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"Eco-morphological principles and patterns of development among minnows, loaches and catfishes". Part II. Ecological groups of fishes and patterns of their distribution

by S. G. Kryzhanovskii

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Akademiya Nauk SSSR. Trudy Instituta Morfologii Zhivotnykh im. Akad. A. N. Severtsova

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Part II

(237*)

Ecological groups of fishes and patterns of their distribution

by S. G. Kryzhanovskii UNEDITED TRANSLATION

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I Ecological groups of fishes

Information seulement

Adaptations of fish to the conditions of propagation and development, reflect not only the essential ecological stages of the embryonic period, but also the essential stages of all other periods in their life cycles. They predetermine the biology of adult fish, the nature of migrations, the potential for transplantations and the boundaries of their areas of distribution.

*Numbers in the right-hand margin indicate the corresponding pages in the original.

Two factors play leading roles during the embryonic period of life: the predators and the state of oxygen availability. All other factors are reduced to these two and together they create an extraordinary variety of adaptations associated with development. However, the various forms of propagation and the sites of egg release predetermine the respiratory conditions and the potential for defense against predators, and hence to a considerable degree, they predetermine the nature of the adaptations associated with development. Therefore, the astounding multitude of adaptations associated with development reveal the ecological patterns which reflect the essential relations of fish in nature.

The understanding of these patterns helps to subdivide fish into ecological groups. The description of these groups will be given later. The names of most of them include indications of the site of egg deposition (lithophilous, phytophilous and other groups) because the site of egg release, as was mentioned, predetermines the nature of the adaptations associated with development and the specificity of the ecological groups.

1. Lithophilous group--Cyprinidae.

The fishes of this group are adapted to develop on sandy-rocky shoals or on lake bottoms which are usually oligotrophic, and near non-overgrown, sandy-rocky shorelines where the water is very clear. The current per se is not

essential for them: the same species can reproduce in swiftly flowing rivers or in still lake water as long as they find all necessary bottom conditions in either of them. They can even deposit the eggs on plants. However, in overgrown, slack waters with retarded flow where silt deposits on the bottom, and in overgrown ponds and lakes, they are not able to develop; for this reason, in these bodies of water, lithophils are completely absent unless there are inflowing rivers or brooks into which they can enter for spawning.

The lithophilous group of the Cyprinidae ranks first in number of species in our fresh water ichthyofauna. It (238) consists of about 89 species (subspecies included), i.e. more than all the other groups taken together, and almost four times more than the next most important group in European rivers--the phytophilous group which represents about 24 species (Table 64). Fifty-two of the species, i.e. the major part, inhabit mountain rivers and lakes and 37 are inhabitants of flatland bodies of water.

The group consists of Barbina and Leuciscina, i.e. on the whole it is heterogeneous.

The lithophilous Barbina and Leuciscina only partially inhabit the same bodies of water. Mostly they are adapted to different conditions of life and development; therefore, although having numerous common adaptations, at the same time they differ to such an extent that they must be studied separately--as independant ecological subgroups.

Among Barbina, apparently all the genera belong to the lithophilous group, in any case the genera Barbus, Varicorhinus, Diptychus and Schizothorax, encompassing altogether some 28 species. Only four of them inhabit the flatland rivers of Europe. All others inhabit mainly rapidly flowing mountain rivers and the lakes of the Caucasus and Middle Asia.

They inhabit not only such high mountain lakes as Sevan and Issyk Kul but also the higher ones and even penetrate the upper reaches of rivers almost up to the glaciers, i.e. higher than any other related fish not yielding in this respect to the trout. In Siberian and Far-Eastern rivers they are absent.

The lithophilous Barbina reproduce at a temperature of 12 to 17 C, i.e. at lower temperatures than fish of any other ecological group, excepting the lithophilous Leuciscina. Some of them (osman, marinka) begin spawning in early spring at a temperature of 12 C and end in summer or fall when the temperature is 17 C. Others (barbel, khramulya) spawn during the first half of summer, preferring temperatures of 16 to 17 C. Another distinguishing peculiarity of lithophilous Barbina is that their spawning is very protracted: from 1.5 to 6 months, i.e. a very long period. Among them there are species which spawn in spring, summer and fall, but none of these species have a short, simultaneous spawning period which is typical for the lithophils of our flatland rivers (this statement does not apply to the Dniepr River barbel

and a few other species of barbels in European flatland rivers, the spawning habits of which are practically unknown). This can be explained by the fact that in the mountain lakes and in many rivers the water is always very clear and therefore the roe in these waters is always in great danger of being destroyed by predators, the main ones being the numerous chars and gudgeons (in the Issyk Kul). This is because in these water bodies there are no spring flood-water periods such as are observed in the flatland rivers and which help to conceal the roe of the fish which spawn there and thus predetermine short spawning periods. Moreover, in these waters, there are no predator fish to which the other fish should align their own spawning periods by advancing or postponing them. A simultaneous spawning would result in overloading the spawning beds with eggs and would unfavorably increase the losses of roe to predators and to the other unfavorable side-effects of such an overload. In contrast, when there is a coincidence of these conditions, a very protracted spawning period in mountain water bodies is very advantageous in that it decreases the number of reproducers present on the spawning grounds at the same time and consequently the amount of roe deposited, thus lowering the level of destruction considerably. This interdependence of the length of the spawning period and the nature of the mountain water bodies is of such a regular nature that even the fish of other ecological groups which have entered these bodies of water follow this rule (except the phytophils) (Table 66).

Table 64

(239)

1) Quantitative distribution among ecological groups of the genera and species of Cyprinidae studied

Таблица 64

1 Количественное распределение изученных родов и видов карповых рыб по экологическим группам

2 Экологические группы и подгруппы		3 Р о д ы	4 Количество видов (или подвидов)		
			5 общее	6 горных водоемов	7 равнин- ных во- доемов
8 Л и т о ф и л ь н ы е	10 подгруппа Barbina	1. <i>Barbus</i> 2. <i>Varicorhinus</i> 3. <i>Diptychus</i> 4. <i>Schizothorax</i>	13 7 3 5	9 7 3 5	4 — — —
		11 Итого видов в подгруппе	28	24	4
	12 подгруппа <i>Leuciscina</i>	5. <i>Leuciscus</i> 6. <i>Aspius</i> 7. <i>Abramis</i> 8. <i>Chalcalburnus</i> 9. <i>Vimba</i> 10. <i>Phoxinus</i> 11. <i>Chondrostoma</i> 12. <i>Alburnoides</i>	13 3 2 6 4 19 7 6	6 2 — 4 2 5 5 4	7 1 2 2 2 14 2 2
		11 Итого видов в подгруппе	60	28	32
		13 Всего видов в группе	88	52	36
	14 Промежу- точные	<i>Leuciscus</i>	1	—	1
	15 Фитофильные	1. <i>Cyprinus</i> 2. <i>Carassius</i> 3. <i>Tinca</i> 4. <i>Scardinius</i> 5. <i>Abramis</i> 6. <i>Blicca</i> 7. <i>Rutilus</i> 8. <i>Alburnus</i> 9. <i>Leucaspilus</i> 10. <i>Phoxinus</i>	2 2 1 1 1 2 9 5(?) 1 1	— — — — — — 1 4(?) — —	2 2 1 1 1 2 8 1 1 1
		13 Всего видов в группе	25(?)	5(?)	20
	16 Псаммофиль- ные	1. <i>Cobio</i> 2. <i>Gnathopogon</i> 3. <i>Hemibarbus</i>	13 2 2	6 — —	7 2 2
		13 Всего видов в группе	17	6	11
17 Пелагофиль- ные	1. <i>Pelecus</i> 2. <i>Ctenopharyngodon</i> 3. <i>Hypophthalmichthys</i> 4. <i>Hemiculter</i> 5. <i>Xenocypris</i>	1 1 1 2 1	— — — — —	1 1 1 2 1	

Table 64 (continued)

Таблица 64 (продолжение)

2 Экологические группы и подгруппы		3 Р о д ы	4 Количество видов (или подвидов)		
			5 общее	6 горных водоемов	7 равнин- ных во- доемов
Не охраняющие 8	17 Пелагофильные	6. <i>Parabramis</i>	1	—	1
		7. <i>Megalobrama</i>	1	—	1
		8. <i>Erythroculter</i>	2	—	2
		9. <i>Culter</i> (?)	1	—	1
		10. <i>Elopichthys</i>	1	—	1
		11. <i>Opsariichthys</i> (?)	1	—	1
		12. <i>Pseudaspius</i>	1	—	1
		13. <i>Paraleucogobio</i>	2	—	2
		14. <i>Sarcochilichthys</i>	7*	—	7*
		15. <i>Armato gobio</i>	1	—	1
	Остракофиль- ные 18	16. <i>Rostrogobio</i>	1	—	1
		17. <i>Gobiobotia</i>	4*	—	4*
		13 Всего видов в группе	29	—	29
	Остракофиль- ные 18	1. <i>Rhodeus</i>	2	—	2
		2. <i>Achilognathus etc.</i>	9*	—	9*
		3. <i>Acanthorhodeus</i>	8*	—	8*
	Остракофиль- ные 18	13 Всего видов в группе	19	—	19
Охра- няющие 19	16 Псаммо- фильные	1. <i>Pseudogobio</i>	—	—	1

20 * Цифры со звездочкой обозначают общее количество видов, остальные — только количество видов в нашей ихтиофауне.

