^{\circ}$ and in October to $+8^{\circ}$. Towards December the temperature at the surface drops to $+2^{\circ}$, and in the northern regions, to 0 and 1° .

Sandy bottoms are widespread over the entire mainland shoal. Twelve flounder species dwell here. Of these, four belong to the winter-spring and spring groups, three (five?) to the summer group, and three to the fall and winter group (see Table 80).

Table 80

The Spawning Seasons of Flounder off the Western Coast of Kamchatka

Species	January	February	March	April	May	June	July	August	September	October	November	December
<i>A. evermanni</i>					+++++						+++++	
<i>R. bip. matsurae</i>					+++++						+++++	
<i>H. bip. stenolepis</i>					+++++						+++++	
<i>L. glacialis</i>					+++++							
<i>Lep. bil. bilineata</i>						+xxxxxxx+						
<i>Pl. quadrituberculata</i>						xxxxxxxx++						
<i>H. elassodon</i>						xxxxxxx						
<i>Pl. stellatus</i>						xxxxx						
<i>L. punct. proboscidea</i>							xxxxxxx					
<i>L. aspera</i>							xxxxxxx					
<i>A. nadeshnyi</i>								+++++				
<i>Gl. stelleri</i>								xx+++				

A northern-boreal, Sea of Okhotsk and Bering Sea species -- the northern rock sole -- reproduces in spring, in March and April, in the lower levels of the sublittoral, at depths of about 100 to 150 m and at a water temperature of about 0° at the bottom. A subarctic-boreal species -- the Alaska plaice -- lays its eggs in April and May, for the most part at a depth of about 100 m and at water temperatures of 0 to +1°. A northern-boreal, Sea of Okhotsk-Bering Sea species -- the Okhotsk flathead flounder -- reproduces somewhat later, from the middle of April to the beginning of June, closer to the shore, at depths of 50 to 150 m and at water temperatures of 0 to +2° at the bottom. A pre-eminently boreal species -- the starry flounder -- reproduces from the end of April and the beginning of May to June, at depths of 75 m and less and at water temperatures of 0 to +3° at the bottom.

Of the flounders that spawn in summer, the yellowfin sole and a northern-boreal, Sea of Okhotsk and Bering Sea species -- the snout sole -- reproduce from the end of May to the beginning of September, for the most part at a depth of 50 m and water temperatures at the bottom of 2 to 5°. Spawning by the long flounder has been noted in August. The spawning periods of the tuberculate [literal translation; possibly an oblique reference to the Alaska plaice] and slime flounders have not been established. Pacific Ocean boreal species -- the arrow-toothed, Greenland and true halibuts -- reproduce in the autumn and winter on the edge of the mainland shoal.

The spawning accumulations of spring- and summer- 424 spawning forms are large and are of great commercial importance;

they are concentrated mainly in the southern area of the coast, in the region from Cape Lopatka to Ust'-Bol'sheretsk; the density of these accumulations decreases considerably towards the north.

First in the number of eggs per square metre is the yellowfin sole, which during the mass spawning period yields up to 1,000 eggs at the mouth of the Ozernaya River. Next is the starry flounder, which in May in the region of Cape Kambal'nyi yields up to 757 eggs. In third place are the Alaska plaice, which in April in the region northwest of Cape Kambal'nyi yields 355 eggs, and the flathead flounder, which in May off Cape Ozernoi yields up to 372 eggs.

Northeastern part of the Sea of Okhotsk. The thermal conditions of the water are characterized by a small annual amplitude of fluctuations; most of the year, however, a low temperature prevails. Here, in the region of Shelekhov Gulf, dwell six (+ one?) flounder species (see Table 76). Of these, three spring-spawning species reproduce in Penzhina Bay in May and June. These species include the northern flathead flounder, yielding up to 100 eggs per square metre, the starry flounder, giving up to 30 eggs per square metre, and, in much smaller quantity, the Alaska plaice, yielding only two eggs per square metre.

Spawning by the summer-spawning yellowfin and snout soles has been noted in August. The spawning period of the spiny flounder has not been established.

Mainly spring-spawning forms reproduce in the Tauiskii Bay region; their spawning periods, however, are shifted to the summer months.

Eggs of the northern flathead flounder (from 8 to 20 per square metre) and of the starry flounder (from 6 to 12 per square metre) have been disclosed in small quantities in this area from 29 June to 14 July.

Summer-spawning species evidently do not reproduce in the region between Iona and Elizaveta Islands, since in summer (21 to 22 July) eggs of only the spring-spawning starry flounder have been discovered.

Eastern coast of Kamchatka. "The offshore zone of eastern Kamchatka is characterized by a very narrow mainland shoal that is close to the coast and widens somewhat in the latter's southernmost area. Sandy bottoms, which only off Capes Shipunskii, Kronotskii and Kamchatskii are replaced by hard, and frequently even rocky, bottoms, are widespread over the entire mainland shoal." Hydrological conditions, as off the western coast, are severe. "The temperature of the water at the surface in April 1951 varied for the most part from 0 to $+0.5^{\circ}$, and only a large part of Kronotskii Gulf contained water at a below-zero temperature. In April 1951 the demersal temperature ranged on the average from $+0.5$ to 2.5° and in May to 1.0° . In the region from Cape Lopatka to Cape Shipunskii, and further in Kronotskii Gulf, the temperature at the bottom ranged from 1 to 3° " (Atlas of Charts of Oceanographic Data on Fishing Regions in the Bering Sea and the Sea of Okhotsk, 1955). Eleven +3? species dwell in this region. The vast majority belongs to the spring-spawning forms (see Table 79, fig. 81). The northern rock sole reproduces in spring, in March and April; the Alaska plaice, in April and May; the Sea of Okhotsk flathead flounder, from the middle of April to the beginning of June,

and the starry flounder, from the end of April and beginning of May to the beginning of June. Of the summer-spawning forms, the yellowfin and snout soles reproduce, evidently, from the end of May to the beginning of September.

The spawning period of the spiny flounder has not been established. Halibut reproduce in the autumn and winter, while a pre-eminently Pacific Arctic species -- the arctic flounder -- probably reproduces in the winter.

Table 81

The Spawning Season of Flounders off the Eastern Coast
of Kamchatka

Species	January	February	March	April	May	June	July	August	September	October	November	December
A. evermanni				+++++							+++++	
R. hip. matsurae				+++++						+++XXXX		
H. hip. stenolepis				+++++++						+++XX		
L. glacialis				+++++						++		
L. bil. bilineata				+XXXXX++								
Pl. quadrituberculata					XXXXXX++							
H. elasodon					XXXXXX++							
Pl. stellatus					XX+++++							
L. punct. proboscidea						XX+++++						
L. aspera						XXXXXXXX						
A. nadeshnyi							+++++					
Gl. stelleri							+++XXX					

The conditions under which the above species reproduce resemble those off the coast of Kamchatka. /425

Mass spawning accumulations of all species of flounder are confined to the extensive shallows of the mainland shoal and to bays running inland. Among such places are Kronotskii and Avacha Gulfs and Avacha Bay and the southernmost part of

the eastern coast, where the 50- to 100-metre isobaths diverge from the coast and go far out to sea.

Extremely large commercial accumulations have been noted in Kronotskii Gulf (in its northern part -- Khrapkova, 1959), and Avacha Gulfs, which in May yield up to 277 starry flounder eggs and up to 102 flathead flounder eggs per square metre. In addition, mass spawning by the flathead flounder takes place off the southern area of the coast, where up to 134 eggs per square metre of ocean surface have been noted in May.

We have not traced the course of Alaska plaice spawning. There is, however, reason to assume that the Alaska plaice spawns in no less quantity than the flathead flounder, since at the very beginning of spawning up to 100 eggs per square metre have been noted in the central area of Kronotskii Gulf, and up to 65 eggs, in the southern part.

As regards the yellowfin sole, our investigations covered only the beginning and end of spawning; an assessment, therefore, of the comparative intensity of spawning has been hampered. The 34 eggs per square metre that were noted at the beginning of spawning, and the large accumulations of prespawning specimens indicate the presence of large spawning populations of this flounder off the coast of Eastern Kamchatka, particularly in Kronotskii Gulf.

Kamchatka Gulf, which is characterized by a very narrow shoal, where the 50- to 100-metre isobaths approach the shore, is of no great importance to flounder reproduction, and the accumulations of spawning specimens here are small.

Off the eastern coast, note should be made of Avacha Bay (Gulf), which runs deep into the peninsula. The fauna of the Bay, according to the data of A. M. Popov, (1935) is of a subarctic character, with a small admixture of boreal forms on the one hand, and arctic forms on the other. The Arctic flounder¹ reproduces here in winter, while the northern flathead and starry flounders, yielding 64 and 277 eggs /426 per square metre respectively, reproduce in the spring, from the end of April to the beginning of June, at a depth of about 25 metres. Reproduction by the yellowfin sole in this Bay in spring has not been noted, and it must be assumed that it occurs in summer, from June to August.

The Bering Sea (see Table 82) has many gulfs and bays running into the mainland. The mainland shoal is characterized by sandy bottoms, particularly in the northern area, and in places is well developed. Hydrological conditions, particularly in the north, are severe.

Table 82

The Spawning Seasons of Flounders in the Bering Sea

Species	January	February	March	April	May	June	July	August	September	October	November	December
A. evermanni			+++++							+++++		
R. hip. matsurae			+++++						+++++			
H. hip. stenolepis			XXX++						+++++			
L. glacialis			+++++									++
L. bil. bilineata					XXXXX+							
Pl. quadrituberculata					+XXXXX+							
H. robustus					XXXX+							
H. classodon					XXXXX+							
Pl. stellatus						++XXXX+						
L. punct. proboscidea						XXXXX++++						
L. aspera						+XXXX+						
A. nadeshnyi							+++++					

¹ A. M. Popov's indications concerning the presence of the banded flounder in Avacha Bay need confirmation.

Ten (plus one?) flounder species dwell in the Korfo-Karaginskii fishing region. Mass spawning by the summer-spawning yellowfin sole, yielding up to 1,700 eggs per square metre of ocean surface, has been noted in August and at the beginning of September. It should be assumed that the arctic flounder spawns here in winter and that the rock sole, the Alaska plaice, and the Sea of Okhotsk, northern flathead, and starry flounders spawn in the spring and summer months. The snout sole and the spiny flounder, in addition to the yellowfin sole, reproduce in summer (see Table 82).

Olyutorskii Gulf is wide open and characterized by a comparatively narrow mainland shoal with a predominance of sandy bottoms with pebbles and a abrupt drop-off-in-depth.

At the beginning of summer (June) the water temperature at the bottom varies from 1.5 to 3°; in the surface layers, the water is warmed to 4 and 5° in the open part and up to 10° near the shore.

Here, at the end of June, within the limits of the 50-metre isobath, mass spawning by the yellowfin sole has been noted wherein this species has yielded up to 807 eggs per square metre in the region of Sommeniya and Lavrov Bays; single specimens of snout sole [eggs] have also been observed. To judge from the occurrence of specimens approaching spawning, as well as of larvae and juvenile fish, the rock sole, the Alaska plaice, and the starry, Sea of Okhotsk, flathead and spiny flounders reproduce in the Olyutorskii Gulf area (see Table 82).

The narrow band of shallows extending from Cape Olyutorskii to Cape Navarin is of far less spawning significance.

Here the same spring-spawning species reproduce as in Olyutorskii Gulf; of the summer-spawning species, only the yellowfin sole and longsnout flounder, whose spawning accumulations here are very small, ascend to this area.

A special distinction should be made for the shallows extending in a southeasterly direction from Cape Navarin, where large accumulations of the eggs of the following spring-spawning species have been noted: the Alaska plaice (up to 107 eggs per square metre) and the flathead flounder (up to 34 eggs per square metre). /427

Anadyr Gulf is characterized by a shallow depth, an even bottom relief and very severe hydrological conditions. The central and eastern parts of the Gulf are considerably chilled, and their temperature throughout the greater part of the year is low. The area with the warmest water is the western region, in which sandy bottoms are widespread.

In June the greater part of the Gulf is covered with floating ice. The maximum temperature in the surface layer at this time is observed in the Cape Navarin region (from 0 to +3°), and the minimum, in the southeastern part of the Gulf and near the edge of the ice (-0.5 and -1.5°).

The surface temperature of the water in Anadyr Gulf at the end of August and in the first half of September 1950 stayed mainly within the limits of 7 to 8.5°, and only in the region of Cape Chukotka dropped to 3°.

In the first half of October the temperature of the water was everywhere 4 to 5°; with the exception of the areas around Cape Navarin and Cape Chukotka, where it dropped to 3°.

In June 1952 the demersal temperature fluctuated from 0 to 1.5° in the southwestern part and from -0.5 to -1.5° in the region of St. Lawrence Island; in August and September 1950 demersal temperature ranged from 0 to 2°, and in the western part of the Gulf, from the mouth of the Anadyr Estuary to Cape Navarin, it fluctuated from 3 to 8°, and in October 1951, from 1 to 3° (Atlas of Charts of Oceanographic Data on Commercial Fishing Regions in the Bering Sea and the Sea of Okhotsk, 1955).

In Anadyr Gulf in June¹ we noted the reproduction of only five species of spring-spawning flounder: the flathead flounder (Sea of Okhotsk and northern), the Alaska plaice, the starry flounder and the rock sole. Spawning was confined almost exclusively to the western part with the warmest water; no reproduction whatever took place in the centre of the Gulf, and only single specimens reproduced in the northeastern part. North of Anadyr Gulf, in the Chukchi Sea, there remained only a winter-spawning species -- the arctic flounder -- and one spring-spawning species -- the northern flathead flounder. The spawning periods of the latter had shifted to the summer months.

Of the five flounder species reproducing in Anadyr Gulf, those forming the largest spawning accumulations of commercial importance were the Alaska plaice, which yielded up to 217 eggs per square metre, and the northern flathead flounder, which yielded up to 71 eggs per square metre. The remaining species were of no commercial importance.

As is evident, a large and diverse group of flounders dwelling in Soviet Far Eastern waters reproduces throughout

¹ Studies were conducted in June and August-September.

the entire year, but different species reproduce and develop at different times, under different temperature conditions and at different salinities.

According to their spawning times and conditions, flounder may be divided into five seasonally spawning groups, which again fall into bathymetric subgroups, reproducing in different layers of water on the mainland shoal (see Table 83).

Larvae, too, appear in plankton in accordance with the time of spawning. The earliest to appear are the larvae of the winter-and spring-spawning species, while those of the summer-spawning species appear later. The larvae of the first group of species are larger than those of the second group. The bulk of the larvae in the pelagic region appears in the spring and summer and, as is known, is the richest 428 in plankton.

The number of reproducing flounder species declines from south to north. The largest number of species dwells and reproduces in Far Eastern waters, off the coast of Japan, in Peter the Great Bay and Aniva Gulf, and off Hokkaido and the South Kurile Islands. Far fewer species lay their eggs off the coast of Kamchatka, and even fewer in the Bering Sea and in the southwestern part of the Sea of Okhotsk. At the same time, the further north one goes, in addition to a decrease in the total number of species, there is a decrease primarily in the number of summer-spawning species, which in the northwestern part of the Sea of Okhotsk, in Anadyr Gulf and in the Chukchi Sea almost entirely disappear.

Table 83

Conditions of Mass Flounder Reproduction

Group	Species	Depth, in m.	Spawning season	Water temperature, in °C
Winter	<u>L. glacialis</u> <u>L. pinnifasciata</u>	10 to 15	From the end of December to February	About -2
Winter-spring	<u>L. obscura</u> <u>L. bilineata bilineata</u> <u>L. bil. mochigarei</u>	100 to 150	From the end of February to April, mainly in March	About 0
Spring	<u>Ps. yokohamae</u> <u>Pl. stellatus</u> <u>Pl. quadrituberculata</u> <u>Hippoglossoides spp.</u>	5 to 10 10 to 70 50 to 100 50 to 100	From the end of March to May, mainly in April (Sea of Japan); May-June (in the Sea of Okhotsk off Kamchatka and in the Bering Sea)	0 to 2 --
Summer	<u>Cl. herzensteini</u> <u>Ps. herzensteini</u> <u>L. aspera</u> (in Peter the Great Bay)..... <u>L. punctatissima punctatissima</u> <u>Ac. nadeshnyi</u> <u>Gl. stelleri</u> <u>L. aspera</u> <u>L. aspera</u> (population off the coast of Kamchatka and in Olyutorskii Gulf)	20 to 50 20 to 30 20 to 30 20 to 30 About 100 About 50 20 to 50 20 to 50	June-July (in Peter the Great Bay) From the middle and end of June to the beginning of September (Kurile-Sakhalin region)	5 to 15 1 to 4
	<u>L. punctatissima proboscidea</u>	Up to 50	May-August (?)	--
Autumn-winter	<u>A. evermanni</u> <u>R. hip. matsurae</u> <u>H. hip. stenolepis</u>	Near the drop-off (more than 150 to 200)	November-February-March	2 to 3

With regard to temperature during the period of reproduction and development, the group of flounders in Soviet Far Eastern waters, in conformity with their spawning periods and the geographical position of their spawning grounds, is fairly diverse. The majority of the representatives (14) have however, a preference for cold and reproduce in the winter and spring for the most part at water temperatures of -2 to $+4^{\circ}$ at the bottom.

Among the species with a preference for cold there should also be included the yellowfin sole population dwelling off the coast of Kamchatka and in the Bering Sea, whose spawning takes place at water temperatures of 1 to 4° . Taken as a whole, the group of flounders in Far Eastern waters is 429 a eurythermal group of fish reproducing within an extremely wide water temperature range, from -2° to 20 and 22° . The temperature range within which the reproduction and development of individual species takes place is closely related to the geographical position of the spawning grounds and the time of year.

The offshore summer-spawning forms have the widest temperature range; furthermore, the nearer the shore the spawning grounds are situated, the greater is the thermal range of the species that spawn there.

In northern regions flounder spawn later and at a low temperature because of the longer winter and the severe hydrological conditions. An example is the yellowfin sole, which has two forms differing in respect to temperature: the southern, which reproduces in the Sea of Japan at a water temperature ranging for the most part from 6 to 12° , and the

northern, a population which has a preference for cold and which reproduces off the shores of Kamchatka and in the Bering Sea, mainly at water temperatures of 1 to 4°.

The spawning places of flounders, in addition to those of halibut, are located within the limits of the mainland shoal, for the most part no deeper than the 100- and 150-metre isobaths. The greatest number of specimens reproduces where there is a broad continental plateau with a gradually falling bottom, in gulfs and bays with masses of water that move little, that are outside the zone of the ocean current streams and that are rich in food resources. The bulk of hatched prolarvae and larvae keeps to this zone. The localization of flounder spawning grounds under the conditions of waters that are little subject to motion is, as P. A. Moiseev has previously noted, an extremely favourable factor in flounder reproduction: the eggs that are laid and the prolarvae that hatch from them are not carried away, but rather remain where they are, in the conditions necessary for their further development and fattening.

Regions characterized by a narrow mainland shoal with sharply altering depths are not ^{of} much spawning importance for flounder.

Within the limits of the mainland shoal the spawning grounds of the various species are for the most part demarcated and situated in a strictly defined order, 13 flounder species laying their eggs in the 5- to 75-metre zone closest to the shore, 5 species mainly at depths of 50 to 150 m, and 3 species of halibut, on the slope of the mainland shoal at depths in excess of 150 to 200 m.

An analysis of our material permits it to be divided into the following bathymetric groups.

1. The offshore species, reproducing in the upper layers of the sublittoral, mainly within the limits of 5 to 15 m. This zone is characterized by sharp fluctuations in temperature; in the winter it is almost entirely covered with ice, and in the summer its upper layers are subjected to considerable warming. The arctic and banded flounders reproduce in this zone in winter under stable conditions; the black flounder reproduces in the winter and spring period, and the Japanese flounder, in the spring.

2. Species reproducing within the limits of the upper-middle area of the sublittoral zone, at depths of up to 50 and 75 m, and for the most part at 20 to 50 m. These species include the yellowfin sole, and the longsnout, sohachi, long, yellow-striped, starry, Sea of Japan and flathead flounders and the snout sole.

3. Species of the middle-lower area of the sublittoral zone, which spawn mostly at depths of 50 to 100 m. These include the Alaska plaice and the Sea of Okhotsk flathead flounders, as well as the spiny flounder.