2) ecological groups and subgroups; 3) genera;
4) number of species (or subspecies); 5) total;
6) mountain bodies of water; 7) flatland bodies
of water; 8) do not guard their eggs; 9) litho-
philous; 10) subgroup *Parbina*; 11) total numbers
of species in the subgroup; 12) subgroup *Leuciscina*;
13) total number of species in the group;
14) intermediate; 15) phytophilous; 16) psammophilous;
17) pelagophilous; 18) ostrakophilous; 19) guard
their eggs; 20) numbers with an asterisk denote
the total number of species, the others only
the number of species in our ichthyofauna.

In contrast to the eggs of lithophilous *Leuciscina*, the eggs of *Barbina* are covered with a slightly sticky or non-sticky layer of mucus. Therefore, even if they are stuck to the rocks, they soon peel off and wash under the rocks where they can expect to be protected from enemies. The spawning adult fish also contribute to the drifting of the eggs under the rocks. During the process of spawning they splash the water so energetically that the water is churning, scattering the eggs. The local fishermen of Lake Sevan then say that the fish "churns". Reports that some species (*khramulya*, barbel) bury their eggs in sand so that they will be safe from predators, are without foundation. Eventually, on spawning beds with a sandy bottom and which are frequented by large numbers of spawning pairs, large quantities of eggs can actually be buried under the sand. However this is only a negative side-effect of "churning" on an overloaded spawning ground. All the buried eggs perish from suffocation. (240)

According to observations of N. N. Disler, the egg membrane of many of the *Barbina* at the moment of egg deposition becomes very poisonous (not the yolk sac, as it was assumed previously). This is a primary protection from enemies for the eggs. One and a half hours later the poison is washed out of the membrane and for the most part only those eggs which roll under the rocks in time are protected.

Apparently the mortality in developing Barbina is lower than in fish of other ecological groups; that is why their fecundity is the lowest. Most of them release from 2 to 50 thousand eggs. Although in absolute values this fecundity is only a little lower than the absolute fecundity of their close relatives--the lithophilous Leuciscina which (241) produce from 1 to 193 thousand eggs--in relative terms, this fecundity is considerably lower. Thus, for instance, the Lake Sevan khramulya deposits from 20 to 50 thousand eggs while the chub, which is younger and also smaller in size deposits from 109 to 193 thousand eggs. Moreover, the fecundity of the Barbina is considerably decreased by the fact that they reach sexual maturity at a very late stage--at an age of 7 to 8 years. Fish of all other ecological groups reach sexual maturity at an age of 3 to 4 years and even younger. Finally, most of them spawn once and not intermittently as many other fish do (according to S. K. Troitskii, 1948, Barbus tauricus kubanicus spawns intermittently).

Because they have the lowest fecundity, the eggs of lithophilous Barbina are the largest among all members of the Cyprinidae. Their diameter, without the coating, is from 1.95 to 2.34 mm while in other fish it is from 0.55 to 1.56 mm (only the eggs of the pelagophilous lazy gudgeon reach 1.9 mm).

The lithophilous Barbina develop within the membrane for an equally long period: from 5 to 6 days at a temperature

of 16 to 17 C and longer when the temperature is lower. They all hatch almost identically developed. Their bodies are fully segmented, still fringed by a small, non-paired, fin-fold. The tail is very short and the pectoral fins are still very rudimentary or may be completely absent (Fig. 84A). The blood vascular system is already functioning and embryonic respiratory organs are present as wide but not very long ducts of Cuvier. The lower caudal vein is short and proportional to the length of the tail. There is no pigment in either the eyes or in other parts of the body.

The hatched embryos do not react to light, i.e. they are completely indifferent to the light conditions. The shortened tail is not in proportion with the extremely elongated body which is weighted by the yolk. The under-developed fin-fold and the absence of pectoral fins make any swimming by the hatched embryos impossible. They rest on the bottom and only periodically exhibit sharp, worm-like movements resulting in upward leaps which are followed by resettling to the bottom. The hatched embryo performs up to 16 such vertical leaps in two minutes, then the frequency increases (Table 65).

The leaps facilitate respiration, which, as was mentioned, is performed by the ducts of Cuvier and the caudal vein. They prevent the possibility of lying for a long time in places where the flow is slowed down and where in the very turbid mountain streams abundant sediments,

which in a short time could kill the hatchlings, are deposited. After gill breathing is established and the ability to swim is acquired, the embryos cease leaping.

(242)

Table 65

1) Number of body convulsions (leaps) and opercular movements at various stages of development of the scaleless osman.

Таблица 65

1 Количество вздрагиваний тела (подпрыгиваний) и движений жаберной крышки на разных стадиях развития османа голого

2 Возраст (в сутках)	3 Количество вздрагиваний тела в течение 2 мин.	4 Количество дыхательных движений жаберной крышки в течение минуты	5 Т воды (в °C)
7	1—16	6 Нет	13
8	19—25	»	17
11	14—27	»	13
16	Нет	89	12
19	»	93	12
20	»	108—132	12

2) age in days; 3) number of convulsions in two minutes; 4) number of respiratory movements of the opercula in one minute; 5) water temperature, C; 6) none.

According to the observations of N. N. Disler, swimming embryos do not move upwards but butt the bottom with their heads. These movements are facilitated by the weighted body and particularly by the slightly downwards curved tail. The result is that the embryos, which still do not react to light, in spite of the fact that their eyes are now pigmented, nevertheless finally are able to wedge themselves under stones, thus finding a safe shelter from their enemies. After

the development of the pectoral fins, when the embryos acquire the ability to swim directionally, they become photophobic to a certain degree, but not as intensely as the embryos of lithophilous *Leuciscina*. This helps them to remain in the darkness, under the protection of the rocks. When the larvae reach the pelagic stage, the photophobia disappears.

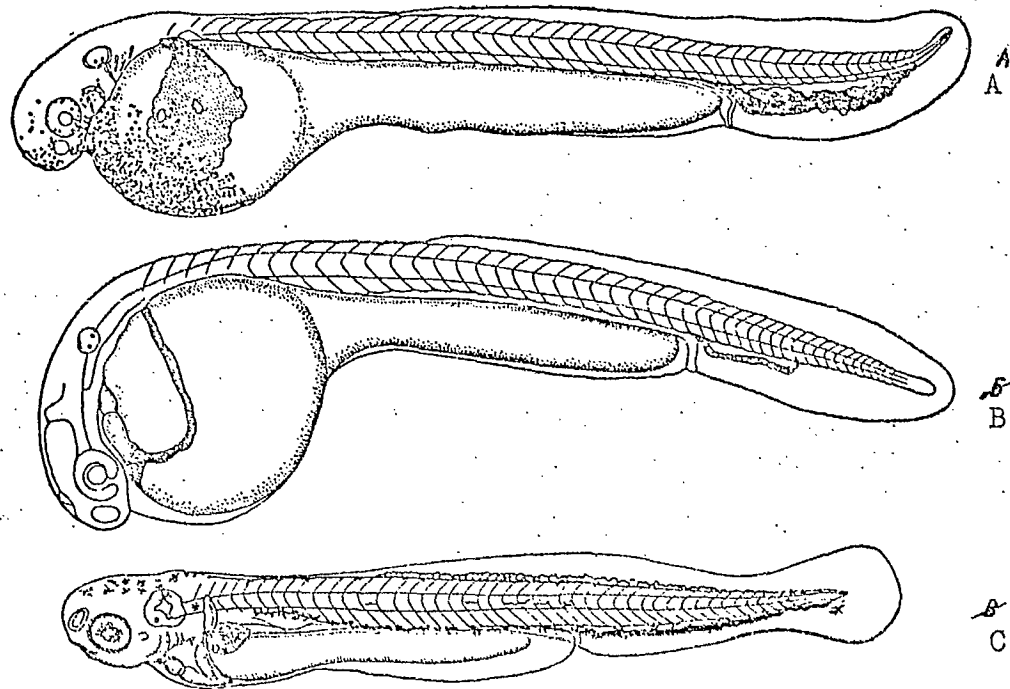


Рис. 84. Вылупившиеся эмбрионы литофильных рыб *Barbini* (A) и *Leuciscini* (B, C)

A — *Barbus goktschaicus*. Возраст около 5½ суток (температура 17°). Органы дыхания — шнуровые протоки и нижняя хвостовая вена. Пигмента нет. Подпрыгивает. B — *Chalcaburnus chalcoides*. Возраст около 2 суток (температура 19°). Кровообращение едва начинается. Прячется под камнями. B — только что вылупившийся пеструх (Leuciscus schmidtii). Возраст около 22 суток (температура 10°). Начинает плавать. В глазах и на теле пигмент. Главный орган дыхания — сосудистая сеть в спинной плавниковой складке. Жабры зачаточны.

Figure 84. Hatched embryos of the lithophilous fish *Barbini* (A) and *Leuciscini* (B and C). A-*Barbus goktschaicus*. Age-about 5½ days (temperature 17 C). Respiratory organs-ducts of Cuvier and lower caudal vein. Pigmentation is absent. Performs vertical leaps. B-*Chalcaburnus chalcoides*. Age-about 2 days (temperature 19 C). Blood circulation is just beginning. Hides under stones. C-just hatched Issyk Kul dace (*Leuciscus schmidtii*). Age-about 22 days (temperature 10 C). Begins to swim. The eyes, body are not pigmented. The main respiratory organ consists of the blood vessel network within the fin-fold. Gills are embryonic.

The eye pigmentation, as was mentioned, appears after hatching, i.e. at a relatively late stage. However, the photophobia in embryos does not coincide with the appearance of pigmentation but appears considerably later. The pigmentation of the body appears at even a later stage than the eye pigmentation. For a long time, pigmentation is rather scarce. This is in accordance with the concealed life style of the embryos which hide under rocks, in darkness.

The initial embryonic respiratory system, which was just discussed, is replaced at later stages by a respiratory system consisting of a venous network underlying the intestinal tract. This network covers a considerable part of the surface of the yolk sac. This explains the progressive shortening of the ducts of Cuvier due to the reduction of the yolk sac and the increasing requirements for oxygen by the embryos (Fig. 85A). Moreover, in some forms (barbel, khramulya) a poorly developed respiratory network appears within the dorsal fin-fold. As an individual variation, but not in all specimens, a similar and even less developed network appears in the marinka (Fig. 85C); and finally in the osman it is completely absent, but in its place a unique web-like structure appears as if indicating its phylogenetic existence. All the respiratory organs described, are completely replaced by gills before the end of the embryonic period. The poor development of auxiliary respiratory networks within the dorsal fin-fold in some of the forms (243)

and their complete disappearance in the others indicates that the development of Barbina takes place in favorable respiratory conditions which, however, are not necessarily identical.

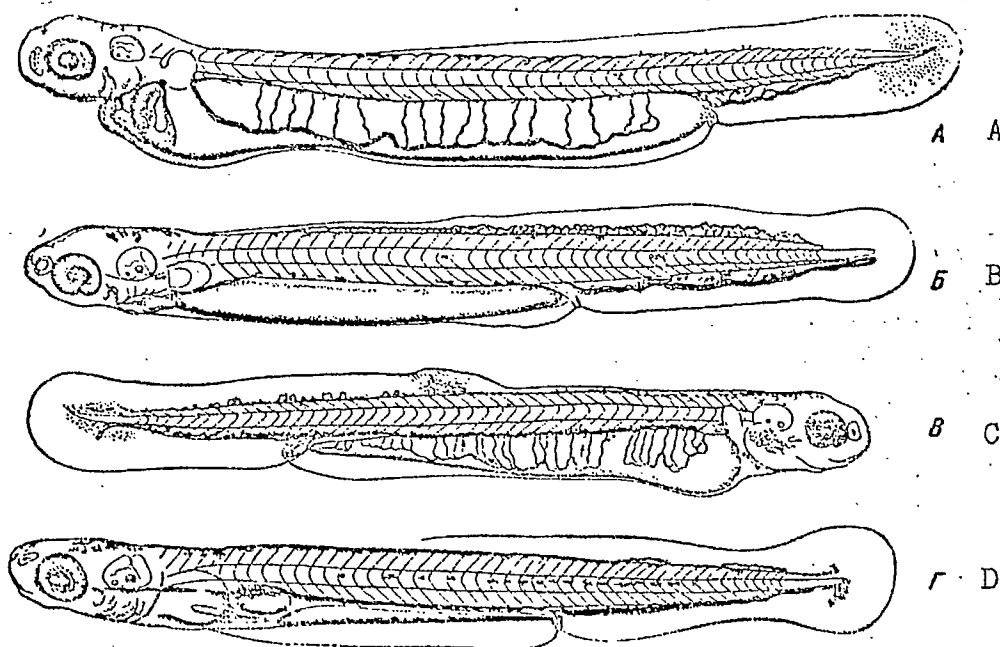


Рис. 85. Органы дыхания Barbini (A, B) и Leuciscini (B, Г).

A — *Diptychus dybovskii*. Дышит подпеченными венами. Жабры зачаточны. Б — *Chalcalburnus chalcoides*. Дышит сосудами спинной и анальной плавниковых складок. Прячется под камни. В — *Schizothorax pseudaksaiensis*. Перед личиночным периодом жизни. Жабры хорошо развиты. Кроме них, имеются дыхательные сосуды желточного мешка и плавниковой складки. Г — *Chalcalburnus chalcoides* в начале личиночного периода жизни. Жабры слабо развиты. Сосуды в непарных складках значительно редуцированы.

Figure 85. Respiratory organs of Barbini (A, C) and Leuciscini (B, D).

A-*Diptychus dybovskii*. Respiration is by means of a venous network underlying the digestive tract. The gills are rudimentary. B-*Chalcalburnus chalcoides*. Respiration is via the blood vessels of the dorsal and anal fin-folds. Hides under stones. C-*Schizothorax pseudaksaiensis* in a prelarval stage. The gills are well developed. In addition there are respiratory blood vessels on the yolk sac and fin-fold. D-*Chalcalburnus chalcoides* at the beginning of the larval stage. Gills are poorly developed. The blood vessels in the unpaired folds are considerably reduced.

The poorly developed embryonic respiratory organs and the belated appearance of pigmentation in the eyes and on the body are typical of the lithophilous Leuciscina, while hatching at the same stage of development and the peculiar behavior of the hatched embryo--the leaping and the relatively long period of the indifferent attitude towards light--are features typical only of the Barbina.

Among the Leuciscina, 8 genera and about 60 subspecies belonging to the lithophilous group are known (Table 64); there is no doubt that they are actually more numerous. The other remaining known genera and species of the Leuciscina belong to the phytophilous and pelagophilous groups. The lithophilous Leuciscina are the most numerous in the European freshwater fauna. They are almost 2.5 times more numerous than the phytophils. Some 33 species of them, i.e. a little more than half, inhabit mainly the rivers and lakes of the flatlands. The remaining 28 species inhabit bodies of water (244) in the mountains. However, in contrast to the Barbina, the latter do not dwell in swiftly running mountain streams and except for individual exceptions such as the Issyk Kul dace, they do not go into high mountain lakes.

The Kura River has the greatest abundance of lithophilous Leuciscina, followed by the Volga River and finally by all other European rivers. In the eastern direction their abundance decreases and in Kamchatka they are completely absent.

Spawning of the lithophilous *Leuciscina* which inhabit flatland rivers coincides with the spring spate. Thus, the eggs deposited on stones are better protected from being eaten by small fish (gudgeons) because only during the spring spate is the water in the flatland rivers very murky. Moreover, spawning at this time coincides with the spawning of pike and thus the danger that the newly-hatched larvae of the lithophilous *Leuciscina* would be eaten by the larvae of the pike hatched at the same time is reduced. At this time both larvae are of the same size and for this reason the *Leuciscina* larvae cannot be eaten by the pike larvae. The synchronization of spawning with spring flooding also means that it begins at a lower water temperature than the spawning of all other ecological groups of fish, namely at 3 C and ends, for the majority of species, when the water temperature is still low--about 10 to 15 C. Another consequence of the coincidence of spawning and spring flooding is that the spawning is simultaneous and of short duration. For most of the species it lasts only a few days (Table 66).

The specimens that spawn separately and at a later time lose all those advantages with respect to their enemies which the species that spawn early and simultaneously have. In the clarified water, their eggs would be eaten in great numbers by the gudgeons while their larvae would be eaten by earlier hatched and already grown pike larvae.