4. Semi-deepwater species, reproducing in the lower zone of the mainland shoal, at depths of 100 to 200 m. 430 These include the rock sole (northern and southern) and, in the drop-off zone, the arrow-toothed, Greenland and true halibuts.

It should, however, be noted that the distribution of spawning grounds by depths varies somewhat depending upon the season and the geographical region. Thus, for example,

in Peter the Great Bay the yellowfin sole reproduces at a depth of about 30 m, in Terpenie Gulf, at depths of 50 to 60 m, and in the Korfo-Karaginskii and Olyutorskii Gulfs, at a depth of about 50 m. The long and Sea of Japan flathead flounders at the beginning of spawning lay their eggs in shallower places and, as the water warms, they move to greater depths.

Thus during the period of reproduction and development flounders occupy different ecological niches; a large quantity of species can therefore exist within the limits of the overall geographical range. The demarcation of spawning by time and space has great biological significance. Each new group of larvae begins feeding actively when the preceding group has converted to a new form of food. Of no less importance is the distribution of spawning grounds in an area, which reduces the competition for food among the larvae of individual species and results in the most expedient use of food.

All flounder, even a eurythermal form such as the starry flounder, reproduce in seawater of normal salinity (30 to 33‰). Exceptions are the arctic and banded flounders, which reproduce in somewhat freshened water with a salinity of about 28‰. It should be added that the development of the eggs of the banded flounder, according to our observations, proceeds best in slightly freshened water.

The duration of the spawning seasons of individual species depends upon favourable conditions for reproduction and development. At the same time, the food habits of larvae differ in various geographical regions. In most species, spawning continues mainly for a month and a half to two months. In Peter the Great Bay, because of the rapidly

changing hydrological conditions and the intensive increase in water temperature in the spring and summer, the spawning season of the sohachi flounder and yellowfin sole lasts for about a month and a half to two months, that of the flathead flounder, three months, and that of the long flounder, about two and a half months.

The more prolonged spawning period of the latter two species is explained by the fact that their spawning begins in the offshore zone and, as the temperature rises, shifts to greater depths, where a water temperature favourable for the reproduction and development of eggs and larvae lasts longer than at the shore. In the southwestern part of the Sea of Okhotsk and mainly off the coast of Kamchatka and in the Bering Sea, in spite of the later onset of biological spring, the spawning of the yellowfin sole, as indicated above, begins and attains considerable development in the same calendar periods as in Peter the Great Bay. In contrast, however, to the latter, because of the slow and limited warming of the water in summer, favourable conditions for the reproduction and development of eggs and larvae are retained in the former areas until September; accordingly, the spawning period of the yellowfin sole in these regions lasts for about three and a half to four months.

The observations of P. A. Moiseev (1953), and our own, have shown that the overall duration of the period within which males are found with ripe sex products is greater than the corresponding space of time in females; males with ripe sex products are the first to appear at the beginning of spawning and are the last to disappear at the end.

As Moiseev has noted previously, this phenomenon is of great biological significance, since it makes it possible to fertilize the eggs of early- and late-maturing females.

The Zoning of the Reproduction Areas of Different /431
Spawning-Ecological Flounder Complexes

During the period of their reproduction and development, flounders, particularly in the egg and larval phase, have an increased sensitivity to changes in their environment and primarily to fluctuations in temperature. Hence we have attempted to zone the spawning-ecological complexes of flounders and to compare the results with known zoogeographical regions.

At the basis of zoning is the predominance of one or another seasonally spawning group relative to other flounder groups, expressed in percentages of the total number of flounder species reproducing in a given region.

In conformity with the geographical distribution of flounder spawning grounds in the Far Eastern waters of the USSR (see Table 84) the following areas and regions are outlined which coincide with the geographical regions accepted by A. P. Andriyashev (1935 and 1939), L. G. Vinogradov (1948) and P. A. Moiseev (1953).

The Reproduction Zone of the Winter
and Spring Spawning Species

The Chukchi Sea -- Chukchi (temperate-arctic) Province
[sic] (Andriyashev).

Under this heading are included two northern species -- a winter-spawning (L. glacialis), and a spring-spawning species

(H. robustus), which [actually] spawns in the summer months.

The Reproduction Zone of the
Predominantly Spring-Spawning Species

1. Anadyr Gulf -- the northern Bering Sea Region (of a subarctic character) (Andriyashev).

Reproduction of predominantly northern spring-spawning species. The spring-spawning species reproduce in the last months of spring and the first months of summer.

2. Koryak Coast -- Eastern Kamchatka (boreal) province, and the Koryak (northern-boreal) Okrug^{*} (Andriyashev).

Reproduction of northern, predominantly spring-spawning species. Spring-spawning species reproduce in the spring months and the first months of summer.

3. Olyutorskii and Korfo-Karaginskii Gulfs and the eastern coast of Kamchatka (northern portion) -- Eastern Kamchatka (boreal) Province and the Avacha (temperate-boreal) Okrug.

Spawning of northern, predominantly spring-spawning species. The spring-spawning species reproduce in the spring and at the beginning of the first month of summer.

4. Sea of Okhotsk. The Western Kamchatka Northern-Boreal Region.

Spawning, for the most part, of northern species, with a predominance of winter-spawning species.

5. Shelekhov Gulf. Insufficient data. Tauiskaya Gulf -- the Sea of Okhotsk Glacial Region (Vinogradov).

^{*} A Russian word meaning "district".

Table 84 (continued on next page)

Correlation of Flounder Species Reproducing in Different Regions

Group and species	Region							
	Chukchi Sea		Anadyr Gulf		Koryak Coast		Olyutorskii and Korfo-Karaginskii Gulfs and eastern coast of Kamchatka	
	Number of species	%	Number of species	%	Number of species	%	Number of species	%
<u>Winter</u>								
<u>L. glacialis</u>								
<u>L. pinnifasciata</u>								
<u>Winter-spring</u>								
<u>L. obscura</u>								
<u>L. bilineata bilineata</u>	1	50	1	14,3-16,6	1	12,5	1	11,1
<u>L. bilineata mochigarei</u>								
<u>Spring</u>								
<u>H. elassodon</u>								
<u>H. robustus</u>			1		1		1	
<u>H. dubius</u>	1		1		1		1	
<u>P. yokohamae</u>		50		57,1		50,0		44,5
<u>Pl. quadrituberculata</u>			1		1		1	
<u>Pl. stellatus</u>			1		1		1	
<u>Summer</u>								
<u>Cl. herzensteini</u>			1?	14,3?	1		1	
<u>L. aspera</u>					1	25,0	1	33,3
<u>L. punctatissima punctatissima</u>							1	
<u>L. punctatissima proboscidea</u>								
<u>Pl. herzensteini</u>	2	100	6-7	100	8	100	9	100
<u>Ac. nadeshnyi</u>								
<u>Gl. stelleri</u>								
<u>K. bicoloratus</u>								
<u>P. olivaceus</u>								
<u>Total</u>								

Table 84 (cont'd)

Correlation of Flounder Species Reproducing in Different Regions

Group and species	Region							
	Western Coast of Kamchatka		Tauiskaya Bay		Tatar Strait and Maritime Coast		Peter the Great Bay	
	Number of species	%	Number of species	%	Number of species	%	Number of species	%
<u>Winter</u>								
<i>L. glacialis</i>								
<i>L. pinnifasciata</i>								
<u>Winter-spring</u>								
<i>L. obscura</i>								
<i>L. bilineata bilineata</i>								
<i>L. bilineata mochigarei</i>					1	7,1	1	7,1
<u>Spring</u>								
<i>H. elassodon</i>	1							
<i>H. robustus</i>	1	11						
<i>H. dubius</i>					1	14,3	1	14,3
<i>P. yokohamae</i>					1		1	
<i>Pl. quadrituberculata</i>								
<i>Pl. stellatus</i>								
<u>Summer</u>								
<i>Cl. herzensteini</i>	1							
<i>L. aspera</i>	1	44,5						
<i>L. punctatissima punctatissima</i>								
<i>L. punctatissima proboscidea</i>								
<i>Pl. herzensteini</i>					1		1	
<i>Ac. nadoshnyi</i>					1		1	
<i>Gl. stelleri</i>					1		1	
<i>K. bicoloratus</i>					1	50	1	
<i>P. olivaceus</i>					1		1	57,2
<i>Cl. herzensteini</i>					1		1	
<i>L. aspera</i>					1		1	
<i>L. punctatissima punctatissima</i>					1		1	
<i>L. punctatissima proboscidea</i>					1		1	
<i>Pl. herzensteini</i>					1		1	
<i>Ac. nadoshnyi</i>					1		1	
<i>Gl. stelleri</i>					1		1	
<i>K. bicoloratus</i>					1		1	
<i>P. olivaceus</i>					1		1	
Total	9	100	3-4	100	14	100	14	100

Spawning of northern, almost exclusively spring-spawning species, for the most part during the summer months -- from the end of May to July.

6. Sakhalin Bay Region.-- no data.

Transitional Zone

433

Tatar Strait. Maritime Coast (northern-boreal region). Spawning of northern and southern species. The quantities of winter-spring and summer-spawning species are equal.

The Zone of Predominantly Summer-spawning Species

1. Peter the Great Bay, according to L. G. Vinogradov, is a southern-boreal, and according to P. A. Moiseev, a transitional, but mainly northern-boreal, region.

Spawning of northern and southern chiefly summer species. We have not as yet established the reproduction of Cl. asperrimum, V. Variegatus, V. moseri or M. achne, but it is nonetheless evident that, as in other southern species, it takes place in summer. Without our taking these species into account, Peter the Great Bay, in its zoogeographical characteristics, approaches the pattern outlined by P. A. Moiseev.

2. Aniva Gulf. The spawning periods of some species have not been established, but there is reason to assume that here the summer-spawning species prevail; 27% are species whose reproduction has not been established (P. clivaceus, M. achne, C. asperrimum, Ver. variegatus and K. bicoloratus).

The region of the South Kurile Islands and the northern Coast of Hokkaido. The spawning periods of many species have not been established, but again there are grounds for assuming

that summer-spawning species prevail here.

4. The eastern coast of Hokkaido and further to the south, along the Pacific coast of Japan.

Here the winter-spawning banded flounder disappears, the number of spring spawning species decreases, and that of summer-spawning species increases; at the same time, the reproduction periods of the spring-spawning species shift to the winter and winter-spring months, and those of the summer-spawning species, to the spring and early summer months.

An analysis of written material shows that there is a direct link between the amplitude of seasonal fluctuations in water temperature and the diversity of flounder species reproducing in one region or another. The greater the gradients of seasonal fluctuations in water temperature (other conditions being equal), the ecologically richer and more diverse is the complex of flounder species reproducing in this region. Thus in Peter the Great Bay the reproduction has been noted of five seasonal-ecological groups with a large number of species. In the Chukchi Sea and the southern area of the Sea of Japan, where the seasonal water temperature gradients are extremely low, the reproduction of two such groups has been noted (the winter- and spring-spawning groups in the Chukchi Sea, and the spring- and summer-spawning groups in the Sea of Japan). Only a single winter-spawning species - L. glacialis - reproduces in the Laptev Sea.

The Quantitative Distribution of Eggs as an
Indicator of the Size of Spawning Stocks

Before proceeding to an assessment of the quantitative distribution of eggs and larvae, we shall pause to consider their vertical distribution.

An analysis of the vertical distribution of pelagic flounder eggs and larvae is somewhat hindered by the fact that at many stations only through (continuous) fishing has been carried out from the bottom to the surface. [The results of] vertical series fishing in a horizontal direction, which has been more or less adequate for the analysis of egg distribution, are available for only three species (H. elassodon, Pl. quadrituberculata and Pl. stellatus). We have borrowed data for L. aspera from published sources (Polutov and Tripol'skaya, 1954).

A large quantity of eggs in surface horizontal fishing, and research on their vertical distribution, show that pelagic flounder eggs develop in the surface layers of the water. 434

It may be seen from the data in Table 85 and Fig. 70 that the bulk of pelagic eggs keeps to the upper 0- to 25-metre level of the water. A large number of eggs, however, of the Sea of Okhotsk flathead flounder and of the Alaska plaice have been noted in the 25 to 50-metre layer.

We have not succeeded in making a layer-to-layer differentiation for the 0- to 10-, or 10- to 25-metre levels in respect to the eggs of the starry flounder.

In water layers deeper than 25 m, the number of eggs decreases considerably. Deeper than 100 m eggs are either caught in negligible quantities or are entirely absent.

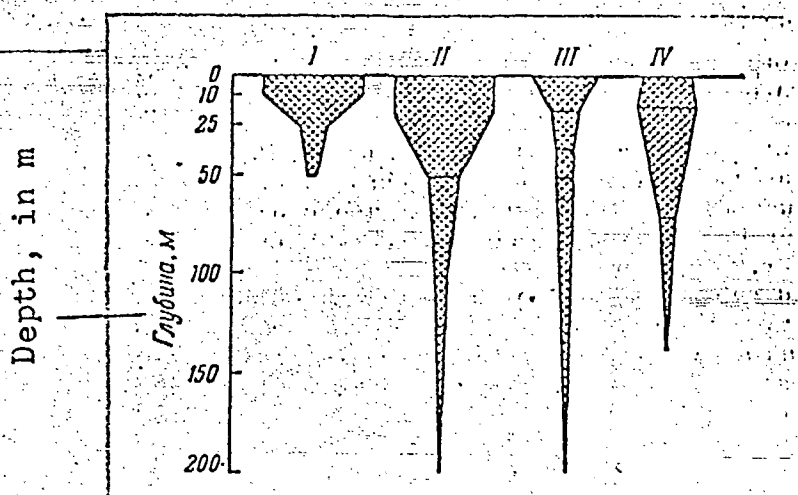


Figure 70 - The vertical distribution of flounder eggs.

1.- L. aspera; 2.- H. elassodon; 3.- Pl. quadrituberculata; 4.- Pl. quadrituberculata (later stages)

In late stages of development the eggs become heavier and sink somewhat deeper. The greatest quantity of flathead flounder eggs stays at the 10- to 25-m layer, where the number of eggs in the first and second stages, taken together, drops from 97 to 85% in comparison with quantities in the 0- to 10-m layer, while the number of eggs in the third and fourth stages increases from 3 to 16%. An analysis of samples (see Table 85) containing Alaska plaice eggs in late stages of development showed that the largest quantity of eggs stayed at the 0- to 20-m level, considerably fewer, at the 25- to 10-m layer, and almost the same quantity [sic 7, in the 25- to 50-m layer. In comparison with the vertical distribution of eggs in the first stages, the quantity of eggs in late stages decreased in the 0- to 25 m layer (from 71.5 to 65%), and increased in the 25- to 50-m layer (from 16.5 to 23.9%). The large catches of eggs of the southern, flathead, sohachi, longsnout, yellow-striped and long flounder in the upper layers of the water, and the developing eggs observed in 435 our experiments at the very surface of the water, indicate that the development of the eggs of these species also takes

place in the surface layer. By analogy with the eggs of the yellowfin sole, the Alaska plaice and the starry flounder, it should be assumed that the bulk of the eggs stays in the 0- to 25-m layer, and that in deeper layers their quantity decreases considerably.

The vertical distribution of halibut eggs in Soviet waters cannot be established because of a lack of material. Off the coast of America, according to Thompson and Van Cleave (1936), the largest quantity of true halibut eggs (68%) stays within a stratum of water between 85 and 212 m; considerably fewer eggs (20%) are at depths of 212 to 425 m, and an even smaller amount (12%), at depths of 425 to 580 m.

In view of the small quantity of material taken according to individual levels of the open water, it is almost impossible to give a description of the vertical distribution of the larvae of the majority of species. An analysis of our samples taken at various water levels shows that larvae are found in different layers of water depending upon their age.

Recently hatched prolarvae and larvae usually stay near their spawning areas at different depths corresponding to the structure and specific gravity of their eggs. Thus the bulk of the prolarvae and early larvae of the flathead, spiny, long and starry flounders and the Alaska plaice keep to the surface layers of the water. Similar prolarvae and larvae of the sohachi and longsnout flounders and the yellowfin sole keep to lower depths, evidently in the 5- to 10- and 5- to 25-m layer, since they are usually not caught in surface, horizontal fishing.

Table 85

Vertical Distribution of Pelagic Flounder Eggs

Level of catch, in m	Flathead flounder		Yellowfin sole*		Alaska plaice				Starry flounder	
					first stages		last stages			
	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%
0-10	366	50,2	1125	29,8	468	71,5	117	40,9	225	67,4
10-25	174	23,9	1550	41,1	—	—	69	24,1	—	—
25-50	140	18,3	1087	28,8	108	16,5	68	23,9	104	31,1
50-100	44	6,1	—	—	78	12,0	25	8,7	5	1,5
100-200	4	0,5	9	0,3	—	—	7	2,4	—	—
Total	728	100	3771	100	654	100	287	100	334	100

* According to data from I. A. Polutov and V. N. Tripolskaya

Later on, at about the time that the fins form, the larvae of all flounders gradually sink to the lower layers of the water, and, at the end of metamorphosis or after it, convert to a bottom mode of life.

Rock sole prolarvae have been found in the 50- to 200-m layer, and halibut prolarvae, even deeper. The older prolarvae of these flounder rise to the upper layers of the water and move closer to the shore, to shallow depths.

Similar behaviour by prolarvae and larvae is also observed in the American true halibut. According to the data of Thompson and Van Cleve (1936), hatched prolarvae 7.8 to 15.0 mm long keep mainly to depths in excess of 750 m in a stratum of water extending from 170 to 950 m in depth; older prolarvae from 9.8 to 17.8 mm long stay at depths of 425 to 935 m in a water layer extending from 70 to 950 m in depth. The largest quantity of both kinds of prolarvae has been noted in a layer of water extending from 400 to 700 m in depth. Younger larvae from 11.2 to 18.5 mm long stay in a

stratum of water from 25 to 700 m deep until their unmatched fins begin to form. Accumulations of larvae have been noted in the 650- to 700-, 400- to 450- and 150- to 200-m layers. Older larvae from 15.0 to 19.9 mm long in various stages of formation of unmatched fins rise to the upper layers of water, from 170 m to the surface, and move towards shallower depths. The largest accumulation of larvae has been noted in the layer of water extending from 0 to 70 m. Large larvae from 17.9 to 20.8 mm long, half of whose left eye rises above the profile of the head, have been taken from the bottom with a trawl at depths of 10 to 25 m.

As indicated previously, the extent of the spawning grounds of each species almost coincides with its geographical range. Accordingly, the starry flounder and the yellowfin sole, whose geographical ranges in Soviet waters are situated from Peter the Great Bay in the south to the Bering Sea and the northern part of the Sea of Okhotsk, have the largest spawning ground area. First in intensity of spawning is the yellowfin sole, the quantity of whose eggs runs as high as 1,700 specimens per square metre of ocean surface and 14,570 in 10 minutes of surface fishing. The places of intensive spawning, corresponding to the accumulations of spawning 436 stock, have been traced in June in Peter the Great Bay (up to 500 per square metre and as many as 14,570 in 10 minutes of surface fishing); in July and August in Terpeniya Gulf (up to 1,000 eggs per square metre); in June and August off the western coast of Kamchatka (up to 1,000 eggs per square metre in the Ozernoi River region); off the eastern coast [of Kamchatka] (Avacha Bay and Kronotskii Gulf); in Olyutorskii Gulf (up to 800 eggs per square metre), and in the Korfo-Karaginskii region (up to 1,700 eggs per square metre). The

yellowfin sole, a leading form in flounder fishing, undoubtedly represents a biologically progressive form. It has a large geographical range, greater numbers, a prolonged spawning period, and high fecundity, and withstands a wide range of temperature fluctuations during the period of its reproduction and development.

All of this promotes a considerable survival of progeny under different hydrological conditions. A favourable factor in this respect is represented by the food habits of this flounder. The yellowfin sole is a benthopolyphage* (Mikulich, 1954), has a broad feeding spectrum and consumes various and numerous representatives of the basic population of the benthos.

Next in the number of eggs at their spawning grounds are the starry flounder and the Alaska plaice. Their largest spawning stocks are situated off the western coast of Kamchatka (see figs. 53 and 59), and yield up to 757 and 355 eggs respectively per square metre of ocean surface, than off the eastern coast of Kamchatka in the region of Kronotskii Gulf and Avacha Bay (up to 277 and 100 eggs respectively at the beginning of spawning). Note should also be made of the spawning grounds of this flounder in the southwestern area of Anadyr Gulf (up to 217 eggs)¹.