Table 66

1) Interdependence of the nature of the body of water and the duration of spawning of the lithophilous cyprinids.

Таблица 66

1 Зависимость между характером водоемов и длительностью нереста литофильных карповых рыб

2 Горные озера (Севан, Иссык-куль) (нерест не связан с весенним паводком)		3 Теплые горные реки и Арал (нерест не связан с весенним паводком)		4 Равнинные реки (нерест приурочен к весеннему половодью)	
5 название рыбы	6 длительность нереста	5 название рыбы	6 длительность нереста	5 название рыбы	6 длительность нереста
<i>Barbus goktschaicus</i>	7 1½—2 мес.	<i>Vimba vimba</i>	9 Около 1½ мес.	<i>Abramis sapra</i>	10 Около 2 недель или меньше
<i>Varicorhinus capoeta sevangi</i>	1½—2 »	<i>Leuciscus aphipsi</i>	» 1 »	<i>Leuciscus cephalus</i>	11 То же
<i>Diploichthys dybowskii</i>	8 Около 5 мес.	<i>Chalcalburnus chalcoides aralensis</i>	» 4 »	» <i>danilewskii</i>	» »
<i>Schizothorax pseudaksaiensis</i>	» 5 »			» <i>idus</i>	» »
<i>Leuciscus schmirni</i>	» 5 »			<i>Phoxinus phoxinus</i>	» »
<i>Nemachilus (Diplophysa) sp.</i>	» 3 »			<i>Chondrostoma nasus</i>	12 Около 1 мес. (в устье Волги)

2) mountain lakes (Sevan, Issyk Kul) (spawning does not coincide with the spring spate); 3) warm mountain streams and Lake Aral (spawning does not coincide with the spring spate); 4) Flatland rivers (spawning coincides with the spring spate); 5) name of the fish; 6) duration of spawning; 7) 1.5 to 2 months; 8) about 5 months; 9) about 1.5 months; 10) about 2 weeks or less; 11) same; 12) about 1 month (in the Volga River delta).

The length of the spawning periods of the lithophilous (245) *Leuciscina* inhabiting bodies of water not influenced by spring floods, (for instance in Lake Aral or Lake Issyk Kul), are determined by other factors and the spawning period may be very protracted. Thus, in Lake Aral, the spawning period of the shemaia lasts about 3 months; the dace in Lake Issyk Kul spawn over about 5 months, i.e. as long as or even longer than the lithophilous *Barbina*, which inhabit the same waters. This similarity is due to the previously mentioned reasons, the main one being the disadvantage of depositing large amounts of eggs in clean, transparent water where they can be readily destroyed by predators. In the small, warm, clear streams of the Caucasus, the natures of which are very unstable and determined by rain fall, the spawning period of the lithophilous *Leuciscina* is also protracted (from 1 to 1.5 months) and like the phytophils, they spawn when the water temperature is high (from 18 to 24 C). According to S. K. Troitskii, the vimba, shemaia and snipe spawn at water temperatures of 12 to 20 C.

The fecundity of the lithophilous *Leuciscina* is higher than that of the *Barbina*, however the fecundity of the *Leuciscina* is lower than that of the fish of the other ecological groups (except the ostracophils). As indicated previously, they deposit up to 193 thousand eggs and sexual maturity is reached probably not later than at four years of age. In some species spawning is intermittent (snipe,

riffle minnow, data of S. K. Troitskii; vimba, data of T. B. Berlyand). The egg size is from 1.17 mm to 1.56 mm, i.e. they are smaller than the eggs of *Barbina* but larger than those of the phytophils and other fish (except those of the lazy gudgeon).

The relatively efficient egg protection of the lithophilous *Leuciscina* made a very high fecundity superfluous and by lowering it, provided the potential for reproducing after the phytophilous fish and for increasing the size of the eggs, almost to the same diameter as the eggs of the predator (the pike). This is necessary not only to insure that the size of the larvae at the time of hatching would not be considerably less than that of the pike's larvae, but also that the larvae would be able to feed efficiently and not fall behind in size during the growth period. During development in early spring, the abundance of small planktonic organisms (rotifers) is low, but at a later date they appear in great numbers and serve as the primary food for the smaller size phytophilous larvae. However, there are also crustaceans larger than the rotifers but they cannot be consumed unless the larvae are sufficiently large.

The egg membrane of the lithophilous *Leuciscina* is not poisonous and in various species it is covered with a sticky, hair-like outgrowth which varies in shape and length. In the lithophilous *Barbina* the sticky coating is very thin and continuous and in some species it is completely absent (Fig. 58).

The released eggs become securely fastened to the stones immediately and remain there until the embryos hatch. This arrangement not only saves them from their enemies (particularly the eggs fastened to the lower surfaces of the stones) but also prevents their drifting from the rubble bars into slack, silty water where they are not adapted to develop.

Hatching in various species occurs at very different stages of development and depends on the nature of the body of water inhabited. Species which grow in clear, warm water (from 18 to 24 C), e.g. the vimba, shemaia and snipe, hatch out of the membrane at a very early stage of development, earlier than the lithophilous *Barbina* and the majority of other fish. At the moment of hatching (at an age of approximately two days) tail segmentation is barely complete; although the heart is beating, blood circulation has not yet started or is just about to begin; the non-paired fin-fold is very rudimentary; there is no pigment, etc. (Fig. 84B). This early hatching speeds up the scattering of the embryos and makes hiding easier thus increasing their survival rate. The development of other species, such as the minnow and undermouth takes place in cold water and they hatch at a later, more developed stage, but still without pigment (Fig. 86A); some species of the genus Leuciscus hatch very (246) late--at an age of about 20 days. Their fin-folds are well developed and contain a respiratory network; the eyes are

pigmented as well as the mesentery etc. (Fig. 84C). Hatching at a later stage of development, a good protection for eggs from their enemies, gives the embryos the advantage of remaining for a longer time on the rocky bottoms where aeration is good and of not being carried away when still underdeveloped, into silty places where they would not be able to survive.

In contrast to the embryos of *Barbina*, the hatched embryos of the lithophilous *Leuciscina* do not perform vertical leaps, but take refuge under stones. This is facilitated by the shape of their bodies (Fig. 84B. and 86A) which, at any effort to swim, instead of helping them to get up in the water column, forces them to butt against the bottom. Hidden deep under the stones, the embryos lay quietly and only when disturbed do they make a new effort to swim. When the ocular pigmentation appears, the embryos become extremely photophobic, which is another feature distinguishing them from the *Barbina*. The photophobia forces them to actively search for shelter under stones and to stay there, thus increasing their survival rate.

At the beginning of the larval stage, the photophobia disappears and the larvae, in contrast to the embryos, begin an open, pelagic way of life.

The embryonic respiratory organs in both the lithophilous *Leuciscina* and the *Barbina*, are moderately developed in accordance with the favorable aeration conditions of the inhabited bodies of water. Morphologically, however, the

structure of these organs differs somewhat. In *Leuciscina* there is no sub-intestinal venous respiratory network within the yolk sac, instead there is always a network of segmented blood vessels within the dorsal fin-fold (Fig. 85B); the development of the gill respiratory system is slow (Fig. 85D) and it becomes fully functional only during the second half of the larval period. As yet the historical reasons for these differences between the *Leuciscina* and *Barbina* are not known.

The black pigmentation of the eyes and body of the lithophilous *Leuciscina* and *Barbina*, in accordance with the concealed way of life of their embryos, appears late--later than in phytophils (Fig. 86 A and B). The yellow pigment in the body coverings also appears considerably later than in the phytophils (see Table 68 which compares the phytophilous and lithophilous species of minnows). Apparently, this is a consequence of the favorable aeration conditions in which the lithophils develop.

The main distinguishing features of *Leuciscina* and *Barbina* are shown in Table 67.

2. Phytophilous group of Cyprinidae

Among the Cyprinidae, the *Cyprina* and some *Leuciscina*, a total of about 10 genera and 25 species belong to the phytophilous group (Table 64). In the European ichthyofauna this group occupies a position almost equal to the lithophilous

group. However, in terms of the total number of species it does not represent more than one quarter of the latter group.

The phytophilous cyprinids are most abundant in the Volga River (11 species) and in the European rivers. In the rivers of Middle Asia and Siberia they are half as numerous, they are very scarce in the Amur River (3 species) and in Kamchatka they are completely absent.

The fish of the phytophilous group are adapted to develop on plants, either living or dead, (on the roots and stems of grasses, branches and so on; Fig. 52), more or less remote from the bottom. Therefore, in contrast to the lithophils they are relatively indifferent to the conditions of aeration at the very bottom and are even able to develop in bodies of water where the bottom is covered with decaying organic detritus, where there is no influx of fresh water and where oxygen is absent. However they are not adapted for development on clean, sandy-rocky bottoms or in swiftly running rivers. Therefore, in contrast to the lithophils, they inhabit mainly flatland bodies of water. Some of them inhabit almost every overgrown, eutrophic, or even oxygen deficient lake and pond but they are not found in oligotrophic mountain lakes nor in swiftly running mountain rivers which do not have overgrown slack waters, nor suitable conditions for reproduction. Among the phytophilous genera only the roach has produced one mountain subspecies and only the bleak has produced several (four) mountain subspecies. The latter, because of its adaptations, is similar to the lithophils in some ways.

Table 67

(247)

Comparison of lithophilous *Barbina* and *Leuciscina*

Lithophilous <i>Barbina</i>	Lithophilous <i>Leuciscina</i>
1. Mainly inhabitants of mountain streams and lakes of the Caucasus and Middle Asia.	1. Mainly inhabitants of flatland rivers and lakes of Europe, Siberia and the Far East.
2. Spawning is not linked to spring floods and is very protracted (up to 6 months), confined to temperatures from 12 to 17 C.	2. Spawning in most of the species is confined to the period of spring spate and mainly to low temperatures (from 3 to 10 C). The spawning period is very short.
3. The lowest fecundity; most of the species release less than 60 thousand eggs. Sexual maturity is reached relatively late (at age 7 to 8).	3. Higher fecundity; many species release more than 100 thousand eggs. Sexual maturity is reached early (at age 5 to 4 years).
4. Have the largest eggs (1.55 to 2.34 mm in diameter).	4. Eggs are smaller in size (1.17 to 1.56 mm in diameter).
5. Eggs stick to the stones only loosely or not at all.	5. Eggs stick solidly to stones.
6. All species hatch at the same stage of development.	6. Various species hatch at various stages of development.
7. The hatchlings perform vertical leaps for a long time, do not hide under stones.	7. The hatchlings do not leap, but seek refuge under stones.
8. After the appearance of eye pigmentation, the embryos become photophobic gradually and only to a slight degree.	8. Embryos become very photophobic as soon as their eyes become pigmented.

The phytophils release their eggs later than the lithophils and their enemies, i.e. in late spring and summer, and in warm water, mainly at temperatures ranging from 18 to 25 C. Only a few of them begin to spawn when the temperature is from 11 to 15 C (roach, vobla, minnow) but none of the species spawn in colder water (?).

Because they spawn later than the predators and their larvae become food of the predator larvae, their mortality rate is higher than that of the lithophils; for this reason their fecundity is considerably higher. Many of the phytophilous species deposit more than 200 thousand eggs, and the wild carp releases more than 1.5 million eggs while the majority of the lithophils deposit less than 50 thousand eggs and only one of their species--193 thousand. All of them reach sexual maturity at an early age--not later than 3 to 4 years old. Moreover, many of them spawn intermittently thus further increasing the fecundity because in this manner more eggs are released over the whole spawning period than would be possible in a single egg release. According to studies by B. I. Cherfas their mortality rate is at its highest during the larval period while the eggs (248) suffer lower losses from the predators.

The spawning of phytophilous fish does not coincide with the peak of spring flooding but takes place later and usually not in murky waters. For these reasons simultaneous, short term spawning would lose all those advantages for them

which it has for the early spring spawners, the lithophilous *Leuciscina*. In contrast, the protracted spawning period becomes a necessity for them because it provides the potential for intermittent spawning, i.e. increases reproduction and decreases the temporary overloading of the spawning territory with eggs thus lowering the rate of their destruction. For these reasons, most of the phytophilous species have long spawning periods lasting from one to three months. Only the roach, which spawns earlier than the other species and in colder waters, has a spawning period that lasts a few days.

Due to the elevated fecundity, the eggs of phytophilous cyprinids are smaller in size than the eggs of the lithophilous species; the egg diameter of the former is from 0.84 to 1.3 mm while the diameter of the latter is from 1.13 to 2.34 mm. For this reason the larvae of the phytophils are also smaller than those of the lithophilous species: the initial length of the former is 6 to 7 mm while the length of most of the latter varies from 8.2 to 14.25 mm. There is a relation between the reduced size of the larvae of phytophilous fish and the status of plankton. The beginning of the life cycle of the larvae of lithophils coincides with the appearance, in abundant quantities, of the small size planktonic organisms (rotifers and others), necessary for their food.

The eggs of all phytophilous cyprinids are provided with a very sticky coating with which they fasten solidly to plants, more or less remote from the bottom and frequently

to floating leaves at the very surface (Fig. 52). Because of this, they are in satisfactory conditions of aeration and are not in danger of dying for lack of oxygen. Oxygen deficiency often occurs in overgrown places and at the bottom of bodies of water used by phytophilous fish for reproduction (eggs of the bream, for instance, are sometimes deposited on sunken leaves and most of them perish).

The duration of development within the egg of phytophils is not identical for all species. However, none of these fish hatch as early as some of the lithophils. Whereas the very early hatching of the latter is advantageous because it allows the embryos to scatter and take shelter under stones, thus providing better protection from enemies, this would be intolerable for the phytophils because their poorly developed embryos, which are unable to swim upwards, would perish at the bottom midst decomposing vegetable and other detritus and where oxygen is absent. For this reason the phytophils do not hatch before reaching the developmental stage at which they are able to rise to the surface at least for short moments. In their less developed representatives, the tail end of the body is temporarily, slightly curved upwards (Fig. 86B). Because of this, at any attempt to swim, they are forced to move upwards and do not butt their heads into the bottom as do the embryos of the lithophils. Moreover, all of them (except the *verkhovka*), in contrast to the embryos of all other fish, have glandular adhesive

organs on the front part of their heads. When making an attempt to swim to the surface they accidentally butt into the stems or leaves of grass, adhere to them by their heads, quiet down and continue to develop in this suspended position. If they accidentally become detached or fall to the bottom, they make a new effort to swim up and attach themselves. They can also develop by lying quietly on the bottom if it is sufficiently clean and irrigated by good quality water. When the yolk is quite reduced, the embryos cease to be suspended and begin to swim continuously, their swim bladder becomes filled with air and they change over to the pelagic larval way of life.

As mentioned, among the phytophils only the verkhovka does not have adhesive organs. In contrast to the other fish it develops inside the egg membrane for such a long period of time, that at the moment of hatching it is more developed, with a negligible quantity of yolk and is immediately capable of assuming the pelagic way of life. Thus it does not need the adhesive organs (Fig. 86D).

Due to the fact that embryos of the phytophilous (249) fish avoid the bottom, and usually develop in a suspended position some distance from it, they strive towards light, avoiding only bright sunlight and giving preference to diffused light. This is in contrast to the embryos of lithophilous fish which hide under stones. Among the embryos of phytophilous cyprinids only the embryos of the bleak are

strongly photophobic. Like the lithophils, the bleak partly prefers to live and develop only in well aerated bodies of water and may even deposit eggs on a sand and stone bottom. Therefore the photophobia of its embryos has a positive biological reason.

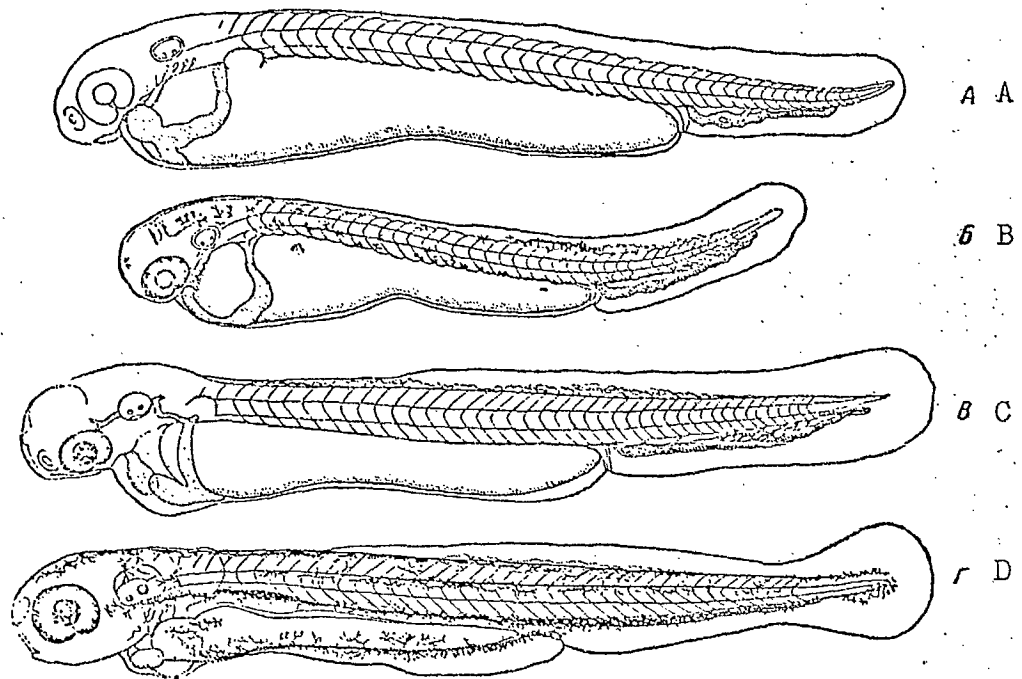


Рис. 86. Стадии вылупления литофильной (А) и фитофильных (В — Г) рыб.