Catches of flathead flounder eggs run as high as 372 per square metre off the southwestern coast of Kamchatka. A somewhat smaller accumulation of eggs has been noted off the eastern coast, mainly in Avacha Bay (up to 102 eggs) and Kronotskii Gulf (up to 100 eggs)².

* Translator's note: This word, of obvious meaning and Greek origin, has been taken directly from the Russian.

1 To judge from catches of prolarvae and larvae, there are commercial accumulations of rock sole in these regions and Olyutorskii Gulf.

2 For flounder laying bottom eggs, catches of recently hatched prolarvae.

In Peter the Great Bay, in addition to yellowfin sole (up to 505 eggs per square metre) in June there are commercial accumulations of longsnout, yellow-striped and sohachi flounder yielding a total of up to 325 eggs per square metre.

The spawning grounds of the arrow-toothed, Greenland and true halibut, which are situated on the slope of the western and central depressions of the Bering Sea, at depths in excess of 160 to 200 m, are worthy of attention.

The large quantity of flounder eggs collected in Ussuri Bay and in Terpenie, Korfo-Karaginskii and Olyutorskii Gulfs and off both coasts of Kamchatka is characteristic of the concentration in these places of shoals of mature pre-spawning and spawning specimens.

In research work, egg catches² permit a rapid and simple estimation of the reserves of local flounder stocks. These operations do not require much effort and may easily be carried out on ships of any size. It is necessary to know the identifying features of flounder eggs. We are supplying the appropriate egg key (see Appendix).

Our research has shown that the pelagic eggs of flounders keep for the most part to the upper (0- to 50-m) levels of the water; therefore, for a quantitative egg estimate, fishing only from this upper layer is quite adequate.

It should be noted that we have been far from complete in our treatment of the course of flounder spawning. Our knowledge of the course of spawning by all flounder in the western area of Peter the Great Bay, in Tatar Strait and Terpenie Gulf, off the coast of Kamchatka, in the Bering Sea

² For flounder laying bottom eggs, catches of recently hatched prolarvae.

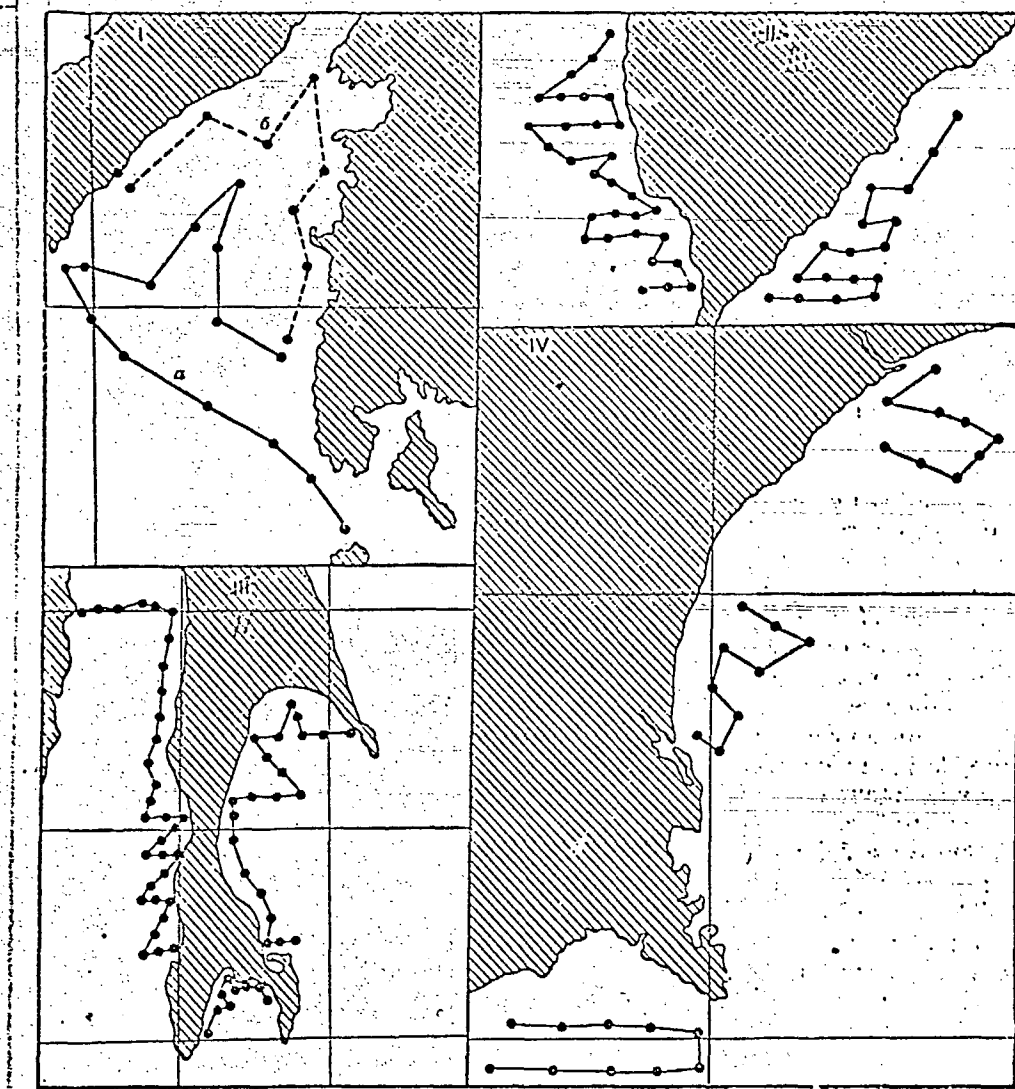


Figure 71 - Diagram of test cross sections.

I - in Ussuri Bay; a - in May, b - in June; II - off the coast of Sakhalin; III - off the coast of Southern Kamchatka; IV - in Avacha Bay and Kronotskii Gulf. Stations are marked with dots.

and other regions, is insufficient. Data are completely lacking on the reproduction of flounder in the northwestern area of the Sea of Okhotsk. For fuller treatment of this question it will be necessary to make regular catches of mature specimens and of eggs and larvae developing in the sea throughout the year. The absence of systematic observations over several years precludes the solution of the problem of the fluctuation in the numbers of laid and developing eggs and,

together with this, the question of the size of the spawning population in individual years. In order to resolve this problem it will be necessary to arrange a yearly estimate of the quantity of eggs that are being laid per unit of ocean surface. For this it will be sufficient to establish several series of regular cross sections on which catches should be made of the eggs of one species or another once or twice a month during the period of mass spawning. Since 1927 detailed studies have been made of halibut off the coast of North America and of sardine off the coast of Japan.

The cross sections that we recommend for checking 438 the intensity of reproduction in basic spawning regions are shown in fig. 71.

Catches of flounder eggs in these regions will enable us to estimate the comparative intensity of spawning in the year under investigation.

DEVELOPMENT

Features of the Structure of Flounder Eggs in Relation to Ecological Factors

Many scientists have believed that all flounder, with the exception of Ps. americanus, have pelagic eggs that develop in the surface layers or in the main body of the water (Norman, 1954; Nikol'skii, 1954; Shelbourne, 1956, and others). Our data compel a reconsideration of the concepts that have accumulated. Of the 23 flounder species and subspecies that we have investigated, 4 species and subspecies (Ps. yokohamae, L. obscura, L. bilineata bilineata and L. bilineata mochigarei) have bottom eggs that develop either at or on the bottom, in contrast to the pelagic eggs, typical of flounder, that float in the surface layers or in the main body of the water.

The structure of pelagic eggs in different groups that have a different geographical distribution, is not uniform. Tropical and subtropical species have for the most part small eggs with a fat drop; in the eggs of the family Bothidae there is one fat drop, and in those of the family Soleidae, several small drops, while in Rombosoleidae their number varies. As one moves further north, because of the increased density of the water, species that have eggs with a fat drop are replaced by those having eggs without a fat drop. The eggs of species of the family Pleuronectidae, prevalent for the most part in the northern area of the temperate zone, have no fat drop¹.

Orton and Limbaugh (1953) have found that the eggs of not all species of Pleuronectidae are devoid of a fat drop. In the eggs of Hypsopsetta guttulata (family Pleuronectidae) they discovered a clearly visible fat drop, representing a primitive feature of flounder eggs of the family Pleuronectidae. It is evident that the fat drop previously existed in all species of this family, but upon subsequent evolution it almost entirely disappeared, being retained up to the present only as an exception in some species, as, for example, H. guttulata. Thus the eggs of this primitive flounder represent a connecting link between the initial eggs of ancestors of the family Pleuronectidae, containing a fat drop, and the modern eggs that have none.

The pelagic eggs of Soviet Far Eastern flounder of the family Pleuronectidae are devoid of a fat drop, which exists only in the eggs of a single representative of the family Bothidae -- the bastard halibut (P. olivaceus), which

¹ The feature of the presence or absence of a fat drop is included in the diagnostics of families (Norman, 1934; Rass, 1947 and 1953)

is found from time to time in the southern regions of Soviet Far Eastern waters. The pelagic eggs of flounder in Far Eastern waters have a characteristic thin membrane and contain a small quantity of plasma. The base of the blastodisc, which yields material for the establishment of the embryo, is smaller than the diameter of the yolk, and its height represents no more than one quarter of that of the latter. Following the terminology of S. G. Kryzhanovskii, we class them with the group of oligoplasmatic eggs.

In contrast to pelagic eggs, bottom eggs have a thick, sticky membrane consisting of several layers; hence they adhere to all objects with which they come in contact. Their yolk is very compact and after fixation becomes almost hard. There is a great deal of plasma. The blastodisc is large as compared with that of pelagic eggs; its height represents about half of the diameter of the yolk, and the 439 base completely covers the yolk from above. These eggs are polyplasmatic. Neither the reasons for the formation of pelagic or bottom eggs in various fish nor the link between the mode of life of the fish and the character of the eggs has been established. Some pelagic fish, such as herring, capelin and others, have demersal eggs, while others, like tiulka, mackerel, anchovy and mullet, have pelagic eggs.

It has been customarily assumed that pelagic eggs are primitive, since they are not protected by the parents and are, as a rule, laid in large numbers.

Since most flounder have pelagic eggs, it is to be assumed that bottom flounder eggs are of secondary origin and that their initial [forms] were pelagic eggs. The evolution of bottom eggs involved thickening of the membrane, condensation

and partial dehydration of the yolk, and an increase in the quantity of formative plasma. In the [eggs] of the Japanese flounder (Ps. yokohamae) there formed an additional thick layer of gelatinous substance, which was probably a protective adaptation to the development of the eggs of this species under the conditions of the shallow zone, which is affected by water disturbances brought about by winds and tides.

Why do pelagic flounder eggs change into bottom eggs?

P. A. Moiseev (1953) has put forward the hypothesis that the adhesive bottom eggs of flounder and cod in Far Eastern waters were formed under the influence of constant and intensive currents, the demersal character of the eggs "ensuring limited dispersion by currents and development at the levels with the most favourable temperatures. In addition, the demersal character of the eggs protected them from the harmful effect of floating ice". Moiseev is substantially correct, but in addition, attention should be directed to the following facts: 1) by no means all species that have bottom eggs reproduce in regions with strong currents; 2) bottom eggs have been formed only in those flounder species which reproduce and develop during the winter and spring, at the time that the ice breaks up, and in the spring-spawning species that lays its eggs near the shore, in the zone of intensive water movement. These species of Far Eastern flounder include L. obscura, L. bilineata bilineata, L. bilineata mochigarei and Ps. yokohamae, and, of the Atlantic flounder living off the eastern coast of North America, Ps. americanus; 3) flounders off the Atlantic coast of Europe, where unfavourable temperatures do not usually occur, have only pelagic eggs.

The formation of bottom eggs in Atlantic and in all Pacific winter-spawning species is doubtless related to similar ecological conditions that have favoured this process. It may be assumed that the formation of bottom eggs in the winter-spring flounder occurred as a result of these species' adaptation to reproduction during the period of the breakup and shifting of ice under conditions where high current speeds prevailed. The movement of the ice and the extreme freshening of the upper layers of the water furthered the sinking of the eggs to lower, denser layers of water; moreover, the heavy eggs sank down, while the lighter eggs were probably broken up and perished.

The sinking of the eggs to the bottom, the thickening of the membrane, the condensation of the yolk and the increase in the quantity of plasma proved to be biologically advantageous. Conditions for development in the new environment were favourable. When the ice melted, the upper layer of the water freshened greatly; this layer, because of its lighter specific gravity, did not participate in the convection currents and did not fall to the bottom. Hence the eggs located on the bottom remained under favourable conditions of salinity and oxygen. According to the data of K. A. Gomoyunov (1926 and 1928) the oxygen 440 content in early spring in the demersal layer of Peter the Great Bay is close to normal, and in this respect the demersal water layers differ little from the surface layers.

Depending upon their size, the eggs of flounder in Far Eastern waters may be divided into three main groups: large -- from 1.7 to 4.0 mm; medium -- from 1.1 to 1.7 mm; small -- from 0.7 to 1.1 mm.

Of the large eggs, note should be made of eggs with a large perivitelline space. Large eggs usually contain an even larger yolk. The group of large eggs with a small perivitelline space includes the eggs of the Greenland and true halibut, as well as of the Alaska plaice. The eggs of all flathead flounder constitute the group of large eggs with a large perivitelline space. The group of medium eggs includes those of the long, banded, and arctic flounders.

Most Far Eastern flounders have small eggs. Among the latter are the eggs of the sohachi, long-snout and yellow-striped flounders and the yellowfin and snout soles, and all flounder having bottom eggs -- the rock sole, and the Japanese and black flounders.

The diameter and structure of the pelagic eggs, and their yolk sizes, vary greatly depending upon the geographical position of the spawning grounds, and reproduction conditions, and reveal a regular connection with the time and the conditions under which they are laid. The largest eggs are proper to the species that reproduce in the winter and in the winter and autumn (see fig. 72). Smaller eggs are to be found among species reproducing in spring (see fig. 73), and the smallest eggs, in species that reproduce in summer in high temperatures (see fig. 74).

The eggs of flounder reproducing in the open, deepest area of the sea are especially distinguishable by their size. Of eggs of the winter-spawning species, the largest are those of the halibuts, and, of the spring-spawning group, those of the flathead flounder. The Sea of Okhotsk flathead flounder, which reproduces in the most open area, has the largest eggs; of the group of summer-spawning species, the long flounder has the largest eggs.

It should be noted that within the limits of each ecological group the eggs of the large-mouthed flounders are, as a rule, noticeably larger than those of the small-mouthed flounders. Thus halibut eggs are larger than those of the banded and arctic flounders; the eggs of flathead flounders are larger than those of the Alaska plaice, and the eggs of the sohachi and spiny flounders are larger than those of the yellowfin sole or of the longsnout and yellow-striped flounders, all three of which reproduce simultaneously. All large-mouthed flounder, with the exception of the sohachi flounder, reproduce in areas of the sea that are relatively open and chilled in comparison with the shallow offshore zone. The same regular pattern is observed in the analysis of egg sizes in series of close species or within the limits of the same species, depending upon the geographical distribution of the spawning grounds. The further north the spawning grounds are situated, the larger are the eggs, and vice versa. A different situation is observed in the widely distributed yellowfin sole species and in flathead flounders. The eggs of the yellowfin sole, which reproduces in the northern area of its geographical range, in Shelekhov Gulf, are no larger, and are on the average even smaller, than in the south. Approximately the same phenomenon is observed in Olyutorskii Gulf, where the eggs of the yellowfin sole, aside from differences in size, as indicated above, also differ morphologically. It is evident that this is associated with the presence of a special form of yellowfin sole in these regions. It is possible that eggs from Shelekhov and Olyutorskii Gulfs, which deviate from the typical eggs of the yellowfin sole, belong to special forms of this species. The same is observed within the limits of the genus of flathead flounders. The Japanese and the Sea of Okhotsk flathead flounders

conform to the same regular pattern as other flounder species, i.e., the eggs of the southern species are smaller than those of the more northerly species.

The northern flathead flounder, which reproduces 4/4/4 under severe arctic conditions, has smaller eggs than the Sea of Okhotsk species; at the same time, the eggs of the flathead flounder are almost equal in diameter to those of the southern species. The reason for this is, evidently, the fact that mature specimens of the northern species are smaller than their southern counterparts and reproduce in a shallower offshore zone.

An increase in egg size in series of near species from south to north and from shallow to deep water is also observed among bottom eggs that are atypical of flounder. The eggs of both representatives of the genus Lepidopsetta, which reproduce in a more open area of the sea, are larger than those of L. obscura or Ps. yokohamae, while the eggs of the northern rock sole are larger than those of the southern rock sole. We have also noted the same regular pattern among Caspian shad (Pertseva-Ostroumova, 1951).

The regular patterns which have been observed coincide with the rules established by Hess (1924) for invertebrates and by T. S. Rass (1941) for fish: "The sizes of the eggs of water animals correspond to the temperatures at which reproduction occurs. In series of closely related species the egg sizes are inversely proportional to the temperatures of the environment at the moments when the eggs are laid: the nearer to the pole the geographical range of the species is situated, the larger are the eggs" (Rass, 1941). The size of the eggs, in our opinion, depends not only upon the temperature

at which they are spawned, but also upon the temperature at which the eggs grow and mature. At a low temperature, the process of egg maturing is retarded, and during the period of yolk formation, the nutrient substances are received over a more extended length of time; large eggs, therefore, with a large yolk, develop.

A comparison of egg sizes with fecundity shows an inverse relationship between fecundity and egg sizes. Flounder that have small eggs are characterized by great fecundity. The only exception is the small longsnout flounder, whose absolute fecundity, in spite of its very small eggs, is a little over one-third that of the yellowfin sole.

P. A. Moiseev (1953) indicates that the incubation period in most species lasts for only two or three, or, rarely, five days. According to our observations, the incubation period of the various species differs sharply, is directly related to the sizes of the eggs (or more correctly, of the yolk) and of hatching prolarvae and is in inverse relation to the temperature. The larger the eggs and the lower the water temperature at which development occurs, the longer is the period of embryonic development, and vice versa. P. A. Moiseev's statements concerning the higher rates of development of Pacific, as compared with Atlantic, flounder, are not confirmed. The duration of the incubation periods of both Atlantic and Pacific flounder, temperature and other conditions being equal, is more or less the same (see Tables 86 and 87).