А — *Phoxinus lagowskii*. Прячется под камни, тело изогнуто вниз. Без пигмента и без дыхательных сосудов в спинной складке (по А. И. Смирнову). Б — *Phoxinus peronurus mantschuricus*. Всплывает, подвешивается к растениям. Хвост изогнут вверх, покрыт пигментом. Дыхательные сосуды в спинной складке (по А. И. Смирнову). В — *Abramis brama*. Всплывает, подвешивается к растениям. Г — *Leucaspis delineatus*. Плавает сразу после вылупления. Тело прямое. Дыхательная система слабо развита.

Fig. 86. Stages of development of lithophils (A) and phytophils (B-D) at the moment of hatching. A-*Phoxinus lagowskii*. Hides under stones, the body is bent downwards. No pigment nor respiratory vessels within the dorsal fold (A. I. Smirnov's data). B-*Phoxinus peronurus mantschuricus*. Swims towards the surface and attaches to plants. Tail is bent upwards, pigmented. Respiratory vessels within the dorsal fold (A. I. Smirnov's data). C-*Abramis brama*. Swims towards the surface, attaches to plants. D-*Leucaspis delineatus*. Swims immediately after hatching. Body is straight. The respiratory system is poorly developed.

Embryonic respiratory organs in phytophilous fish are developed to various degrees depending on the ecological conditions. In those which live and develop in the worst possible conditions of aeration, i.e. in very densely overgrown or oxygen deficient lakes, for instance the lake minnow, the respiratory organs are developed to a very high degree (Fig. 86B and 87A, D). In addition to the extended ducts of Cuvier, and yolk sac with a more enlarged anterior part than in other fish, they have a very dense network of vessels in the dorsal finfold which persists for a long period and continues to function for some time during the larval period simultaneously with the gills (Fig. 87D, A. I. Smirnov's data). Furthermore, in phytophilous fish these organs are developed earlier, i.e. the vascular network fills the finfold at that stage of development at which, in the lithophilous fish, which develop in more favorable aeration conditions, the network is not yet present (compare Fig. 86A and B). In other phytophils which deposit their (250) eggs in less unfavorable conditions (roach, bream) the embryonic respiratory organs are somewhat less developed and at the beginning of the larval period they have ceased to exist (Fig. 87, B and E). Finally, in fish which develop in very favorable conditions of aeration, the respiratory organs are quite insignificant. The bleak, which releases its eggs in relatively fast running water, and the verkhovka which releases its eggs at the surface of the water, almost never have the vessels in the dorsal finfold (Fig. 87C and F).

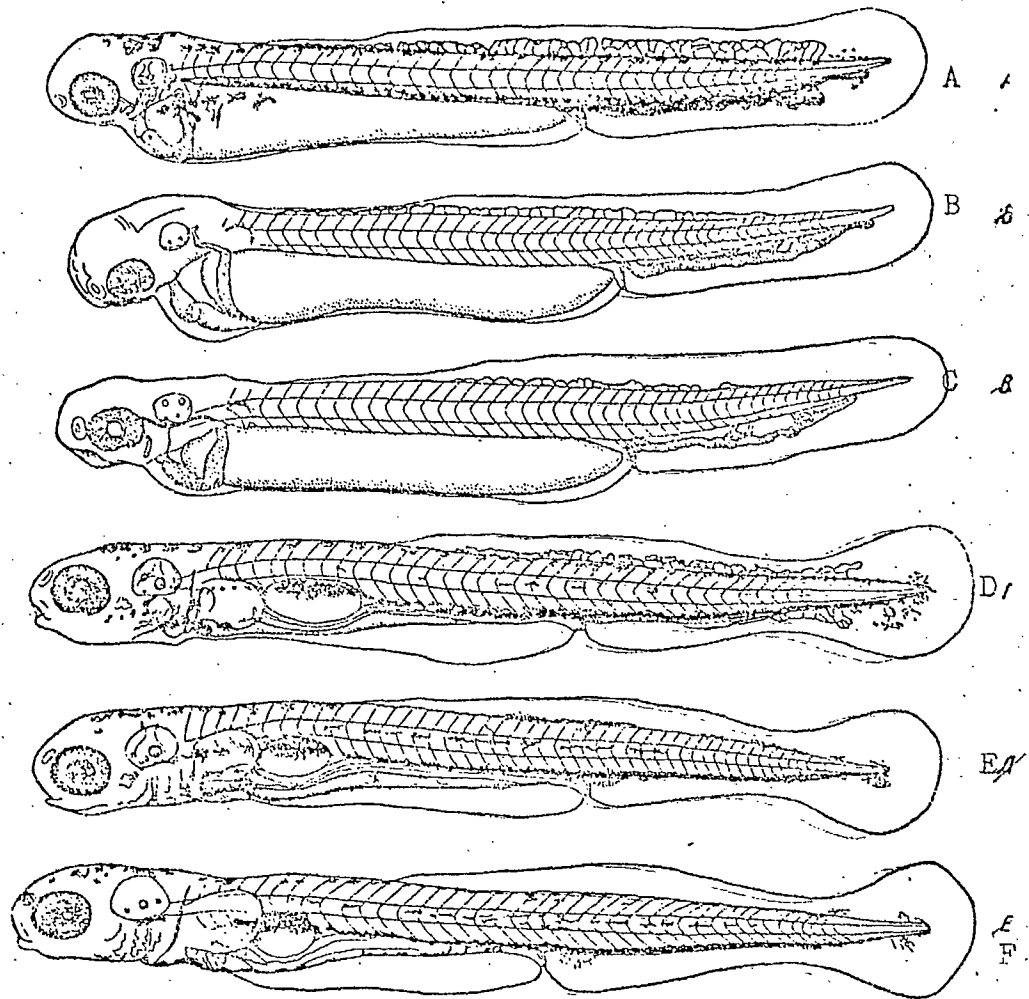


Рис. 87. Органы дыхания у эмбрионов (А—В) и личинок (Г—Е) разных фитофильных рыб.

А — *Phoxinus peronurus mantschuricus*. Сосудистая дыхательная сеть в непарных складках очень большая (по А. И. Смирнову). В — *Abramis brama*. Дыхательная сеть менее значительная. В — *Alburnus alburnus*. Почти нет сосудов в спинной плавниковой складке. Г — *Phoxinus peronurus mantschuricus*. Начало личиночного периода жизни. Имеется значительная сеть сосудов в спинной и анальной плавниковых складках (по А. И. Смирнову). Д — *Abramis brama*. Дыхательная сеть в плавниковых складках почти совсем исчезла. Е — *Alburnus alburnus*. Плавниковые складки без сосудов.

Fig. 87. Respiratory organs in embryos (A-C) and larvae (D-F) of various phytophilous fish.

A-*Phoxinus peronurus mantschuricus*. The vascular respiratory network within the unpaired folds is very large (A. I. Smirnov's data). B-*Abramis brama*. The respiratory network is less developed. C-*Alburnus alburnus*. The respiratory network in the dorsal fin fold is almost completely absent. D- *Phoxinus peronurus mantschuricus*. Beginning of the larval life period. A considerable vascular network is present within the dorsal and anal fin folds (A. I. Smirnov's data). E-*Abramis brama*. The respiratory network in the fin folds has practically disappeared. F-*Alburnus alburnus*. The fin folds are without vessels.

The eye and body pigmentation in phytophils appears earlier than in lithophils. At the moment of hatching or even before, most of the phytophils are covered with black pigments to varying degrees, whereas the lithophils at the same stages of development are completely devoid of any pigmentation (Fig. 86., Table 74). This is determined by the various biological conditions of life of these two groups and not by the direct influence of light. Such an assumption (251) can be made because the pelagophils which develop in an even more intensely illuminated environment (at the surface of running water and in the absence of vegetation) acquire pigmentation at a much later stage than the phytophils and even the lithophils which develop, for a long period, in darkness. It may be that the early appearance of the melanin in embryos of phytophilous fish has a cryptic significance.