Both the pelagic and the bottom eggs of Far Eastern flounder develop under good breathing conditions in water

Species

Depth, in m

Months

Eggs

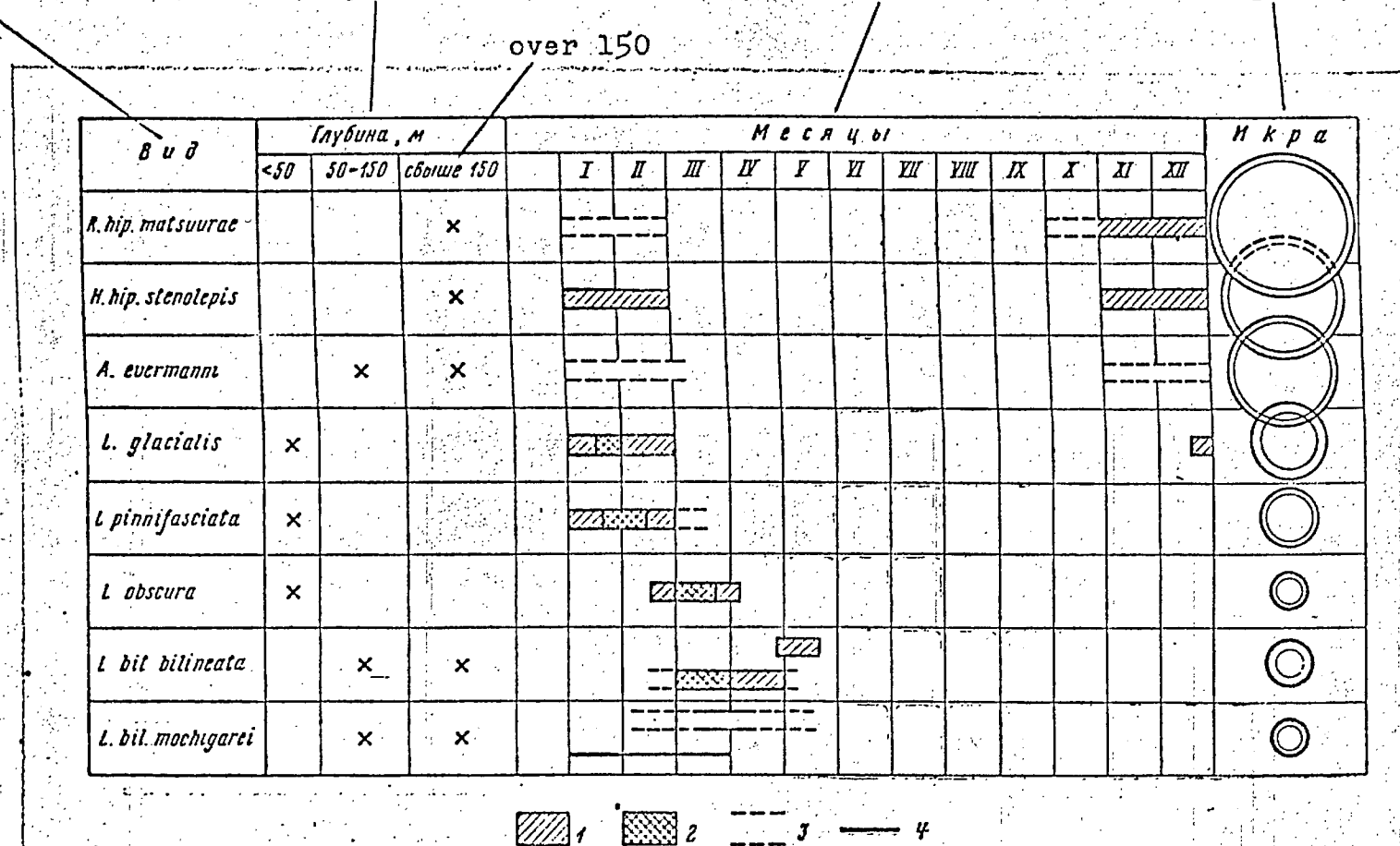


Figure 72 - Spawning time of winter-, winter-spring-, and winter-autumn-spawning flounder off the coasts of the USSR and Hokkaido

The outer circles represent the diameter of the eggs, and the inner circles, yolk sizes; 1 - observed spawning; 2 - mass spawning; 3 - assumed; 4 - off Hokkaido

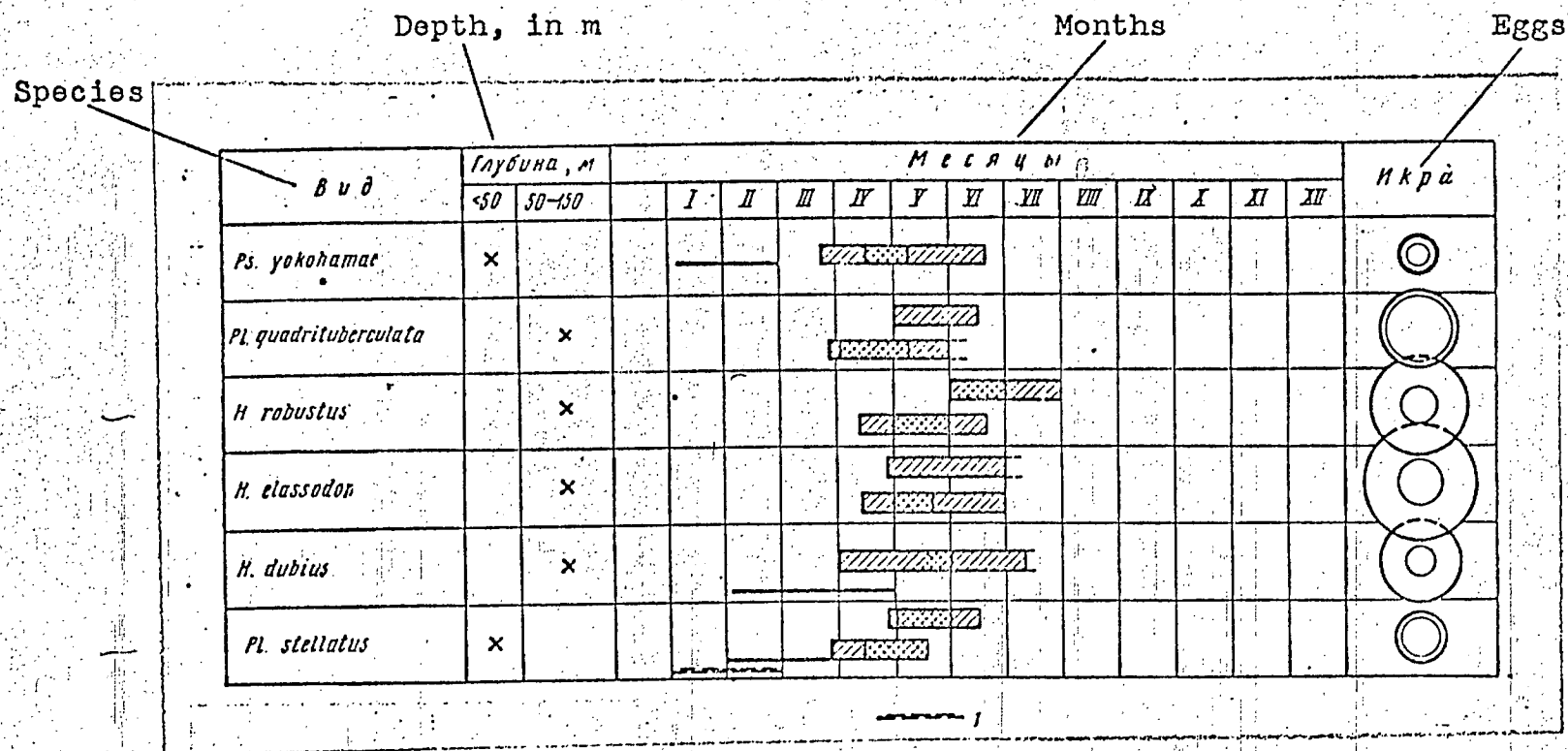


Figure 73 - Spawning time of spring-spawning species off the coasts of the USSR, Hokkaido and America

1 - off the coast of America. For remainder of legend see fig. 72

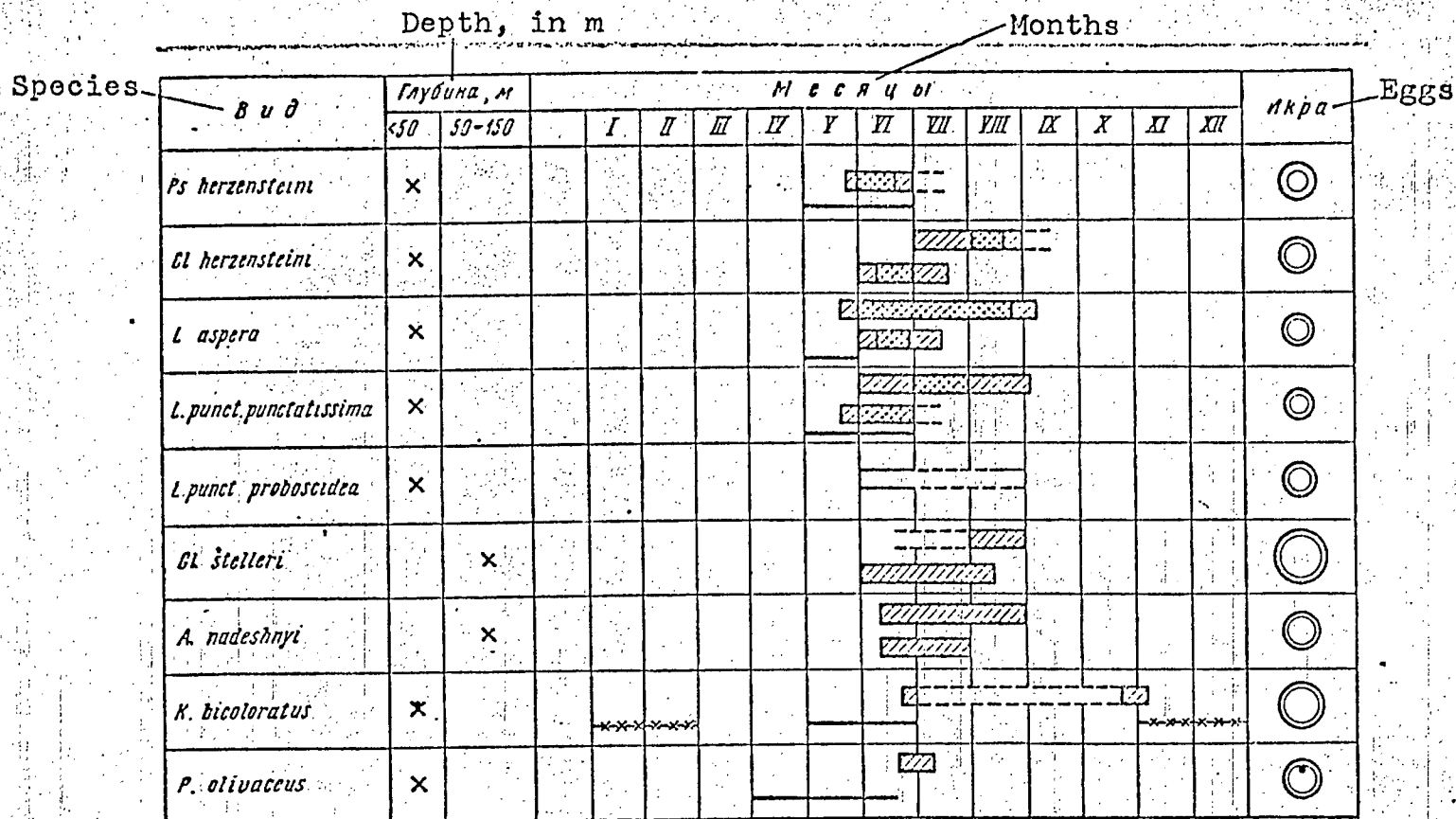


Figure 74 - Spawning time of summer-spawning fish off the coasts of the USSR, Hokkaido and Southern Japan

1 - off Southern Japan. For remainder of legend, see fig. 72

containing a sufficient quantity of oxygen. In embryos, throughout the whole of the embryonic period of life, no special breathing organs develop, erythrocytes are absent, and the beating heart drives only a homogeneous plasma devoid of blood corpuscles.

The sizes of prolarvae that have just hatched correspond to the sizes of their eggs, and in this way repeat the regular patterns observed for eggs. It should be noted that noticeably smaller prolarvae hatch from pelagic eggs that are of the same size as bottom eggs; this phenomenon is related to the larger 447 amount of formative material in bottom eggs. The prolarvae and larvae of winter, winter-spring and autumn-winter species are larger than the prolarvae of spring and summer species, and, in turn, the prolarvae of species that spawn in the open areas of the sea are larger than those that are proper to offshore areas. In addition, it should be noted that the majority of prolarvae of the first three groups and of the open parts of the sea hatch not only larger, but also morphologically more developed. Alaska plaice prolarvae, for example, hatch with an open mouth, pigmented eyes, a head separated from the yolk sac to the level of the rear edge of the auditory capsule or of the pectoral fins, and with small and probably already mobile pectoral fins whose bases are situated vertically. The prolarvae of the Sea of Okhotsk flathead flounder hatches at an earlier stage of development (but at a later stage than the prolarvae of summer-spawning species).

The prolarvae of winter-spring species which have bottom eggs, under natural conditions hatch less developed than the prolarvae of the Alaska plaice and the typical flathead flounder, but more developed than summer species. The forward

Table 86

The Correlation between Egg Sizes, Duration of Incubation Period and the Length
of Hatched Prolarvae of Far Eastern Flounder

Species	Egg diameter, in mm		Yolk sizes in mm		Water temperature during incubation, in °C		Length of incubation period [*] , in		Length of hatched prolarvae, in mm		Data
	range	average	range	average	range	average	days	hours	range	average	
<i>H. hip. stenolepis</i>	2,9—3,8	3,25	—	—	3,0	—	—	—	7,8—15	11,2	Thompson and Van Cleve, 1936
<i>Pl. quadrituberculata</i>	1,9—2,05	0,97—1,01	1,26—1,84	1,32—1,73	4,8—9,2	6	16	18	5,85	—	Our own
<i>H. dubius</i>	2,02—2,34	2,27	0,97—1,1	1,03	9,8—12,1	10,8	5	15	2,6—3,13	3,0	Same
<i>Gl. stelleri</i>	1,23—1,49	1,36	0,80—1,19	1,11	11,6—16,4	13,6	7	—	4,1—5,2	4,64	"
<i>L. pinnifasciata</i>	1,45—1,61	1,54	1,20—1,43	1,35	—2,0—+5,0	+1,3	24	—	3,07—3,34	3,25	Yusa
<i>Pl. stellatus</i>	0,97—1,01	—	—	—	2,0—5,4	3,7	14	17	2,58—3,36	—	Orcutt
Тот же	0,89—0,94	—	—	—	11,3—14,8	10,5	4	14	1,93—2,08	2,0	—
<i>Cl. herzensteini</i>	0,9—1,00	0,93	0,64—0,87	0,71—0,80	16,4—19,0	13,1	4	9	—	—	Our own
Тот же	0,9—1,00	0,93	0,64—0,87	0,71—0,80	15,4—19,4	17,6	2	18	2,17—2,59	2,4	—
<i>Ps. herzensteini</i>	0,81—1,00	0,88	0,64—0,79	0,74	11,0—15,2	16,6	2	16	2,05—2,29	2,16	Same
<i>L. aspera</i>	0,76—0,88	0,83	0,57—0,76	0,64—0,73	15,9—19,0	13,1	4	14	1,87—2,44	2,24	"
<i>L. punct. punctatissima</i>	0,71—0,80	0,74	0,51—0,69	0,59	—	17,6	2	14	1,79—2,21	2,08	"
<i>P. olivaceus</i>	0,93—1,03	—	0,71—0,81	—	—1,0—+8,6	20,4	2	—	1,14—2,27	—	"
<i>L. obscura</i>	0,81—0,94	0,87	0,55—0,8	0,63	—0,2—+8,2	+2,4	22	5	2,32—3,21	2,67	"
<i>L. bil. bilineata</i>	1,02—1,09	1,07	0,76—0,94	0,85	+4,8—+7,8	+3,5	22	15	3,60—4,00	3,8	"
<i>L. bil. mochigarei</i>	0,87—0,95	0,93	0,54—0,65	0,62	4—12	+5,6	19	—	3,26—3,84	3,51	"
<i>Ps. yokohamae</i>	0,73—0,83	0,78	0,44—0,64	0,57	—	8,4	8	10	2,4—2,7	2,55	"

* Prior to mass hatching

The Correlation between Egg Diameter, Duration of Incubation Period and
Length of Hatched Prolarvae of Atlantic Flounder

Species	Diameter of eggs, in mm	Water temperature during incubation, in °C		Duration of incubation period, in days	Length of hatched prolarvae, in mm	Data
		range	average			
True halibut						Taning, 1936; Dannevig, 1895
Ocean (plaice)						Dannevig, 1894
Same	3,0-3,8	—	6,0	16	6,5-7	
"	1,6-2,08	5,2	—	21	—	
"	—	—	6,0	18 ¹ / ₄	—	
"	—	—	10,0	12	5	
"	—	—	12,0	10 ¹ / ₂	—	Cunningham, 1893
"	—	6,0-8,5	7,0	16 ¹ / ₂ -18 ¹ / ₂	4,10	
"	—	—	10,0	12	6,0-8,0	Ehrenbaum, 1897
Flathead flounder	—	—	3,9	11-14	4-6	Huntsmann, 1918; Ehrenbaum, 1905 and 1909
Long flounder	1,07-1,25	7,7-9,4	—	7-8	4-9	Bigelow and Welsh, 1925
Fluke	0,91-1,03	—	10,0	5	2,23-3,29	Cunningham, 1882
Yellowtail flounder	0,81-0,92	7-11	—	7	2,46-2,67	Cunningham, 1887; Ehrenbaum, 1897
Yellowtail flounder	0,74-0,85	2,8-3,1	—	15-18	3,0-3,5	
Winter flounder	0,87-0,94	10,0-11,1	—	5	—	Bridger, 1924
Rusty	—	—	—	—	—	Bigelow and Welsh, 1925

end of the head is usually separated from the yolk sac, and pigmentation of the eyes is beginning. Finally, the prolarvae of flounder that reproduce in summer hatch poorly developed: their heads are tightly appressed to the yolk sac, there is no mouth, and the pectoral fins have the appearance of minute, vertically standing laminae whose bases are situated parallel to the longitudinal axis of the body. The eyes are unpigmented. Long flounder prolarvae from the open part of the sea hatch more developed, a phenomenon related to temperature conditions.

It is known from experiments and observations in nature that the higher the incubation temperature (within limits possible for the development of each species), the more rapidly and less developed the prolarvae hatch. An example confirming our assumption is to be found in the larvae of the Atlantic winter flounder (Ps. americanus), which hatch more developed than the larvae of the dab and other summer-spawning forms. The prolarvae of the flathead sole and the plaice in the North Sea are smaller and hatch less developed than in the Barents Sea. On the basis of the foregoing material, the following assumption may be formulated: the sizes and the degree of development of flounder prolarvae that have just hatched correspond to the temperature at which the eggs develop. In series of closely related species, the degree of development of prolarvae that have just hatched is inversely proportional to the temperature during the period of development of the eggs and hatching.

The degree of development of closely related forms in series increases from south to north and from shallow to deep water. Prolarvae feed differently and have different body proportions in accordance with their size and degree of

development. Large and more developed prolarvae, of the winter-spring forms, shortly after hatching (and some, probably, immediately after hatching), side by side with their endogenous feeding, convert, on the basis of the yolk that they contain, to active feeding and thus have mixed food habits. They are very mobile, and have a long tail and, correspondingly, a short distance from the end of the snout to the insertion of the anal fin.

As indicated above, species that lay large eggs are of a comparatively low fecundity. Their small quantity of eggs is compensated by the large sizes of more developed hatching prolarvae. A high degree of mobility and active procurement of food give them a definite advantage in the struggle for existence. This reduces the mortality and maintains the numbers of the species. The feeding of just-hatched prolarvae of the summer ecological-morphological group of flounders takes place exclusively on the basis of the reserves of the yolk sac. Consequently, they are of limited mobility and have a short tail and a correspondingly 448 long distance from the end of the snout to the insertion of the anal fin.

Because of their limited mobility, the prolarvae, as compared with the larger and more mobile prolarvae of the winter-spring groups, are subjected to greater danger: a large number die from various unfavourable conditions and fall prey to their enemies. Their high mortality is compensated by a high fecundity. (All species reproducing in summer in the offshore zone have a greater fecundity in comparison with winter- and spring-spawning species.) Also of no little importance in maintaining the numbers of the species is the

shorter period for which the prolarvae and larvae of the summer-spawning forms stay in pelagic depths.

Prolarvae that have hatched from pelagic eggs lead a pelagic mode of life, and at first keep to the places at which they hatch. Nor do prolarvae of the black, and Japanese flounders or of the rock sole that have just hatched from bottom eggs, remain on the bottom. Performing peculiar movements, they gradually rise up. They swim upwards almost in a straight line and evenly, alternately resting for periods in which they sink passively. Since the length of the path covered in ascent is greater than that during sinking, in each ascent in turn the prolarva is higher and higher and in the end rises to the upper layers of the water. Prolarvae that have risen up lead the same pelagic mode of life as larvae that have hatched from pelagic eggs.

In this connection it is interesting to note that, according to our observations, prolarvae and larvae hatching both from pelagic and bottom eggs have a positive phototaxis towards scattered light and behave negatively towards direct sunlight. We have not studied the behaviour of older larvae towards light, but by analogy with the larvae of bottom invertebrates (Thorson, 1946) it may be assumed that as larvae grow, the positiveness of phototaxis diminishes, and towards the completion of metamorphosis they become photonegative. Special experimental observations are required for the final solution of this question.

The prolarvae of the arrow-toothed, Greenland and true halibuts, which, as is known, hatch at great depths, also shift to the higher (but not the surface) layers of the water.

The distribution of larvae in the upper layers of the water coincides with that of plankton, the bulk of which also stays within the upper levels.

The Metamorphosis of Flounder Larvae

As indicated above, the development of prolarvae generally proceeds in the same way as in all other fish: as the yolk sac is absorbed, the mouth apparatus is formed, and the intestine opens and communicates with the oral cavity. At the same time, the pectoral fins increase in size and acquire mobility, the tail lengthens and, in addition, the mobility of the prolarvae increases, a necessary condition for the pursuit and grasping of food.

When flounder larvae develop, they undergo very complex changes (metamorphosis), in the process of which the entire organism of the larvae as a whole adapts to a certain group of external conditions in a definite ecological niche -- in this case, to dwelling on the bottom.

It has been known for a long time -- since the beginning of the second half of the nineteenth century -- that flounder prolarvae, when they hatch, are fully symmetrical, with eyes situated, as in normal fish, on both sides of their heads. It was previously believed that the flat body shape of flatfishes resulted from sinking to the bottom and that it originated from a demersal mode of life. Actually, not only asymmetry, but all the features of family, genus and species develop in the course of life under pelagic conditions. An external visible feature of asymmetry is the beginning of the shift of the eye of the future lower side to the other side. This external process of metamorphosis of flounder larvae was noted very long ago, and its internal development studied much later in detail (Kyle, 1923). /449

The process of metamorphosis takes place at different rates of speed in different species. Hence even the sizes of flounder vary greatly. The largest larvae are those of the long flounder of the genus Glyptocephalus and the smallest, those of Ps. americanus and L. obscura (see Table 88).

The duration of the pelagic period of life of larvae, which is of great importance in the preservation and settlement of a species, is closely related to the environment. If larvae in all stages of metamorphosis are grouped by sizes, it will be found that metamorphosis takes place most rapidly in offshore forms, which develop at high temperatures, and that this process is slower in species living in the open sea.

We have not established the reasons for the more rapid rates of metamorphosis of larvae of the genus Platessa, as compared with species of the genus Limanda.

Peculiarities of Larval Pigmentation

The colouring of fish in individual stages of development, and of mature specimens, has interested many scientists. To this question has been devoted an enormous number of studies, which Bronn (1927) collated and generalized. Of later works, mention should be made of research by V. V. Vasnetsov (1934) devoted to the evolution in the colour of bony fishes. Vasnetsov, in the introduction to his article, writes: "The problem of the phylogenetic relationships of groups of bony fishes cannot be considered to have been adequately treated, /450 neither in relation to small taxonomic units such as families or genera, nor in relation to suborders or, as they are now understood orders. Therefore an interest in solving the problem of this feature (colouring) is highly desirable..."

Table 88

The Sizes of Flounder Larvae Towards the Moment of
Passage of the Eyes to the Other Side

Species	Length of body, in mm	Data
<u>Gl. cynoglossus</u>	About 40	Petersen, 1904
<u>Gl. stelleri</u>	" 40 to 50	Our own
<u>R. hippoglossoides</u>	More than 30	Jensen, 1935
<u>H. h. stenolepis</u>	22.3 to 28.8	Thompson and Van Cleve, 1936
<u>H. h. hippoglossus</u>	35 to 40	Schmidt, 1904; Taning, 1936
<u>H. platessoides</u>	30	Petersen, 1904
<u>H. p. limandoides</u>	30	Our own
<u>H. elassodon</u>	30	Same
<u>A. nadeshnyi</u>	About 20	Same
<u>L. bilineata bilineata</u>	About 20	"
<u>L. limanda</u>	About 15	Schnakenbeck, 1928
<u>L. aspera</u>	" 15	Our own
<u>P. platessa</u>	14 to 15	Ehrenbaum, 1905-1909
<u>Pl. stellatus</u>	About 10	Ehrenbaum, 1905-1909
<u>Pl. flesus</u>	" 10	Orcutt, 1950
<u>Ps. americanus</u>	" 8 to 9	Bigelow and Schröder, 1953
<u>L. obscura</u>	" 8 to 9	Our own and Kurata's, 1956

An understanding of the evolution of colouring is moreover necessary for investigating the regular patterns of the evolutionary process. Vasinetsov writes further that "Colouring on the one hand is highly variable under the direct influence of environment; and on the other hand it is constantly being determined by hereditary factors, while a definite character is proper to whole groups of animals, and to genera and families..."

An analysis of flounder pigmentation at different stages of development has permitted us to establish, as for other fish (Rass, 1949), three basic types of pattern -- scattered, row, and that which has the appearance of stripes or spots and accumulations (in the sense of the distribution of pigmentary cells over the bodies of embryos and larvae), by which or by a combination of which the whole range of colouring is formed.

In the ontogenesis of flounder the first to appear is the scattered, then the row, and last, the spot-band type of pigmentation. The last two types at the beginning of their formation are usually combined with scattered cells, some of which subsequently become part of the accumulations, while others disappear entirely.

Pigment which has appeared is, in the character and distribution of the cells that compose it, generally similar in all species, but as early as the time of embryonic development, specific features are outlined which subsequently appear more and more distinctly. It is in larvae that have not been fully formed that the specific characteristic of pigmentation attains its greatest prominence. After rays are established in the fins, these differences even out somewhat, and towards

the close of metamorphosis the pigmentary pattern, losing none of its specificity, in the majority of species acquires common features (upper, lower, and lateral rows of spots) because of the transition to similar dwelling conditions on the bottom. When the pigment patterns of the flounder larvae that we have studied are compared, common characteristic features are seen, on the one hand for a group as a whole, and on the other, for genera and individual species.

It is characteristic of larvae of all species as a whole that the lower portion of the body is more intensively pigmented than the upper portion, and that the trunk, head and abdomen are coloured differently from the tail. A row-type, scattered and unformed accumulation of cells is characteristic of the lower portion of the body. The corresponding characteristic feature of the trunk is a row-type, transverse-oriented accumulation that intersects the body in the form of bands. In establishing the species of larvae, the most important feature is the pigmentation of the tail.

Let us examine the group and generic features. In all of the species that we have examined of larvae of the group of large-mouthed flounder, with the exception of the arrow-toothed halibut, the end of the urostyle is surrounded with a row of pigmentary cells (see fig. 75, 1-6). This is observed not only in Far Eastern flounder, but to an equal extent in Atlantic flounder. The pigmentation, therefore, of the end of the urostyle may be considered a feature of the entire group. An absence of pigment at the end of the urostyle is characteristic of small-mouthed flounders (see fig. 75, 7-17).

The prolarvae and larvae of the Greenland and true halibut are characterized by a very poor development of pigment;

also characteristic is a primitive scattered-row type of pigmentation. The genus Hippoglossus differs from the genus Reinhardtius in an extensive development of scattered row pigmentation on the dorsal and anal fin folds (see figs. 4 and 7, and 75, 2 and 3). A row distribution of pigmentary cells is characteristic of the genus Acanthopsetta (see figs. 19 and 75, 5); in this respect, it resembles the Greenland and true halibuts. Larvae of the genera Atheresthes, Cleisthenes and Hippoglossoides have a pigmentary pattern which differs sharply from that of the genera Reinhardtius, Hippoglossus and Acanthopsetta. The pigmentary cells on the metameric portion of the tails of these flounders form bands. In larvae of the genus Cleisthenes there are two such bands, while the stripes that compose them are separate along the middle line of the tail, and are extended along the length of the larvae. There are three or four pigment bands (see figs. 11, 13, 15 and 75) in the prolarvae and larvae of the genus Hippoglossoides. It should be noted that in Atlantic flounders the forward band is rudimentary and represented by a small group of cells on the lower edge of the tail. In the southern Verasper, which has a mouth of average size, the end of the urostyle is not pigmented, and the entire body is thickly covered with melanophores, among which two bands stand out weakly on the tail.

The larvae of the vast majority of small-mouthed flounder species have a spot-band pigmentation in the metameric portion of the tail; only in species of the genera Limanda and Platessa is a row arrangement of pigmentary cells observed. Larvae of the genus Limanda have a distinct double row of pigmentary cells on the lower edge of the tail, and an incomplete, deep row of melanophores above the chord, beginning far behind

the anus (see figs. 30 and 75). In larvae of Limanda (Myzopsetta) the row arrangement is disrupted by an accumulation of melanophores on the tail at the beginning of its rear third or near the middle (see figs. 32, 35, and 75).

Larvae of the genus Platessa have a less distinct row on the lower edge of the tail, a short row on the upper edge of the end of the tail, and a long row of deep melanophores above the chord, beginning, as a rule, at the level of the anus (see figs. 43 and 75, 3).

In larvae with a band type of pigmentation the number of bands varies. In species of the genus Liopsetta (L. pinnifasciata and L. glacialis) there is one band on the middle of the tail (see figs. 48, 49, 51, and 75). The species L. obscura stands apart; its larvae have a forward band in addition to a band in the middle. The prolarvae and early larvae of species of the genus Pleuronectes (P. stellatus and Pl. flesus with all of their subspecies) in the character of the pigmentation of their tails display a great similarity to the prolarvae and larvae of L. glacialis and L. pinnifasciata, -- only one band forms at first on the middle of their tails (see figs. 57 and 75, 17). Subsequently, in older larvae of both genera, the band type of pigmentation is replaced by a secondary, scattered-row type. Older larvae of the species Kareius bicoloratus, which resembles the genus Pleuronectes, also have a scattered-row type of pigmentation.

Prolarvae and larvae of species of the genus Lepidopsetta have at first two distinct bands and a rudimentary third band; older prolarvae and larvae have a full second band and an upper stripe of a partially reduced forward band (see figs. 22, 23, 26, and 75, 8). The pigmentation of prolarvae and larvae of

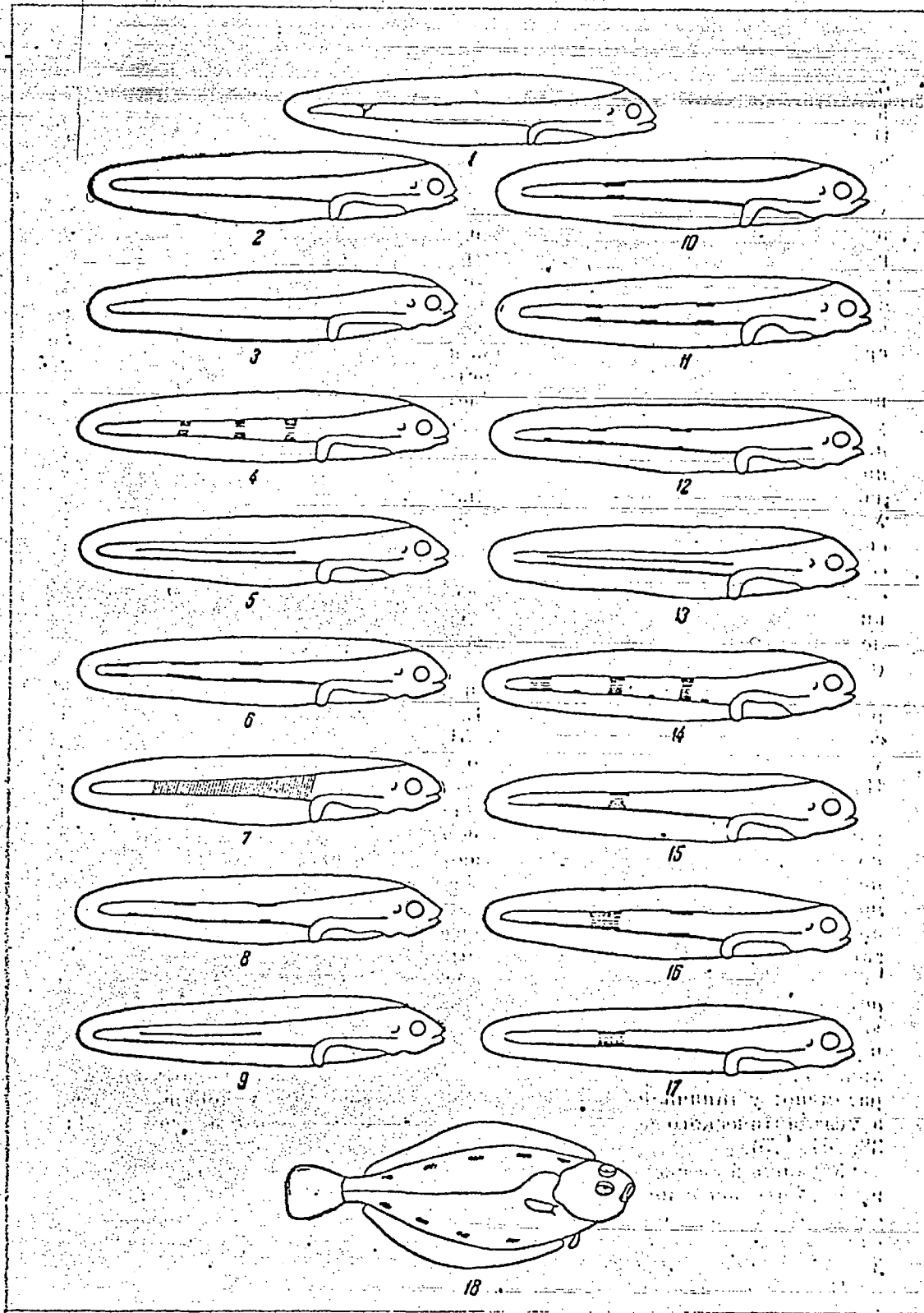


Figure 75 - Diagram of the arrangement of pigmentary cells on the tails of flounder larvae.

1 - *Atheresthes*; 2 - *Reinhardtius*; 3 - *Hippoglossus*; 4 - *Hippoglossoides*; 5 - *Acanthopsetta*; 6 - *Clesthene*; 7 - *Verasper*; 8 - *Lepidopsetta*; 9 - *Limanda*; 10 - *Limanda* (*Myzopsetta*); 11 - *Pseudopleuronectes herzansteini*; 12 - *Ps. yokohamae*; 13 - *Platessa*; 14 - *Olyptocephalus*; 15 - *Lipsetta pinnifasciata*; *L. glacialis*; 16 - *obscura*; 17 - *Pleuronectes*; 18 - *малек (обобщенный)*

18 - fingerling (generalized)

the genus Pseudopleuronectes is not monotypic -- the number of pigmentary cells varies: in the typical Ps. herzensteini. there are three, in Ps. yokohamae there are two, and in the Atlantic species Ps. americanus, there is only one (see figs. 10-11, 38, 41, and 75).

In long flounder of the genus Glyptocephalus there are three short bands, of which the last is situated near the end of the urostyle, but not at its very end, as we have seen in the large-mouthed flounders. In addition, small pigment spots located on the middle of the spaces between the bands (see figs. 13, 56, and 75) are characteristic of species of this genus.

The prolarvae and larvae of the genus Microstomus have four transverse bands.

On the basis of the foregoing it may be assumed that of the large-mouthed flounders, those with the most primitive pigmentation -- colouring -- are the halibuts Reinhardtius and Hippoglossus, while among the small-mouthed flounders, the same applies to L. limanda and L. aspera. The colouring of L. punctatissima punctatissima, L. punctatissima proboscidea and L. ferruginea has deviated somewhat from this type. /453

Lepidopsetta and Pseudopleuronectes, which are close to the genus Limanda, have deviated even more in respect to colouring. Incidentally, atypical (bottom) eggs, and prolarvae and larvae that are unique in their structure and character of movement are, together with a change in colour, characteristic of these highly specialized forms, with the exception of Ps. herzensteini.

The process of the further development of colour in the larvae of all flounder leads without exception to the

convergent formation of the spots of the upper and lower rows of the tail, the completion of which coincides with the moment of completion of metamorphosis and the transition of the larvae to a bottom mode of life. Where there is a band type of pigmentation, the formation of spots takes place mainly through the transformation of the upper and lower stripes which diverged when the body grew in height, and to an insignificant degree through the formation of new pigmentary cells. In larvae with row or scattered-row type pigmentation the formation of spots takes place exclusively on the basis of the regrouping and new formation of pigmentary cells, and always in a strictly determined order -- from back to front.

After juveniles have lain on the bottom, in the process of adaptation to the latter's colouring, pigment markings become intensified on the eye side, since there appear the spots of the middle lateral, and then of the upper lateral and lower lateral rows, and in the end there develops a spotty-checked pigment pattern, subsequently made complex (and at the same time losing its sharp definition) by a large quantity of melanophores scattered among its components. In some species rows of spots are also frequently observed on the dorsal and anal fins. The form, quantity and arrangement of individual pigment spots are different in the fingerlings of different species, and in the same way as in prolarvae and larvae they are of great importance for identification.

The significance of colouring as a biological phenomenon in the lives of embryos, prolarvae and larvae is not entirely clear. In adult flounder it has an adaptive significance and is manifested in different ways under different

conditions. The amazing capacity of flounder to alter their colouring in relation to the colour and pattern of the bottom is well known; in experiments, flounder have reproduced the appearance of the bottom so completely that they have become almost imperceptible (Luk'yanova, 1936; Osborn, 1941 and 1948; Parker, 1948; Breder, 1955, and others).

We have not as yet established the adaptive significance, specific for flounder prolarvae and larvae, of colouring as has been demonstrated for fish of the herring family (Rass, 1937).

Let us see whether there is any kind of link with the ecological conditions under which prolarvae and larvae dwell. The larvae of winter-spawning offshore species (L. glacialis and L. pinnifasciata) have a band type of pigmentation, and the two winter-autumn species of the open sea (R. h. matsurae and H. h. stenolepis), a scattered-row type. The genus and species of the winter-spring group (L. bil. bilineata, L. bil. mochigarei and L. obscura) and one species of the spring group (Ps. yokohamae), which develops from bottom eggs -- all, without exception, have a band-type pigmentation.

Among the spring forms, the offshore species (P. stellatus and Pl. flesus) have a band type of pigmentation, represented by one band, while the forms that dwell in the more open areas (Hippoglossoides) have four bands. The prolarvae and the larvae of the genus Platessa, which develop at the same time, are characterized by a row arrangement of pigmentary cells.

In the group of summer-spawning fish in the offshore zone some species (Limanda) have a row arrangement of pigmentary

cells, while others (Cl. herzensteini and Ps. herzensteini) have a spotty-band arrangement. In precisely the same way, of the two species developing in the more open areas of gulfs, G. stelleri has a spotty-band type of pigmentation, and A. nadeshnyi, a row type.

Thus within the limits that we have established 454 for ecological groupings no distinct relation is disclosed between pigmentation and ecological conditions during the period of development. The prolarvae and larvae of the winter-spring ecological group, as well as those of one species of the spring group, which hatch from bottom eggs, are an exception. Here there distinctly emerges a curious parallelism in the development of the pigmentary pattern (highly similar in all), on the one hand, and in the character of movement, on the other. The fact is that all prolarvae that have hatched from bottom eggs, on rising up perform movements of the same type, described above, with their tails. We do not observe such movements in any other groups. In spite of the fact that the majority of species included in this group differ in details of pigmentation, two bands develop on their tails. Thus two peculiarities of prolarvae and larvae prove to be linked. Where they have bottom eggs, they differ from all flounder developing from pelagic eggs in the unique movement of their tails and in the no less unique pigment on the latter. It should moreover be noted that the prolarvae of the banded and starry flounders, which have a similar pigmentation (a band on the middle of the tail) perform identical movements with their tails; at the same time, their yolk sacs are turned upwards. It is possible that it is in just this that the causal dependence consists, but it is difficult to decide what its nature is without the application of the experimental

method. It is probably that such a conformity is not accidental, and that the development of the pigment pattern on the tail depends directly upon the character of movement.

In this connection it is interesting to note that spotty-row pigmentation is usually on the tail, whose length in pelagic flounder prolarvae with different types of pigment varies towards the moment of absorption of the yolk sac. In most of the species that have a linear-row arrangement of their pigmentary cells, the tail is shorter, while in species with a spotty-band type of pigmentation it is longer; among the latter, those with the longest tails are forms (Hippoglossoides and Glyptocephalus) with three or four bands (see Table 88). The spots of the upper and lower rows that form upon further development are also related to the peculiar movement of the anal and dorsal edges of the body and the fins. An accumulation of melanin pigment is usually accompanied by a corresponding accumulation of lemon-yellow xanthophores, which participate in oxidizing processes. In connection with our discussions it may be assumed that the arrangement of spots on the tail is associated with the zone of the most intensive oxidizing processes, which take place when the myotomes contract and which determine the bending and unbending of the tail. This assumption appears to agree fully with the data of physiologists, which have shown that the consumption of oxygen in the muscles, and, consequently, the oxidation processes, increase when a muscle passes from rest to work. The final solution of the problem involving the relation of the pigment pattern of the tail to the character of its movements needs additional observations specially arranged both in nature and under experimental conditions. The possibility is not excluded of an association between pigmentation

and the geographical occurrence of a species.