In phytophils the yellow pigment also appears earlier than in the lithophils. It appears particularly early in those phytophils which are adapted to the least favorable conditions of aeration. Yellow pigmentation is particularly abundant in the crucian carp, common carp, tench and lake minnow. In the phytophilous lake minnow, for instance, the intensive yellow pigmentation is already apparent at an age of approximately 4 days (Fig. 94E) while in the lithophilous *Lagovskii's* minnow a slight yellow pigmentation appears only at an age of 10 days (Table 68). In other phytophilous fish, adapted to better aeration conditions, there is less of the

yellow pigment and it appears later. In this respect these fish resemble the lithophilous species. The described peculiarities of development of the yellow pigment are related to the developmental stage of the respiratory organs and apparently are determined by some ecological factors, linked to respiratory functions.

Thus, the adaptations of the phytophilous cyprinids are not quite identical and depend on the differences in ecological conditions during development. They may be subdivided into four subgroups.

1. The bleak, in contrast to other phytophils can deposit eggs in swifter running water and on a hard substratum-- on sticks, boards, and even on a sandy-stony bottom (data of P. A. Dryagin and S. K. Troitskii). Egg development takes place in the best possible conditions of aeration and therefore the embryonic respiratory organs are minimal. The embryos are provided with adhesive organs and they are able to suspend themselves; at the same time they are very photophobic and may be hiding. This is due to the good conditions of aeration where their development takes place. The ability to deposit eggs on a sandy-stony bottom and the photophobia are features in which the bleak resembles the lithophils while the ability to reproduce on plants and to adhere make it similar to the phytophils.* The poorly developed embryonic respiratory organs and the strong photophobia prevent the bleak from living in densely overgrown, eutrophic bodies

*Translator's note: "lithophilous" in the original.

of water. The bleak is found mainly in rivers, and as mentioned, it has even produced four subspecies which inhabit mountain streams.

2. The roach, bream and other typical phytophils are adapted to the living conditions in rivers and flatland lakes. The eggs are deposited mainly on live or dead grassy plants, in places with reduced current or in completely still water. The embryonic respiratory organs are moderately developed. The embryos do not hide on the bottom but suspend themselves from plants and avoid only direct sunlight.

3. The crucian carp and lake minnow are adapted to life in heavily overgrown and even oxygen deficient lakes and ponds. Their eggs are deposited on grassy plants. The embryonic respiratory organs are developed to a high degree and persist longer (e.g. in the minnow) than in other fish. The yellow pigmentation appears earlier and is considerably more abundant than in other species. The embryos do not hide but attach themselves to plants and are photophilous.

4. The verkhovka, like the bleak, is adapted to develop in very good conditions of aeration, however, in contrast to the bleak and other fish, it deposits its eggs mainly on leaves, sticks and other objects which are floating on the surface (Fig. 52). Moreover, the verkhovka has extended the period of development within the egg membrane to the limit. Thus the embryos develop in the best possible (252) conditions of aeration, are completely independent of the

Table 68

1) Comparison of lithophilous and phytophilous minnows.

(The fish developed at identical temperatures).

Таблица 68

1 Сравнение литофильного и фитофильного гольянов
(рыбы развивались при одинаковой температуре)

2 Название рыбы	3 Величина яиц без оболочки (в мм)	4 Появление меланина		7 Выгуливание из оболочки*	8 Появление желтого пигмента*	9 Органы приклеивания	10 Отношение к свету	11 Эмбриональные органы дыхания	12 t° воды при нересте (в °C)
		5 в глазах	6 на теле						
13 <i>Phoxinus phoxinus</i> (фитофильный)	1.08	15 суток 16 18 час.	154 суток 16 18 час.	154 суток 16 18 час.	154 суток 16 18 час.	18 Имеются	20 Положительное	22 Значительные	17
14 <i>Phoxinus lagowskii</i> (литофильный)	1.15	17 Около 5 суток	155 суток	156 суток	1510 суток	19 Отсутствуют	21 Отрицательное	23 Менее значительные	12

24* Сроки указаны, считая с момента оплодотворения икры.

2) name of the fish; 3) egg size without the membrane (in mm);
 4) appearance of melanin; 5) in the eyes; 6) on the body;
 7) hatching out of the membrane*; 8) appearance of yellow pigment; 9) adhesive organs; 10) reaction to light; 11) Embryonic respiratory organs; 12) water temperature during spawning (°C);
 13) Phytophilous; 14) Lithophilous; 15) days; 16) hours;
 17) approximately, days; 18) are present; 19) are absent;
 20) positive; 21) negative; 22) considerable; 23) less considerable.

24) *The duration of each period indicated is from the moment of fertilization of the egg.

bottom and are not in danger of sinking to it. They hatch at a sufficiently well developed stage that they do not need to attach themselves and are immediately adapted to a pelagic way of life. For this reason they do not have adhesive organs (Fig. 86D). Development of the embryonic respiratory organs is minimal and similar to that of the bleak. In spite of this, the verkhovka, in contrast to the bleak, can live and multiply, because of a combination of adaptations, not only in rivers but also in very densely overgrown and even oxygen deficient lakes.

As a rule the extent to which the peculiarities of the phytophils are determined by the environment of their habitat, is visible from the comparison of two related species: the phytophilous lake minnow and the lithophilous minnow of Lagovskii, both of which partly inhabit the Amur River (Table 68; Fig. 86A and B). They deposit their eggs in different places, at different seasons, on different substrata and at different temperatures. The phytophilous lake minnow spawns for a longer period of time, mainly in June, at a temperature of 17 C or higher, in flooded lakes and deposits its eggs on grass; the lithophilous minnow has a short spawning period in mid-May, at a temperature of about 12 C, in clear brooks and deposits the eggs on rocks.

The eggs of the phytophilous minnow are smaller, i.e. its fecundity is relatively higher. It hatches slightly earlier with more developed respiratory organs (Fig. 86A and B);

its ducts of Cuvier are longer because the anterior part of the yolk sac is more enlarged and the vessels in the dorsal fin fold are already present. Later they grow much larger and remain up to half of the larval period (Fig. 87D). The tail is curved upwards considerably which makes it possible (253) for the embryo to swim towards the surface; the body is covered with abundant black pigment and the eyes are equally pigmented. The embryo is photophilic, has adhesive organs and suspends itself from plants. At the same stage of development, the yolk sac of the lithophilous minnow is only slightly enlarged, therefore the ducts of Cuvier are shorter; the vessels in the dorsal fin fold are not yet developed; at later stages they expand less and disappear earlier. The tail is not curved upwards; there is no pigment either in the eyes or on the body; the adhesive organs are absent; the embryo is photophobic and develops on the bottom, under rocks etc.

A peculiarity of the phytophilous group of fish is the scarcity of species in their genera (Table 64): most of the genera have only one phytophilous species and only two genera have more than two species while the genera of lithophilous fish have from 3 to 20 species; in the genus Phoxinus, for instance, for each phytophilous species there are at least five lithophilous species. The limited formation of species is inherent not only to the genera with a restricted area of distribution, but also to the genera

which have taken over various regions and have even penetrated into the mountains. For instance, the redbfin in Caucasian lakes is the same as in the flatland bodies of water; the common carp in the Azov Sea, Caspian Sea, the lakes of the Caucasus and in the Issyk Kul, is always the same, while any lithophilous genus, particularly the Leuciscus, not only in remote areas but also in neighboring mountain rivers forms different species.

There are only two genera within the phytophilous group--Phoxinus and Abramis--which besides the phytophilous species also have lithophilous species. All other species are typically members of this group.

On the whole, the phytophilous group, similar to the lithophilous, is heterogeneous because it is formed by species of the subfamilies Barbini and Leuciscini which do not have a direct relationship but have evolved parallelly. It is possible that some phytophilous species of Leuciscini, such as the tench, bream, lake minnow and verkhovka, have also evolved parallelly.

Among the phytophils, as previously mentioned, the bleak is somewhat similar to lithophils in that it is able to deposit its eggs on a rocky-sandy bottom and it is very photophobic. Among the typically lithophilous fish, the Aral shemaia, vimba and the minnow of Lagovskii, when the bottom conditions are suitable, can deposit their eggs on plants and branches like the phytophilous fish, however on the whole they remain typically lithophilous.