T. S. Rass (1935) has noted that the pigmentation of the embryos of arctic forms appears at a later stage of development than in the embryos of related boreal forms. Larvae and fingerlings in colder waters are usually less pigmented. These regularities, which have been established for the eggs and larvae of cods, are only partially observed in Far Eastern flounder in corresponding stages of development.

In observing the time at which pigmentation appears, and its intensity, within the limits of the same species or of the related species of one genus, we have noticed that in different regions of a geographical range pigment appears in embryos at the same stages of development -- the beginning of formation of the tail bud. Subsequently, however, it is 455 not as clearly expressed in embryos in northern as in southern regions. For example, the larvae of the yellowfin sole are less highly coloured in the north than in the south. The prolarvae and larvae of the northern rock sole are noticeably less coloured than those of the southern-temperate-boreal variety. The larvae of the subtropical-boreal two-coloured flounder are far more intensively pigmented than those of a mainly boreal species -- the starry flounder. Unfortunately, we cannot compare the pigmentation of the prolarvae and larvae of H. robustus and the southern form H. dubius. No noticeable difference is found in the pigmentation of embryos prior to hatching. The embryos, prolarvae and larvae of H. elassodon, as indicated above, are appreciably more intensively coloured than those of H. Dubius, which accords fully with the observations of Petersen (1904): "Juveniles of the same species are of different sizes in different waters, and the larvae of

the open areas of the sea are larger and have an appearance different from those in the offshore area. Their pigmentation is frequently more sharply expressed." The more intensive pigmentation of southern forms is evidently associated with an adaptation protecting the nervous system of embryos and larvae from the bright sunlight of the south (Rass, 1935).

In conclusion, it is interesting to note that the pigmentation of flounder prolarvae and larvae of the same age and developing under artificial conditions is usually darker than that of specimens collected at sea. We have noted this phenomenon in Caspian herring (Pertseva, 1939), as has S. G. Kryzhanovskii in perch and other fish (1949 and 1953). The reasons for the more abundant pigmentation of prolarvae and larvae under artificial conditions, according to Kryzhanovskii, consist in the peculiarities of illumination, breathing, and any number of other conditions perceptible with difficulty, in the aquarium, with which we can agree fully.

A Comparison of Far Eastern and Atlantic Flounder Species

As indicated above, ten species of Pacific Ocean flounder have their analogues in the Atlantic. These species are mainly those with a preference for cold: the subarctic-boreal species Pl. quadrituberculata; the mainly boreal species Pl. stellatus; the Pacific-boreal species R. hippoglossoides matsuurae, H. hippoglossus stenolepis, L. aspera, and the northern-boreal Sea of Okhotsk-Bering Sea species H. elassodon. The only exceptions are the temperate-boreal Sea of Japan species Gl. stelleri and the southern-boreal Sea of Japan species Ps. yokohamae. L. glacialis is circumpolar.

The Atlantic flounder of the above species are extremely similar to their Pacific counterparts and differ most frequently only in insignificant meristic features and in the structure of their scale, while the difference between some (the species Reinhardtius and Hippoglossus) are so unimportant that their taxonomic value does not extend beyond the limits of subspecies (Vernidub, 1936; Vernidub and Panin, 1937).

The flounder species of the Atlantic and Pacific Oceans that are similar taxonomically display corresponding regularities in respect to biology. Both dwell, reproduce and develop under similar ecological conditions and have a similar latitudinal change in spawning periods and conditions. Thus H. platessoides platessoides reproduces in Men Gulf from the beginning of March to the middle of July at water temperatures of 2.8 to 4°, and in the Gulf of St. Lawrence in May and July at water temperatures ranging from -1.7 to 0°. H. platessoides limandoides spawns in the North Sea from the middle of January to May, and in the Barents Sea from March to June. L. limanda spawns in the North Sea from the end of January to July, and in the Barents Sea from May to August. P. platessa spawns in the North Sea from the end of November and beginning of December to the beginning of June for the most part at 5 to 6°, and in the Barents Sea from 456 February to the middle of June at 1 to 3°. Pl. flesus reproduces in the North Sea from January to May, and in the Barents Sea from the beginning of April to the end of June. This corresponds to what has been described above for similar Pacific species.

Atlantic flounder lay their eggs within the limits of the mainland shoal, at approximately the same depth as Pacific flounder.

A particularly marked resemblance is revealed in the biology of related flounder of the Asiatic and American Atlantic coasts, where winter- and spring-spawning species reproduce under extremely similar severe conditions. Flounders off the European coast, because of the peculiarities of the hydrological conditions of this region, have a greater preference for warmth, and the water temperature at which they reproduce in the north and Barents Seas is one or two degrees higher than in Far Eastern waters. It should also be noted that the temperature range of the summer-spawning species in Soviet waters is much wider than in European waters.

Great similarity is also observed in all analogous stages of development, beginning with eggs that have just been fertilized and ending with juvenile fish with a completed metamorphosis. They both have eggs and larvae that are similar in size and structure, the same type of pigmentation, and, other conditions being equal, equal rates of development. The complex processes of metamorphosis occur and are completed in them at similar sizes.

The specific features of the flounders under comparison appear most distinctly only after the formation of rays in unmatched fins, in the number of which they differ mainly when they are adults. Atlantic flounder fauna, in contrast to that of cod, undoubtedly originated from the richer Pacific Ocean fauna (Schmidt, 1948 and 1950).

The settlement of Pacific Ocean flounder, like that of other species with an amphiboreal distribution, according to L. S. Berg (1934, 1947 and 1953) and A. P. Andriyashev (1944) occurred mainly in the Pliocene, when a sea existed in the area of what is now Bering Strait, and the average

annual temperature in the surface layers of the water in this region was 5 to 10° higher than now. The transition of these flounder probably took place along the northern coast of Asia and America. When the environment subsequently got colder (during the ice age), all flounders (with the possible exception of the ancestor of L. glacialis) in the central area of the Polar Basin disappeared: some were forced south, and the others became extinct. In the warm period of time that succeeded the ice ages, the flounder that had migrated to the south advanced back closer to the north, but not one spread as widely around the pole, in the Arctic Basin, as L. glacialis. The distribution of the genus Liopsetta, which is limited to regions where the water in winter freezes to below-zero temperatures, and the spawning of all of its species at the coldest season of the year at below-zero temperatures, point to the preference of this species for cold. Since reproduction conditions can serve as an indirect indication of origin (Appelöf, 1912), it may be stated that the genus Liopsetta originated under arctic conditions.

The genus Liopsetta closely resembles the genus Pleuronectes (Platichthys), but, as our investigations have shown, these genera are especially similar at early stages of development. The arctic flounder prolarvae and larvae from the Kara Gulf that are in our possession, from the moment that absorption of the yolk sac is completed to the appearance of rays in unmatched fins, resemble analogous fluke larvae to such an extent that their species can be determined only with difficulty. Hence there arises the question as to whether the genera Liopsetta and Pleuronectes are near kindred and derivatives of an ancestor common to both.

The arctic flounder became adapted under arctic ⁴⁵⁷ conditions to reproduction and development at below-zero temperatures; this capacity became consolidated in heredity, was retained in the period of warmth that then set in, and was transmitted to L. pinnifasciata and L. putnami, which settled far to the south, as far as Peter the Great Bay inclusive in the Pacific Ocean and Massachusetts Bay in the Atlantic. Both of these species, in spite of the far southern boundaries of their geographical ranges, have, in their reproduction and development, fully retained the element of their nature and, similar to the initial form, reproduce in winter at the coldest time and at water temperatures lower than 0°. Moreover, as indicated above, their geographical ranges are limited to regions where such a temperature is established; off the western coasts of Europe and America, where an above-zero temperature that is unfavourable for their reproduction and development exists the year round, there are no representatives whatever of the genus Liopsetta.

In conclusion, I should like to touch, in the most approximate way, upon the age of certain species of Far Eastern flounder. Among the phylogenetically relatively ancient species it is evident that all those should be included which were formed towards the Pliocene epoch and which yielded emigrants to the Atlantic Ocean. These are R. hippoglossoides matsuurae, H. hippoglossus stenolepis, H. elassodon, L. aspera, Pl. quadrituberculata, Pl. stellatus and Gl. stelleri.

All of these retained the pelagic eggs that are typical of flounders. It is evident that the phylogenetically younger species are those that have bottom eggs. These include the Japanese Ps. yokohamae, the dark L. obscura, the southern rock

sole L. bilineata mochigarei, and the northern L. bilineata bilineata. This is confirmed by the following.

1. In the Atlantic Ocean, with the exception of Ps. americanus, which dwells off the eastern coast of America, there is not one species that lays bottom eggs.
2. Most of the flounder that lay bottom eggs are concentrated in a comparatively young water area -- the Sea of Japan, which originated (Jabe, 1929) in the Pleistocene.
3. The possibility of the conversion of pelagic eggs to bottom eggs in a subsequent segment of time (after the settlement of amphiboreally distributed genera) is confirmed by the parallel appearance (during the same period) of bottom eggs in the descendents of an Atlantic ancestor -- the Pacific cod.

Conclusion

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In the Pacific Ocean, as Norman demonstrated, of the flounders of the northern hemisphere, that which for the most part developed and was formed, was the subfamily Pleuronectinae of the family Pleuronectidae. It has 28 genera with 48 species, whereas in the Atlantic Ocean there are only 10 genera with 11 species.

The research into the reproduction and development of Pacific Ocean flounder that we conducted from 1949 to 1957 embraced 24 species -- all the commercial flounder species of the northern and temperate seas off the Asiatic Coast.

Research on Pacific flounder has permitted us to trace biographical and ecological regularities in the reproduction and development of this subfamily, to expose important factors of taxonomy and to outline the biological foundations of the possibilities for practical use of these valuable Far Eastern commercial fish.

In the process of historical development and the formation of species, Far Eastern flounder, in conformity with the vast extent of their geographical range and its diversity of hydrophysical conditions, became adapted to reproduction and development at different seasons of the year, in environments that were specific for each species.

One of the most important environmental factors that determine the beginning and the course of flounder spawning is the temperature of the water. The relationship of each species separately to this factor in large measure determines the species' geographical distribution.

In the main, the following seasonally spawning groups are distinguished: the winter-spawning (Liopsetta glacialis, Liopsetta pinnifasciata); the winter-spring spawning (Lepidopsetta bilineata bilineata, Lepidopsetta bilineata mochigarei, and Liopsetta obscura); the spring-spawning (Hippoglossoides, Platessa quadrituberculata, Pleuronectes stellatus, and Pseudopleuronectes jokohamae); the summer-spawning (Cleisthenes herzensteini, Limanda aspera, Limanda punctatissima punctatissima, Limanda punctatissima proboscidea, Glyptocephalus stelleri, and Acanthopsetta nadeshnyi), and the autumn-winter spawning (Atheresthes evermanni, Reinhardtius hippoglossoides matsurae, and Hippoglossus hippoglossus stenolepis).

The diversity of the seasons in which flounder species spawn is determined by the amplitude of seasonal fluctuations in water temperature. The greater are the gradients in such fluctuations, the richer and more diverse are the seasonally-spawning complexes of species reproducing in this region.

A comparison of spawning seasons in northern (Anadyr Gulf) and southern (Peter the Great Bay) regions reveals that the calendar periods of spawning become regularly later from south to north. In conformity with the general pattern, the number of species of spawning flounder decreases, and there is a decrease primarily in the number of summer-spawning species.

The reproduction of flounder takes place within the limits of their geographical range, in the region of the mainland shoal, for the most part at depths of no more than 100 to 150 m; only halibut reproduce in the drop-off zone. /459
The mass spawning of many species is confined to areas with relatively calm water or a local circular current.

Flounder occupy different niches during their period of reproduction and development. Their spawning is limited in time and space. The arctic and banded flounders reproduce near the shore, at depths of 5 to 15 m in winter under stable conditions; the black and Japanese flounders reproduce in the winter-spring and spring periods respectively, in the same environment. The vast majority of flounder reproduce at depths extending for the most part from 20 to 50 m in spring (the starry, Sea of Japan, and northern flathead flounders), or in summer (the yellowfin and snout soles, and the sohachi, longsnout, yellow-striped and long flounders). The Alaska plaice and the Sea of Okhotsk flathead flounder reproduce in spring at depths ranging for the most part from 50 to 100 m. The spawning of rock sole in the winter-spring period and of the spiny flounder in summer is confined to the lower zone of the mainland shoal (100 to 200 m). Halibut reproduce in the drop-off zone in the fall and winter period.

A comparison of the spawning seasons and of the geographical distribution of the spawning grounds of various seasonally spawning groups enables us to outline the biographical regions of flounder spawning grounds, which are closely related to environmental factors. These regions coincide with the schemes of zoogeographical regionalization of Andriyashev (1939), Vinogradov (1948), and Moiseev (1953).

We have for the first time succeeded in dealing fully with the development of 15 flounder species:

Hippoglossoides dubius, Hippoglossoides elassodon, Cleisthenes herzensteini, Acanthopsetta nadeshnyi, Lepidopsetta bilineata bilineata, Lepidopsetta bilineata mochigarei, Limanda aspera, Limanda punctatissima punctatissima, Pseudopleuronectes

yokohamae, Pseudopleuronectes herzensteini, Platessa
quadrituberculata, Liopsetta pinnifasciata, Liopsetta
obscura, Glyptocephalus stelleri, Pleuronectes stellatus,
and, partially, Atheresthes stomias, Atheresthes evermanni,
Reinhardtius hippoglossoides matsuurae, Hippoglossus
hippoglossus stenolepis, Hippoglossoides robustus, Limanda
punctatissima proboscidea, and Kareius bicoloratus.

On some of the above species, Ps. yokohamae, L.
obscura, L. bilineata mochigarei, and Pl. stellatus, there
are only fragmentary observations of Japanese scientists,
carried out in recent years. It has been ascertained that
the eggs of a whole group of the species L. bilineata bilineata,
L. bilineata mochigarei, Ps. yokohamae and L. obscura are
of the bottom variety and adhesive, whereas pelagic eggs
have been considered characteristic of all flounders.

Bottom flounder eggs are of secondary origin and
were formed from pelagic eggs as a result of the adaptation
of flounders to reproduction and development in a zone of
tidal water movement (Ps. yokohamae), during the period of
breakup and movement of ice combined with heavy currents
(L. obscura and Lepidopsetta spp.).

Developing eggs and larvae of different species and
at different stages of development make different demands
upon environment. The development of the eggs and larvae
of a group of flounders as a whole takes place within wide
fluctuations of temperature ranging from -2° to $+ 21$ and 22°
and higher. The development, on the other hand, of individual
species takes place at different temperatures depending upon
the geographical position of the spawning grounds and the time
of the spawning itself. All transitions, from the stenothermy

of winter-spawning groups developing under the ice at a constant temperature ranging from -2 to -1.7° (the arctic and banded flounders, and, at considerable depths and temperatures varying from $+2$ to -3° , halibut), to the eurythermy of spring- and summer-spawning groups, which reproduce under conditions of periodic temperature fluctuations, are being traced in relation to the temperature during the period of embryonic development. Within the limits of each species, the cleavage stages are related to narrower temperature boundaries than are the later stages. Larvae /460 are more eurythermal and can exist under conditions in which fertilization and cleavage are not always possible.

Experimental data have enabled us to reveal a latent (potential) opportunity for flounder eggs to develop within a wider temperature range than under natural conditions. The amplitude of temperature fluctuations within such a range is specific and is closely related to the environment; at the same time, the more stable are the natural conditions of development, the narrower are the potential opportunities of the latter. This factor is of essential importance in determining the possibility of acclimatizing flounder to other bodies of water.

The duration of the incubation period of eggs is determined by the environment, and depends upon the sizes of the eggs, the structure of their yolks and the temperature of the water.

The stages that are most sensitive to external influences have been established (cleavage and the period prior to hatching).

The sizes of eggs and larvae are determined by hereditary factors and environment, while the degree of development of hatching prolarvae is determined mainly by environment.

A regular geographical, seasonal and ecological pattern has been disclosed in flounder development.

The sizes of eggs and larvae, as well as the degree of development of hatching prolarvae, or among series of closely related species, increase from south to north, decrease from winter to summer, and increase from the coast to the open sea in accordance with changes, parallel in these cases, in the temperatures that determine a different correlation of the rates of growth and differentiation of organisms.

There is a close relationship between egg sizes and biotic environment. Larvae of various sizes are adapted to feeding on various species of plankton and to the process of obtaining the latter. Small larvae of limited mobility that are found in offshore, summer-spawning groups are adapted to neritic plankton, while large, more mobile larvae of the winter-spring spawning groups and in the open sea are adapted to feeding on relatively large items of ocean plankton.

A taxonomy has been developed for and a key prepared to the eggs and larvae of the following flounder species and subspecies:

Family Bothidae

Bastard halibut -- Paralichthys olivaceus (Temminck et Schlegel)

Family Pleuronectidae

Arrow-toothed halibut (Asiatic) -- Atheresthes
evermanni (Jordan et Starks)

Greenland halibut -- Reinhardtius hippoglossoides
matsuurae, Jordan et Snyder

True halibut -- Hippoglossus hippoglossus stenolepis,
Schmidt

Sea of Japan flathead flounder -- Hippoglossoides
ubius, Schmidt

Sea of Okhotsk flathead flounder -- Hippoglossoides
elassodon, Jordan et Gilbert

Northern flathead flounder -- Hippoglossoides
robustus, Gill et Townsend

Spiny flounder (Nadeshny's) -- Acanthopsetta nadeshnyi,
Schmidt

Variable verasper -- Verasper variegatus (Temminck
et Schlegel)

Northern rock sole -- Lepidopsetta bilineata bilineata
(Ayres)

Southern rock sole -- Lepidopsetta bilineata mochigarei,
Snyder

Yellowfin sole -- Limanda aspera (Pallas)

Longsnout flounder -- Limanda punctatissima /461
punctatissima (Steindachner)

Snout sole -- Limanda punctatissima proboscidea,

Gilbert

Yellow-striped flounder -- Pseudopleuronectes herzensteini (Jordan et Snyder)

Japanese flounder -- Pseudopleuronectes yokohamae (Gunther)

Alaska plaice -- Platessa quadrituberculata Linnaeus

Long (smallmouthed) [slime] flounder -- Glyptocephalus stelleri (Schmidt)

Black flounder -- Liopsetta obscura (Herzentein)

Arctic flounder -- Liopsetta glacialis (Pallas)

Banded flounder -- Liopsetta pinnifasciata (Kner)

Starry flounder -- Pleuronectes stellatus (Pallas)

Two-coloured flounder -- Kareius bicoloratus (Basilewsky)

An analysis of data that we have obtained shows that all species in almost all stages, especially larval stages, differ sufficiently well in their morphological features, these differences being expressed far more distinctly in certain species than in adult specimens (an example may be seen in the differences between the Japanese and black flounders).

The most important features of the eggs are the presence or absence of a fat drop in the yolk, which characterizes different flounder families; the size of the eggs; the structure of the membrane, which changes from thin and smooth, thin and wavy, thick and wavy, and thick with a reticulate-wavy [structure] to adhesive, thick and wavy,

and thick and covered with a mucous layer; other most important features include the sizes of the yolk, blastodisc, and perivitelline space. Of essential importance are the structure and character of distribution of the pigmentary cells on the body of the embryo and on the yolk.

The most important features of prolarvae and larvae are the shape and sizes of the body and the distribution of the pigmentary cells, the pigmentation of the tail being of paramount significance.

Characteristic features of pigmentation have been established for a group as a whole on the one hand, and for genera and individual species on the other. Many features of genus, and occasionally of species as well, are disclosed as early as the embryonic period, while features of closely related species, as a rule, become apparent only prior to hatching, and in some species, even after hatching.

In the process of formation of a species the character of pigmentation is to a certain extent determined by the character of tail movement. The disposition of pigment spots on the tail is related to the zone of the most intensive oxydizing processes taking place upon the contraction of the myotomes that cause the flexion and extension of the tail.

A comparison of the reproduction, development and structure of the eggs and larvae of flounders of the Pacific and Atlantic Oceans has disclosed similar regular patterns, with this different aspect, that in conformity with climatic conditions most Far Eastern flounder reproduce and develop under harsher conditions and in a wider temperature range. The eggs and larvae of species of similar genera in the Atlantic and Pacific Oceans have an identical structure and the same nature of pigmentation.

Atlantic flounder fauna, in contrast to cods, undoubtedly originated from the richer Pacific Ocean fauna.

The relatively small seasonal fluctuations in the conditions of Atlantic waters have determined the retention of flounder fauna that has penetrated from the Pacific Ocean. The great diversity of the more or less land-locked ocean basins with their complex hydrological conditions and different histories, and particularly the appearance of the Sea of Japan in the Pleistocene, have led to the formation, in Far Eastern waters, of a whole series of new species, including those possessing bottom eggs, which are not characteristic of the majority of flounder.

The most important factor that has determined the 462 new formation of species is adaptation to reproduction and development in different environments. The flounder species that were formed in the Pliocene and at this time yielded emigrants to the Atlantic Ocean are phylogenetically relatively ancient. The species that are concentrated (and were formed) in a comparatively young body of water -- the Sea of Japan -- are phylogenetically younger. Among these are H. dubius, L. punctatissima punctatissima, L. pinnifasciata, and species with bottom eggs -- Ps. yokohamae, L. obscura, and L. bilineata.

The taxonomy of flounders, as of all fish in general, is based on the comparative morphology of adult fish; the structural features of their eggs, prolarvae and larvae are, as a rule, not used, whereas their use can in a number of cases substantially facilitate the building of a natural taxonomic system. The results of our investigations are helping us to clarify questions of phylogeny, the species of the genera Limanda, Pseudopleuronectes, and Liopsetta, as well as of the genera Pleuronectes and Kareius.

The history of the development of the primitive genus Atheresthes is remarkable in that the larvae of this genus are perch-shaped, with a low body and spines on the gill cover and above the eye, which confirms the descent of flounders from ribbon fishes of the Perciformes type.

Three species of the genus Hippoglossoides are clearly discernible from eggs and larvae in Far Eastern waters, which excludes their being considered as subspecies. Of these, the closest ecologically to the Atlantic flathead sole is H. elassodon, whose ancestors were evidently the parents of all currently existing species of flathead flounder.

Substantial differences in the structure of the eggs and larvae of Ps. yokohamae, Ps. herzensteini, L. obscura and other species of Liopsetta (pinnifasciata and glacialis) raise doubt as to the correctness with which the taxonomic position of these species has been interpreted, which indicates the need to revise their taxonomy.

In the character of the pigmentation of its prolarvae and larvae, the genus Limanda clearly separates into two groups, of which one incorporates L. limanda and L. aspera, and the other, L. punctatissima and L. ferruginea, which confirms the expediency of incorporating the latter two species into the subgenus Myzopsetta, which is evidently on the way to being separated into an independent genus.

The divergence of the ancestors of L. aspera and L. punctatissima evidently occurred prior to the Pliocene, after which the ancestors of L. aspera in the eastern Atlantic yielded L. limanda, and the ancestors of L. punctatissima in the western Atlantic yielded L. ferruginea.

The features of the eggs and larvae of species of the genera Pleuronectes and Kareius confirm the correctness of separating them into individual genera.

It is a known fact that the conditions of reproduction can serve as an indirect indicator of origin.

Hence flounder should be considered as fish of ocean origin, which were formed under the most diverse environments. Species that reproduce in summer are undoubtedly of warm-water origin, while those that reproduce in the autumn-winter period are of cold-water origin, those with the greatest preference for cold being species of the genus Liopsetta (except L. obscura), which reproduce at the coldest time of the year, at below-zero water temperatures and under the ice, indicating their origin under arctic conditions. The ancestral species was evidently that which was most widespread in the Arctic -- L. glacialis, which settled to the south and yielded L. pinnifasciata off the coast of Asia and L. putnami off the eastern coast of North America.

A direct qualitative and quantitative association 463 has been revealed between eggs floating in plankton, the size of a spawning stock and the correlation of individual species in the latter; at the same time, accumulations of eggs coincide with mass spawning, while single eggs indicate the remoteness of mass spawning areas. This is an indisputable premise for determining the volume of a spawning stock by the method of a qualitative and quantitative record of eggs.

Of essential importance are the distribution and size of the spawning shoals of various species. The spawning shoals of flounder are represented by stocks which are isolated

and relatively small in area, ^{and} whose size is determined by temperature and other factors, as well as by the configuration and dimensions of the mainland shallows. The effectiveness of flounder reproduction is determined by the size of the spawning stock, the state of the weather and of the surface layers of water, and the presence of food and predators that consume both eggs and larvae. The most favourable years for the development of eggs and larvae are those with relatively stable hydrological conditions, and calm, storm-free weather throughout the spring and summer, ensuring the normal development of all laid and fertilized eggs. Heavy swells and sharp changes in temperature cause eggs to die in the cleavage stages and in the period prior to hatching.

The largest spawning accumulations of the main commercial flounders are situated in relatively shallow sectors of the mainland shoal (at depths of up to 100 and 150 m) and of gulfs and bays running inland. Such regions include Peter the Great and Avacha Bays and Aniva, Terpenie, Kronotskii, Korfo-Karaginskii, Olyutorskii, and Anadyr Gulfs, and the broad shallows off eastern and western Kamchatka. The most numerous species of the above regions (excluding Anadyr Gulf) is the yellowfin sole. Mass spawning accumulations of this fish have been traced in June in Peter the Great Bay (up to 500 eggs per square metre); in July and August, off the western coast of Kamchatka in the Yavino-Ozernoi region, and off the eastern coast, in Avacha Bay and Kronotskii and Olyutorskii Gulfs (up to 800 eggs per square metre) and in the Korfo-Karaginskii region (up to 1,700 eggs per square metre). There should be very large accumulations on the shoals in northern Tatar Strait and in the Chekhov-Il'insk region.

Next in numbers of eggs at spawning grounds are the Alaska plaice and the flathead flounder. The largest spawning accumulations of these fish have been noted off the western coast of Kamchatka. These concentrations have yielded up to 370 eggs per square metre in April. Smaller spawning accumulations have been observed off the eastern coast of Kamchatka, mainly in Avacha Bay and Kronotskii Gulf (yielding up to 100 eggs per square metre at the beginning of spawning in April). Also worthy of note are the spawning accumulations of Alaska plaice in southwestern Anadyr Gulf, which yield up to 217 eggs per square metre of ocean surface in June.

Mass spawning accumulations have been revealed of Sea of Japan flathead flounder in the open area of Peter the Great Bay (yielding up to 185 eggs per square metre in May), and of longsnout, yellow-striped and sohachi flounder (yielding in all up to 325 eggs per square metre), in the offshore shallow zone.

Shoals of spawning halibut are evidently represented by small schools situated in the drop-off region over a large area from Anadyr Gulf in the north to the coast of Japan in the south. Halibut form their densest accumulations in the Bering Sea off the Koryak Coast.

The spawning accumulations of flounder in the above regions are evidently of great commercial importance and can ensure large catches in each region. Taking into consideration, however, the limited sizes and local nature of individual spawning stocks, and the quick reaction of flounders to the influence of commercial fishing, such fishing should be conducted in various regions in conformity with the sizes 464 of spawning grounds and the extent of the spawning stocks

themselves. In order to avoid overfishing and to maintain the numbers of generations of a given year, strict control should be exercised over fishing involving the main commercial flounders during the period of mass spawning.

An assessment of the size of spawning stocks of flounder, the correlation of individual species in the stock, and a record of fluctuations in reserves and of the effect of commercial fishing on them can and must be carried out by means of regular quantitative removals of floating eggs at the 0- to 25-metre level in conformity with the scheme that we have developed for individual regions, while the species composition of the eggs should be determined from the special keys that we have prepared.

Systematic work embracing all seasons and all of the regions inhabited by these fish makes it possible to characterize individual spawning grounds, the size of a spawning stock and the population dynamics of the stock from catches of eggs and larvae from year to year.

THE TAXONOMIC FEATURES OF AND KEYS TO THE EGGS,
PROLARVAE AND LARVAE OF FAR EASTERN FLOUNDER

These keys are intended for identifying eggs, prolarvae and larvae collected on voyages and fixed in a 2% solution of formalin. The identification of live eggs and larvae that have just been collected is almost impossible under expeditionary conditions in Far Eastern waters. Material for preparing the keys has included eggs, prolarvae and larvae which we and TINRO workers collected in Far Eastern waters from 1948 to 1953. Unfortunately, the collections of ichthyoplankton were made irregularly; therefore the keys that we offer will in all probability be supplemented and detailed.

The fundamentals of the taxonomy of eggs include their shape, the presence or absence of a fat drop, the diameter of the eggs, the dimensions of the perivitelline space, the character of pigmentation and the structure of the anus of the embryo. In describing pigment, melanin (black) pigment is taken into consideration; it is the most important for identifying fixed material, since other types of pigment fade in fixation. The eggs are fixed and preserved in a 2% formalin solution in seawater. In this kind of fixation, the diameter of the eggs changes less than where other preserving fluids are used for fixation. All measurements of eggs are made with the aid of a micrometer eyepiece.

The main taxonomic features of flounder prolarvae and larvae are the shape of the body, the structure of the excretory intestine, the ratio of the length of the trunk to that of the tail, the number of myotomes, and the dimensions of the pectoral fin. Of highly essential importance is the character of the distribution of pigmentary cells on the body, especially on the tail.

Let us examine each of these features separately.

Shape of the body. Flounder prolarvae and larvae are distinguished from the corresponding stages of other fish by the fact that their bodies are never thickened and are constricted from the sides, always to a lesser extent in prolarvae and a greater extent in larvae. In prolarvae the excretory intestine has the appearance of a narrow conical tube; in larvae, it is more or less dilated and opens on the edge of the anal fin fold. The distance from the end of the snout to the insertion of the anal fin is always less than half the length of the body. In prolarvae and early larvae the intestine has the appearance of a straight tube, and in older larvae it forms loops; the rear intestine usually adjoins the preceding section. The pectoral fins are fan-shaped. The tail is at first difficercal and then heterocercal, while in fully-formed larvae it is homocercal.

The seasons in which eggs are found, as indicated in the keys, are given from data obtained for the most part from 1950 to 1954.

Terminology and Methods of Measurement

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1. The diameter of an egg (measured crosswise under a microscope with the aid of a micrometer eyepiece); the figures obtained are converted to millimetres.
2. The diameter of the yolk (measured in the same way as the diameter of the egg).
3. The diameter of the fat drop (measured in the same way as the diameter of the egg).

4. The perivitelline space -- the aperture between the yolk and the egg membrane which is visible in an optical section -- is calculated using the following formula:

$$P = \frac{D-d}{2 \cdot D} \cdot 100,$$

where P is the perivitelline space; D is the diameter of the egg; d is the diameter of the yolk + the blastodisc; in cases where the yolk has an elongated form, it is taken as the arithmetical mean of the greatest length and width.

5. The membrane of the egg. In some species the membrane has a specific structure (the structure is viewed with a surface adjustment of a microscope or a binocular lens).

The length of larvae is measured from the tip of the snout (where the mouth is closed) to the end of the urostyle. The total length of larvae is from the tip of the snout to the end of the fin fold that surrounds the tail. Measurement of the remaining parts of the body is made in accordance with the attached diagram (see fig. 1).

In describing pigment, in the same way as in the case of eggs, only the black pigmentary cells -- the melanophores -- are taken into consideration. Several types of melanophore accumulations are distinguished: rows, spots, stripes and bands. Depending upon their arrangement on the tail, several characteristic rows may be distinguished -- the upper, the middle lateral, and the lower, between which are situated the upper lateral and the lower lateral.

Key to the Pelagic Eggs of Flounder of the Far Eastern

Seas of the USSR

(The numbers of the illustrations are taken from Part II of this monograph)

1(2) The egg yolk contains a fat drop. The diameter of the egg varies from 0.93 to 1.03 mm. The fat drop is smaller than 0.22 mm (0.18 to 0.21 mm). The bastard halibut Paralichthys olivaceus (fig. 2)

2(1) The egg yolk contains no fat drop -- 3

3(6) The eggs have a large perivitelline space, consisting of more than 20% of the diameter of the egg. The diameter of the eggs varies from 2.02 to 3.67 mm -- 4

4(5) Yolk sizes from 0.82 to 1.1 mm. The diameter of the eggs varies from 2.02 to 2.94 mm. Peter the Great Bay, Tatar Strait, Hippoglossoides dubius (fig. 9). Southeastern coast of Sakhalin, Sea of Okhotsk, Bering Sea Hippoglossoides robustus (fig. 14)

5(4) Yolk sizes from 1.1 to 1.5 mm. Diameter of eggs varies from 2.45 to 3.67 mm, Hippoglossoides elassodon (fig. 12)

6(4) Eggs have a small perivitelline space, consisting of less than 20% of the diameter of the egg -- 7

7(10) Large eggs from 3.0 to 4.5 mm -- 9

8(9) Diameter of eggs varies from 4.0 to 4.5 mm. Greenland halibut -- Reinhardtius hippoglossoides matsuurae

9(8) Diameter of eggs varies from 2.9 to 3.8 mm. The true halibut -- Hippoglossus hippoglossus stenolepis (fig. 6)

10(15) Medium eggs, diameter from 1.2 to 2.6 mm /467

-- 11

11(14) Membrane thick and wavy-reticulate -- 12

12(13) Diameter of eggs varies from 1.67 to 2.21 mm. Membrane of a rose-tinted-lilac colour. In an embryo in the third and fourth stages of development the pigment forms no bands on the tail. There are large, starry cells on the surface of the yolk. The Alaska plaice, Platessa quadrituberculata (fig. 43)

13(12) The diameter of the eggs varies from 1.2 to 1.61 mm. The membrane is colourless. In an embryo at the end of the third and in the fourth stage the pigment forms bands on the tail. There are starry pigmentary cells on the entire surface of the yolk. The long flounder -- Glyptocephalus stelleri (fig. 56)

14(11) The membrane is thin and colourless and is occasionally slightly wavy. The diameter of the eggs varies from 1.2 to 2.6 mm. The yolk is of a loose consistency and slightly coloured. The entire body is thickly pigmented, and there are no isolated accumulations of pigment on the tail. The anus is of the flounder type, January to March [sic]. Bering Sea and Sea of Okhotsk. The arctic flounder -- Liopsetta glacialis. The Seas of Okhotsk and Japan. The banded flounder -- Liopsetta pinnifasciata (fig. 48)

15(10) Small eggs, diameter less than 1.2 mm -- 16

16(19) Diameter of eggs varies from 1.00 to 1.2 mm

-- 17

17(18) Colourless membrane. Diameter of eggs varies from 1.03 to 1.15 mm. From the second stage of development of the embryo onwards, the pigmentary cells are scattered throughout the entire yolk. October and November. The two-coloured flounder -- Kareius bicoloratus (fig. 62)

18(17) The membrane is of a rose-tinted-lilac colour. The diameter of the eggs varies from 1.05 to 1.2 mm (1.28). There are pigmentary cells on the yolk only in the region of the pectoral fins. In the south in April and May, and in the north, in May and June. The starry flounder -- Pleuronectes stellatus (fig. 59)

19(16) Diameter of the eggs does not exceed 1.03 mm
-- 20

20(25) Diameter of the eggs varies from 0.87 to 1.03 mm -- 21

21(24) The head of the embryo is not pigmented between the auditory capsules and the eyes at the end of the second stage. The contour of the rear half of the body and subsequently of the lower edge of the tail in the second and at the beginning of the third stage is slightly pigmented (no more than three cells). At the beginning of the third stage the head of the embryo in the region of the eyes is either not pigmented at all, or only 1 to 3 cells enter upon it -- 22

22(23) The back and the upper edge of the tail of the embryo are pigmented. There is no distinct row of cells at the end of the tail of an embryo in the fourth stage of development. There is no pigment at the end of the intestine either before or above the anal pipe; not infrequently, one

melanophore is visible behind the intestine. The sohachi flounder -- Cleisthenes herzensteini (fig. 18)

23(22) Neither the back nor the lower edge of the tail of the embryo is pigmented. The end of the tail of an embryo in the fourth stage is bordered by a distinct row of cells. The spiny flounder -- Acanthopsetta nadeshnyi (fig. 16)

24(21) The head of an embryo in the second stage is pigmented between the auditory capsules and the eyes. The contour of the rear half of the body and, consequently, of the tail, is intensively pigmented (more than three or four cells). There are 1 to 4, and more frequently, 2, melanophores at the end of the intestine in front of or above the anal pipe. The yellow-striped flounder -- Pseudopleuronectes herzensteini (fig. 38)

25(20) The diameter of eggs, as a rule, is less than 0.87 mm -- 26

26(27) The lower edge of the tail and the contour of the rear half of the body are pigmented. There are 1 to 4, and more frequently 2, melanophores at the end of the intestine either above or in front of the anal pipe. The yellow-striped flounder -- Pseudopleuronectes herzensteini (fig. 37)

27(26) The lower edge of the tail and the contour of the rear half of the body are either not pigmented at all or are only very slightly pigmented (there are 1 to 2 melanophores) -- 28

28(31) A middle row of cells is distinctly isolated /468 among the scattered pigment on the trunk of an embryo in the second stage -- 29

29(30) There is always pigment (1 to 2 melanophores) on the lower edge of the trunk (more frequently its rear half) in the second and third stages; in the third and fourth stages there is also pigment on the rear end of the intestine above the anal pipe or in front of it. The lower edge of the tail is either entirely devoid of pigment, or has one, or rarely two, cells at the end of the third and fourth stages. The diameter of the eggs varies from 0.66 to 0.87 and averages 0.77 mm. The longsnout flounder -- Limanda punctatissima punctatissima (fig. 32)

30(29) There are no pigmentary cells on the lower edge of the trunk in the second and third stages, nor are there any on the rear end of the intestine above the anal pipe in the third and fourth stages. The snout sole -- Limanda punctatissima proboscidea (fig. 34)

31(28) There is no distinctly isolated middle row on the trunk of an embryo in the second stage. No pigmentary cells are visible on the lower edge of the trunk. Pigment is lacking at the end of the intestine both above and in front of the anal pipe. The lower edge of the tail is either entirely deprived of pigment or has one or two, and rarely three, melanophores. The diameter of the eggs varies from 0.72 to 0.98 mm and amounts on the average to 0.79 to 0.82 mm. The yellowfin sole -- Limanda aspera (fig. 28)

Key to Prolarvae and Larvae

A Prolarva without a Mouth and with Unpigmented Eyes

1(2) The yolk sac contains a fat drop, and the fin fold is intensively pigmented. The bastard halibut -- Paralichthys olivaceus (fig. 2). June to August. Peter the Great Bay and further south.

2(1) The yolk sac contains no fat drop -- 3

3(4) The melanophores on the tail are small, almost punctate and are sparsely scattered; there are no accumulations in the form of spots or bands, nor are they outlined. The yellowfin sole -- Limanda aspera (fig. 31)

4(5) The melanophores are either branched and more or less thickly scattered, or they form accumulations -- 5

5(14) The melanophores are scattered, and on the tails of older prolarvae there is a tendency towards the formation of accumulations in the form of spots or bands -- 6

6(9) The prolarvae are small, and their length does not exceed 3.0 mm. The melanophores on the tail are either scattered unevenly or are concentrated mainly along the upper and lower edges of the tail

7(8) The fin fold in the region of the rear part of the tail is pigmented. The melanophores on the yolk are situated under the pectoral fins. In older prolarvae a band is outlined near the middle of the tail. The starry flounder -- Pleuronectes stellatus (fig. 60)

8(7) The fin fold is not usually pigmented, but if it is, the melanophores are situated along the edges in the form of a border. In older prolarvae two bands are outlined on the tail. The sohachi flounder -- Cleisthenes herzensteini (fig. 19)

9(6) Prolarvae from 3.5 mm and larger. The melanophores of the younger prolarvae are usually arranged more or less evenly -- 10

10(11) The melanophores are large-branched, and there are four bands outlined in older prolarvae. The flathead flounder -- Hippoglossoides dubius (fig. 11)

11(10) The melanophores are small-branched, and in older prolarvae there is one band outlined that is situated on the middle of the tail.

12(13) Prolarva caught in the northern Bering Sea or Sea of Okhotsk. The arctic flounder -- Liopsetta glacialis (fig. 51).

13(12) Prolarva caught off the coast of Sakhalin or in the Sea of Japan. The banded flounder -- Liopsetta pinnifasciata (fig. 49)

14(5) Melanophores form more or less noticeable accumulations on the tails of younger larvae -- 15 /469

15(22) Melanophores on the tail form a single band-accumulation on or near the middle of the tail -- 16

16(19) Length of prolarvae is less than 4 mm -- 17

17(18) The fin fold is pigmented in the region of the rear portion of the tail. In addition to a band, there are thickly scattered melanophores on almost the entire surface of the tail. The starry flounder -- Pleuronectes stellatus (fig. 60)

18(17) The fin fold is unpigmented. Melanophores on the lower edge of the tail are either entirely absent or are very sparse. The accumulations do not form a solid band. There is a dark spot above the anus. The longsnout flounder -- Limanda punctatissima punctatissima (fig. 33)

19(16) The length of a prolarva is more than 4 mm. The fin fold is not pigmented in the region of the central portion of the tail -- 20

20(21) Prolarva caught in the northern Sea of Okhotsk or Bering Sea. The arctic flounder -- Liopsetta glacialis (fig. 51)

21(20) Prolarva caught off the coast of Sakhalin or in the Sea of Japan. The banded flounder -- Liopsetta pinnifasciata (fig. 49)

22(15) Melanophores on the segmented portion of the tail form two and more band-accumulations -- 23

23(24) Melanophores on the tail form two band-accumulations -- 24

24(27) There are no melanophores on the fin folds; if there are, they are sparsely scattered -- 25

25(26) Accumulations of melanophores are indistinct and faintly outlined; a marked rear accumulation is situated far beyond the middle of the tail. The Japanese flounder -- Pseudopleuronectes yokohamae (fig. 41)

26(25) The band-accumulations are clear; the last accumulation is located near the middle of the tail. The black flounder -- Liopsetta obscura (fig. 53)

27(24) The fin folds are pigmented, and the melanophores on them form accumulations -- 28

28(29) Only the anal fin fold is pigmented. The northern rock sole -- Lepidopsetta bilineata bilineata (fig. 23)

29(28) Both fin folds, the dorsal and the anal, are pigmented. The southern rock sole -- Levidopsetta bilineata-mochigarei (fig. 26)

30(24) The melanophores on the tail form more band-accumulations -- 31

31(34) Melanophores on the tail form three bands -- 32

32(33) In addition to accumulations on the tail, there are accumulations on the trunk above the anus and above the pectoral fins. The prolarvae are large; their length exceeds 3.5 mm. The long flounder -- Glyptocephalus stelleri (fig. 56)

33(32) There are no accumulations on the trunk. The prolarvae are small; their length is less 3.5 mm. The yellow-striped flounder -- Pseudopleuronectes herzensteini (fig. 38)

34(31) Melanophores on the tail form four bands, of which the last surrounds the end of the urostyle. The flathead sole -- Hippoglossoides (figs. 11 and 13)

Prolarva with a Mouth Opening and Pigmented Eyes,
and an Unformed Larva

1(2) The body is thickly pigmented and almost dark. Two spots stand out lightly on each of the upper and lower edges of the tail. The verasper -- Verasper variegatus (fig. 20, B)

2(1) Body is not thickly pigmented -- 3

3(17) The melanophores are scattered or situated in rows; there are no accumulations in the form of spots or bands -- 4

4(7) The prolarvae [are] large, from 8 mm and up -- 5 / 47

5(6) The melanophores of the distal edges of the anal and dorsal fin folds are concentrated in the rear half of prolarvae and throughout the entire length of larvae. The tips of the pectoral fins of larvae go beyond the middle of the abdomen. The true halibut -- Hippoglossus hippoglossus stenolepis (fig. 7)

6(5) The melanophores of the distal edges of the anal and dorsal fin folds are concentrated at the ends of prolarvae and in the rear half of larvae. The tips of the pectoral fins of the larvae do not go beyond the middle of the abdomen. The Greenland halibut -- Reinhardtius hippoglossoides matsuurae (fig. 4)

7(4) Prolarvae smaller than 8 mm -- 8

8(9) The end of the urostyle is bordered by a row of melanophores. The pigmentary cells on the lower edge of the tail do not form a regular double row. There is a lower lateral row. The spiny flounder -- Acanthopsetta nadeshnyi (fig. 17)

9(8) The end of the urostyle is not bordered by a row of melanophores -- 10

10(13) A row arrangement of pigmentary cells predominates on the tails of prolarvae and larvae -- 11

11(12) The prolarvae are small, smaller than 4 mm. The middle lateral row of the tail is short and does not reach the level of the anus. There are no melanophores on the upper edge of the end of the tail. There are pigmentary cells on the pectoral fins. The yellowfin sole -- Limanda aspera (fig. 30)

12(11) The prolarvae are large, larger than 4 mm. The middle lateral row is long, and reaches the level of the anus. On the tail, in addition to the lower row, there is a short rear dorsal row. There are no melanophores on the pectoral fins. The Alaska plaice -- Platessa quadrituberculata (fig. 43)

13(10) A scattered arrangement of pigmentary cells predominates on the tail -- 14

14(15) Scattered melanophores are concentrated mainly in the central third and the lower half of the tail. There is no upper row on the tail. The starry flounder -- Pleuronectes stellatus (fig. 60)

15(14) Melanophores are scattered over the entire surface of the tail. There is an upper row on the tail. The two-coloured flounder -- Kareius bicoloratus (fig. 62)

16(3) On the tail, in addition to melanophores both scattered and arranged in rows, there are accumulations in the form of spots and bands -- 17

17(26) The melanophores on the tail form a single accumulation which is situated either near the tail or on the middle of it -- 18

18(23) Prolarvae are small, smaller than 4 mm -- 19

19(22) The anal fin fold is not pigmented, and there are either no scattered melanophores on the tail, or they are very sparse -- 20

20(21) In addition to an accumulation of melanophores around the middle of the tail there is a well-marked compact spot above the excretory intestine or immediately behind it.

The longsnout flounder -- Limanda punctatissima punctatissima
(fig. 33)

21(20) There is no compact spot above the excretory intestine, and in its place there are several individual melanophores. The accumulation around the middle of the tail has the appearance of a short upper stripe. The snout sole -- Limanda punctatissima proboscidea (fig. 35)

22(19) The anal fin fold of the larvae is pigmented. Scattered melanophores are possible. There is no compact spot above the excretory intestine, and there ^{are} a few melanophores scattered on the latter. The starry flounder -- pleuronectes stellatus (fig. 59)

23(18) A prolarva larger than 4 mm -- 24

24(25) A prolarva or larva caught in the northern Sea of Okhotsk or Bering Sea. The arctic flounder -- Liopsetta glacialis (fig. 51)

25(26) Prolarva or larva caught off the coast of Sakhalin and in the Sea of Japan. The banded flounder -- Liopsetta pinnifasciata (fig. 49)

26(17) The melanophores on the segmented portion of 471 the tail form two and more accumulations -- 27

27(42) The end of the urostyle is not surrounded by a row of melanophores -- 28

28(39) The melanophores on the tail form two accumulations -- 29

29(36) There are usually no melanophores on the fin folds, and if there are, they are sparsely scattered -- 30

30(31) The prolarvae are large and about 7 to 9 mm long. The arrow-toothed halibut -- Atheresthes evermanni (fig. 3)

31(30) The prolarvae are small; their length is less than 7 to 9 mm -- 32

32(33) A rear accumulation (in the form of a compact band) is located near the middle of the tail. The black flounder -- Liopsetta obscura (fig. 54)

33(32) The rear accumulation does not have the appearance of a compact band and is located far beyond the middle of the tail -- 34 (fig. 41)

34(35) The middle ventral row has additional melanophores (fig. 41 -- 4). The Japanese flounder -- Pseudopleuronectes yokohamae (fig. 41)

35(34) Has no middle ventral row of additional melanophores (fig. 20a -- I). The sohachi flounder -- Cleisthenes herzensteini (fig. 19, 20a -- 1.2) 36 (29). Melanophores form accumulations on the fin folds. In some specimens there is a rear, third embryonic band -- 37

37(38) Melanophores form accumulations mainly on the anal fin fold. The northern rock sole -- Lepidopsetta bilineata bilineata (fig. 23)

38(37) Melanophores form accumulations on the dorsal and anal fin folds. The southern rock sole -- Lepidopsetta bilineata mochigarei (fig. 26)

39(28) The melanophores on the tail form three band-accumulations -- 40

40(41) Small prolarvae from 3.5 mm in length; there are no additional pigmentary cells on the lower edge of the tail between the main bands. The yellow-striped flounder -- Pseudopleuronectes herzensteini (fig. 38)

41(40) Large prolarvae from 5.0 mm in length. There are additional pigmentary spots on the lower edge of the tail between the main bands. The long flounder -- Glyptocephalus stelleri (fig. 56)

42(27) The end of the urostyle is surrounded by a row of melanophores -- 43

43(44) There are scattered melanophores on the surface of the fin folds surrounding the end of the tail. Hippoglossoides elassodon (fig. 13)

44(43) There are no scattered melanophores on the surface of the fin folds surrounding the end of the tail. Hippoglossoides dubius (fig. 11)

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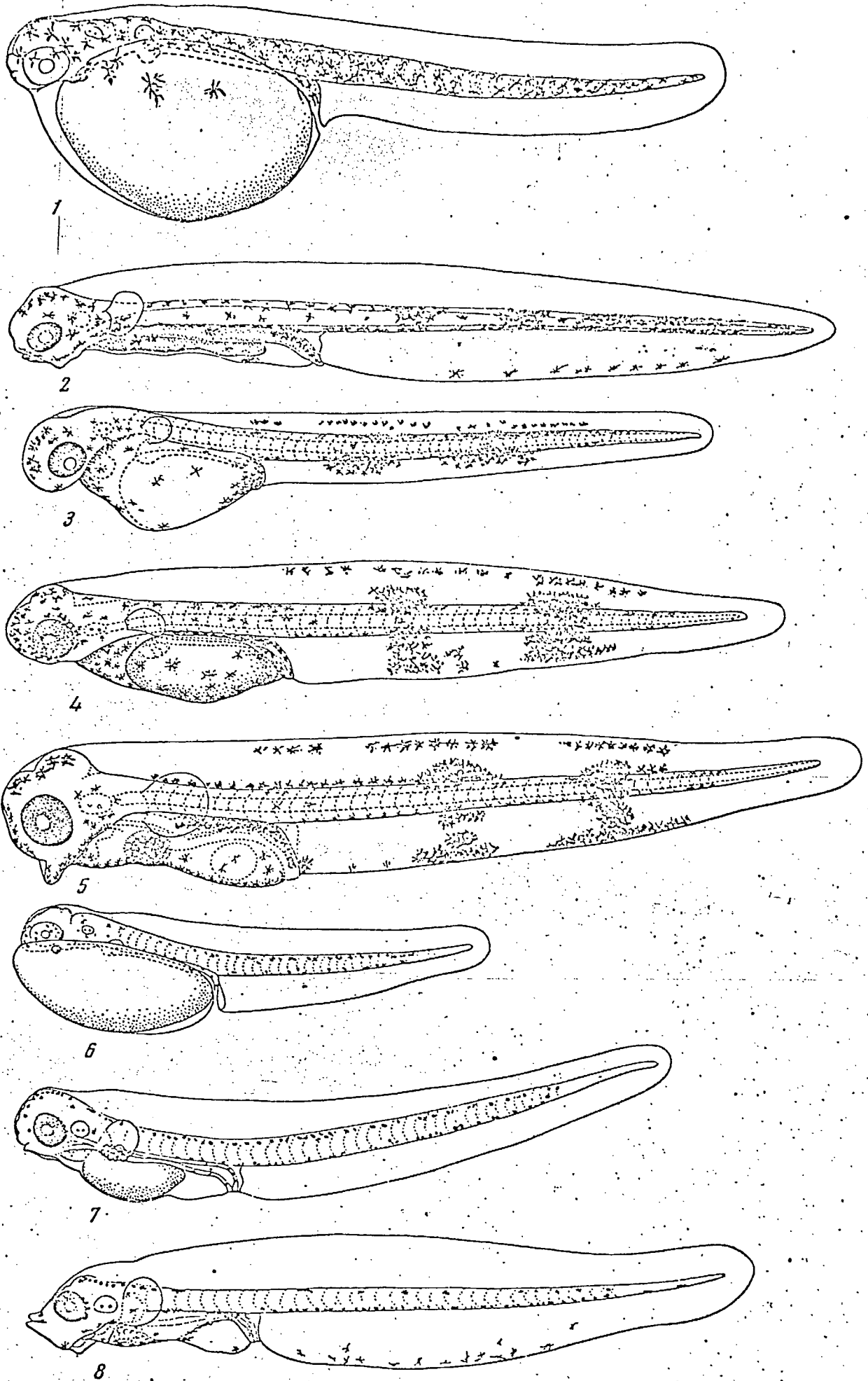
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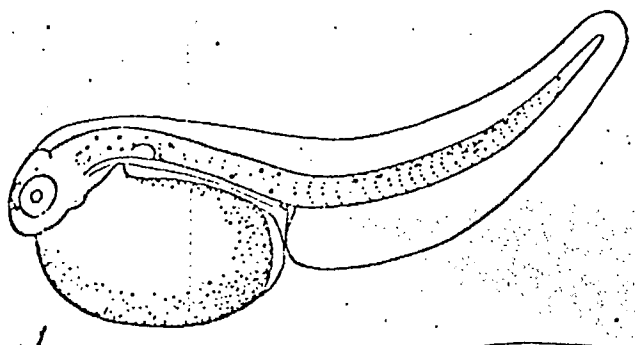
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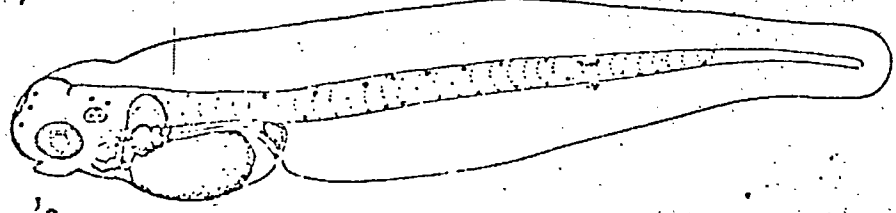


1-2 - *H. dubius*; 3-5 - *L. bilineata bilineata*; 6-8 - *L. aspera*

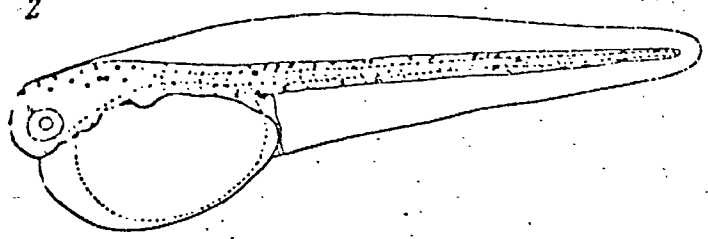
Figure 76 - Flounder prolarvae and larvae



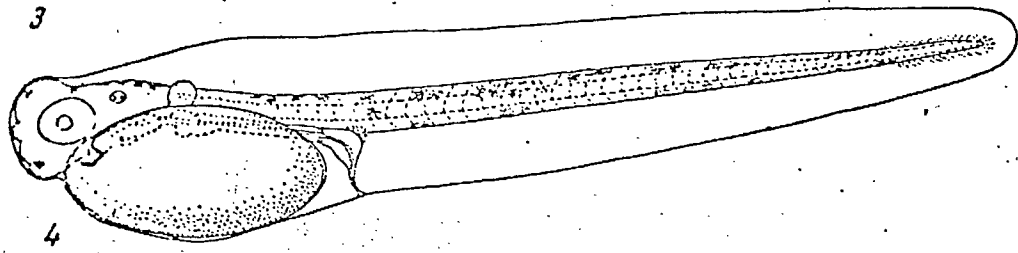
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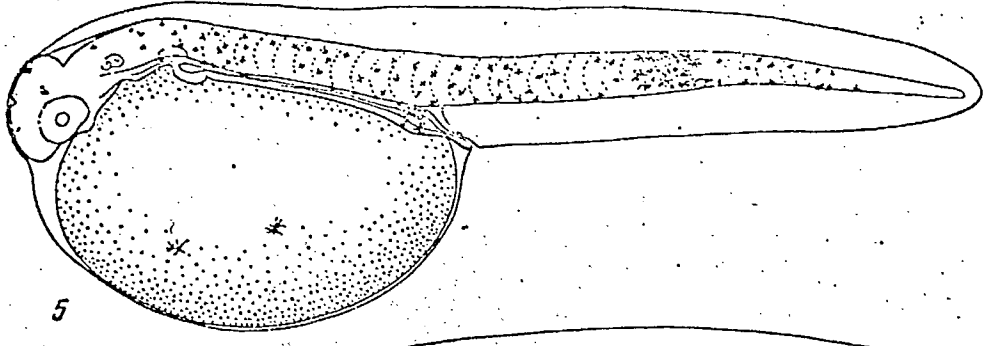
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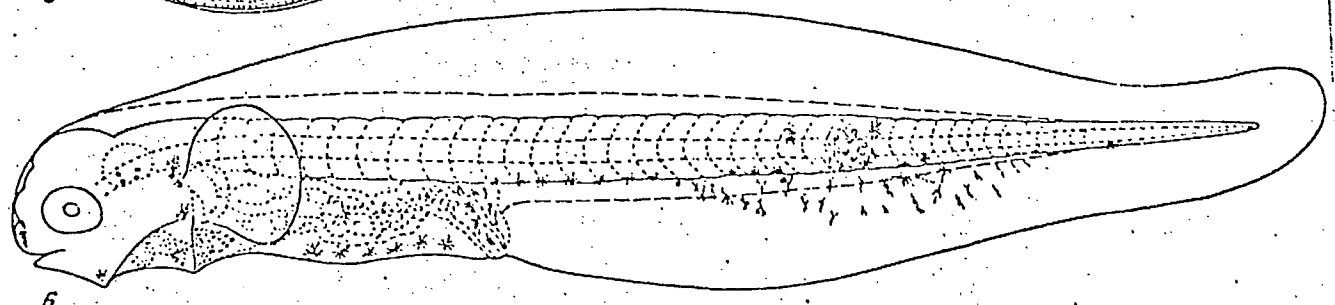
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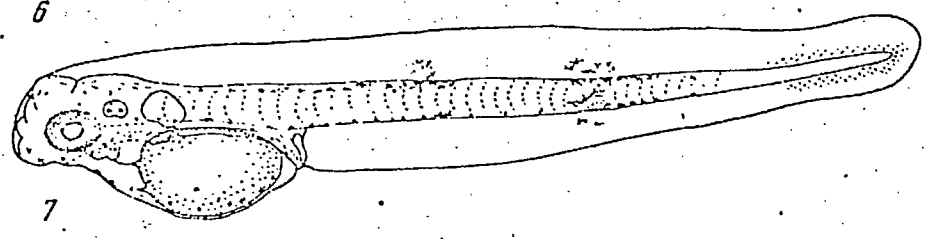
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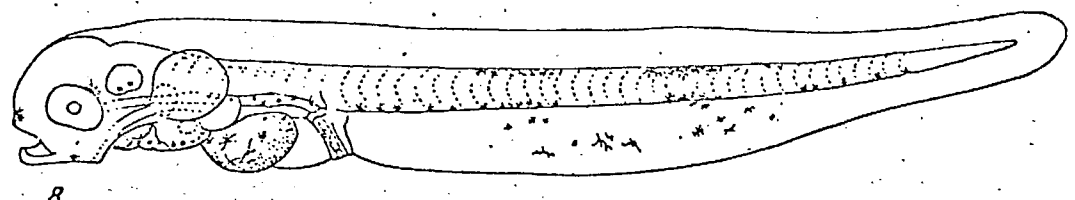
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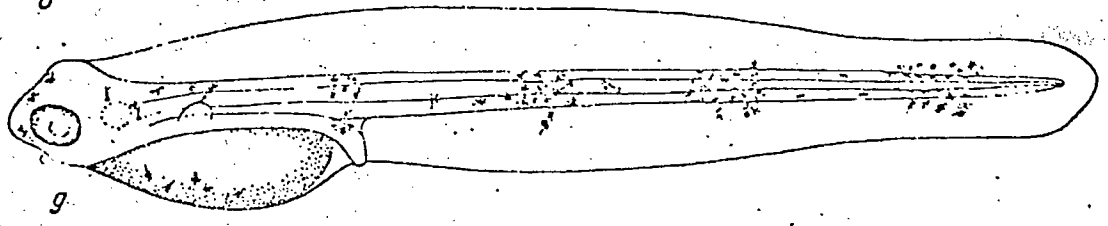
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7



8



9

1-2 - *L. punctatissima punctatissima*; 3-4 - *Ps. herzensteini*; 5-6 - *L. pinnifasciata*; 7-8 - *L. obscura*; 9 - *Gl. stelleri*

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