In contrast to these fish which have preserved their basic adaptations, the ide (and possibly the dace) has combined the features of lithophils and phytophils to such an extent that it is impossible to relate it to either of these groups. It must be studied as a typical representative of an intermediate group. Like the lithophils, its spawning is confined to the period of spring flooding. The egg release is simultaneous, over a short period of time and at a very low temperature--about 5 C. For spawning it leaves the lakes and rivers and enters brooks where it deposits its eggs on rocky shoals where the currents are swift. The eggs stick to the rocks and for a long period of time they develop there in very good conditions of aeration. As is typical for lithophilous fish, the eggs are very large in size (1.43 mm in diameter). This indicates that the fecundity of the ide is rather low.

The embryos at the moment of hatching are at a considerably advanced stage of development and behave like embryos of phytophilous fish. They have adhesive organs, are not photophobic (avoiding only direct sunlight) and are able to swim towards the surface. Therefore, in contrast to the embryos of lithophils, they do not lie on the bottom nor do they hide under rocks. They are carried by the current into silty, slack water regions with vegetation where they become temporarily suspended from the vegetation by their adhesive organs (Fig. 38). Later they begin to lead the

usual, pelagic way of life. Thus the initial period in the development of the ide, up to the hatching of the embryos, (254) is adapted in a manner similar to lithophilous fish; the period that follows it, is adapted in a manner typical of phytophilous fish. The combination of the qualities of both groups of fish, provides the ide with an advantage over the typical lithophilous fish in that it makes the ide less exacting in its choice of spawning grounds and allows it to reproduce in places where the typical lithophilous fish would not be able to reproduce. However, the dace, as a rule, cannot definitely become adapted to small, grassy bodies of water without inflows which are completely suitable for typical phytophilous fish in spite of the fact that it is able to deposit its eggs on plants. This is probably so because it is not adapted against predators of its eggs. Moreover, the eggs are large, the fecundity is low, etc.

3. Psammophilous group.

Fish of the psammophilous group are adapted to develop, after hatching, on an open, sandy bottom.

Among the cyprinids only the Gobionina, which is represented by three genera: Gobio, Gnathopogon and Hemibarbus, comprising a total of about 7 species, are members of this group. In addition, apparently, all the Nemachilini of the loach family are typical psammophils. In our fauna they are represented by some 23 subspecies. Other families and

orders of fish have not produced any psammophilous species. If it is definitely demonstrated that the Nemachilini are derived from the Gobionina, then this group will turn out to be, like the ostracophilous group, completely homogeneous.

The psammophilous cyprinids deposit their eggs at the edges of grassy beds on clusters of very fine roots which have been washed out by the current, in places where they hang over a sandy bottom. The eggs are driven between the roots and adhere to them. Here the eggs develop for some time, protected by the roots. According to S. K. Troitskii, the gudgeons deposit their eggs on a sandy, rocky bottom.

Spawning takes place in the spring and summer, at temperatures of 12 to 20 C. In the Don River (near Voronezh) the gudgeon spawns from the second half of April until the beginning of May, at temperatures of 12 to 15 C, partly simultaneously with the lithophils and partly with the phytophils. In the Amur River, the Amur barbel (Hemibarbus maculatus) spawns during the first half of June, at a temperature of 18 C, simultaneously with the crucian carp; at almost the same time, the Ussuri gudgeon begins to spawn however its spawning period extends up to the end of June.

Most of the species have small size eggs, from 0.8 to 0.9 mm in diameter. Only eggs of the Amur barbel reach a size of 0.97 to 1.15 mm. This indicates that these fish have a relatively high fecundity. In their egg size and

degree of fecundity they are close to the phytophilous cyprinids. Spawning of the gudgeon is intermittent; the ovary contains about 3,357 eggs (data of S. K. Troitskii).

In all species the egg membrane is densely covered with long, sticky villi (Fig. 58), with which the eggs become strongly fastened to the roots. The yolk sac is colorless or grayish and completely devoid of yellow or orange pigments which are typical of the benthonic eggs of all other ecological groups of fish, although sometimes this pigmentation may be very faint. In this respect, the eggs of the gudgeon resemble the eggs of the pelagophils, apparently reflecting the favorable conditions of aeration, in which the eggs of both groups develop.

After hatching, which takes place at various stages of development but not very early (Fig. 88B and 28B), the embryos leave the tuft of roots and sink to the bottom. The embryos achieve this by being restless for a short while immediately following hatching. The tail of the Amur barbel, which hatches earlier than the embryos of other gudgeons, is even curved upwards initially (Fig. 28B). Because of this, (255) when an attempt to move is made, they are forced to swim upwards and are washed off the roots by the current. Having fallen on a clean, sandy bottom, the embryos cease their efforts to swim towards the surface, their tails straighten out and from then on they continue to develop while lying quietly on the bottom. Development in such conditions has

determined all other essential morphological and behavioral peculiarities of the fish belonging to this group. In contrast to the embryos of phytophilous fish, they do not have adhesive organs and therefore they are not adapted to adhere to plants and thus become suspended above the bottom. In contrast to the embryos of lithophilous fish, they are not photophobic, just the opposite, they strive towards the light and therefore they do not become wedged between objects lying on the bottom, but are always moving to clean, open spaces where aeration is better. Good conditions of aeration are responsible for the poorly developed embryonic respiratory organs (Fig. 88, A-B, and Fig. 22): they are represented by only the ducts of Cuvier and the lower caudal vein, the latter being somewhat convoluted while the former undergo shortening at an early stage (i.e. the importance of both of them for respiration is minimal). The gill arches develop very late--during the larval period (at an age of 20 days; see Table 21). Unlike the embryos of lithophilous and phytophilous fish, they are not provided with a segmented vascular respiratory system in the dorsal fin fold; nor do they have the subintestinal venous network on the surface of the yolk sac. Only the pelagophilous fish, which develop from large eggs (chekhon, lazy gudgeon), are comparable to the psammophilous gudgeons with respect to the stage of development of the embryonic respiratory organs. Only the other pelagophilous fish are behind them in this respect.

The most typical peculiarity of the psammophils is the development and use of the pectoral fins. They appear early: towards completion of segmentation of the body, the rudiments are already comparatively large (Fig. 88A), their longitudinal growth rate then increases until they become narrow, unusually long blades. If the pectoral fins of the embryos of other fish are pressed against the body, they cover not more than 4 to 5 myotomes, while in the psammophils they extend over 7 to 8 myotomes (Fig. 88 and 28). They do not carry a vascular network and do not participate in respiration but serve only as support against the bottom. The embryos spread them sideways, the edges touching the ground. With this arrangement, the embryos are able to rest on the ground on their bellies without falling over (Fig. 88, D-E).

The larvae use their pectoral fins in a similar manner. They lie quietly on the bottom supported only by the fins and occasionally flutter from one place to another searching for food. Due to their benthic way of life, their swim bladder is smaller than that of embryos of the pelagic fish of other ecological groups. The pre-anal fin fold is also relatively small (Fig. 28). Later, the size of the pectoral fins decreases and they reach a normal size at the end of the larval period. As was just mentioned, in embryos and larvae of fish belonging to other ecological groups the pectoral fins are not elongated, the larvae use

them for swimming but do not spread them out and do not use the fins as supports. The larvae never rest on their bellies on the bottom but are always in midwater. Consequently the swim bladder and the pre-anal fin fold of these fish are large.

The body of psammophilous cyprinids has a peculiar pigmentation: melanophores first appear only along the ventral surface of the yolk sac, then along the body cavity and caudal vein and finally along the spinal cord and backbone, not above it, as in majority of fish species, but below it (Fig. 28, B, C-E). For a long time the body coverings are almost completely devoid of melanophores. Later the number of melanophores begin to increase, not in the integuments, but mainly along the inner organs, such as the dorsal ventral aortas, the cardinal veins, the spinal cord and the vertebral column. Almost the entire, externally visible pattern of (256) pigmentation of the larvae consists, for a long time, of these melanophores which are visible through the tissue (Fig. 28, E).

In larvae of the fish of other ecological groups, except the pelagophils, the pigment is distributed in bands, at first, mainly in the integument and above the spinal cord (Fig. 42, C), not below it. However, in many pelagophilous cyprinids the spinal cord becomes initially pigmented ventrally. The described peculiarities in pigment distribution in psammophilous cyprinids (and partly in the pelagophilous also) are apparently due to the fact that these fish develop in open places and uniformly illuminated environment.

The psammophilous loaches differ from the psammophilous gudgeons in that they do not deposit their eggs within tufts of exposed roots, but on sparse small grasses, growing on a sandy (257) bottom, on vegetable detritus and directly on the sand. The sticky coating of the eggs becomes covered with sand grains which makes them barely discernable to their enemies (small fish).

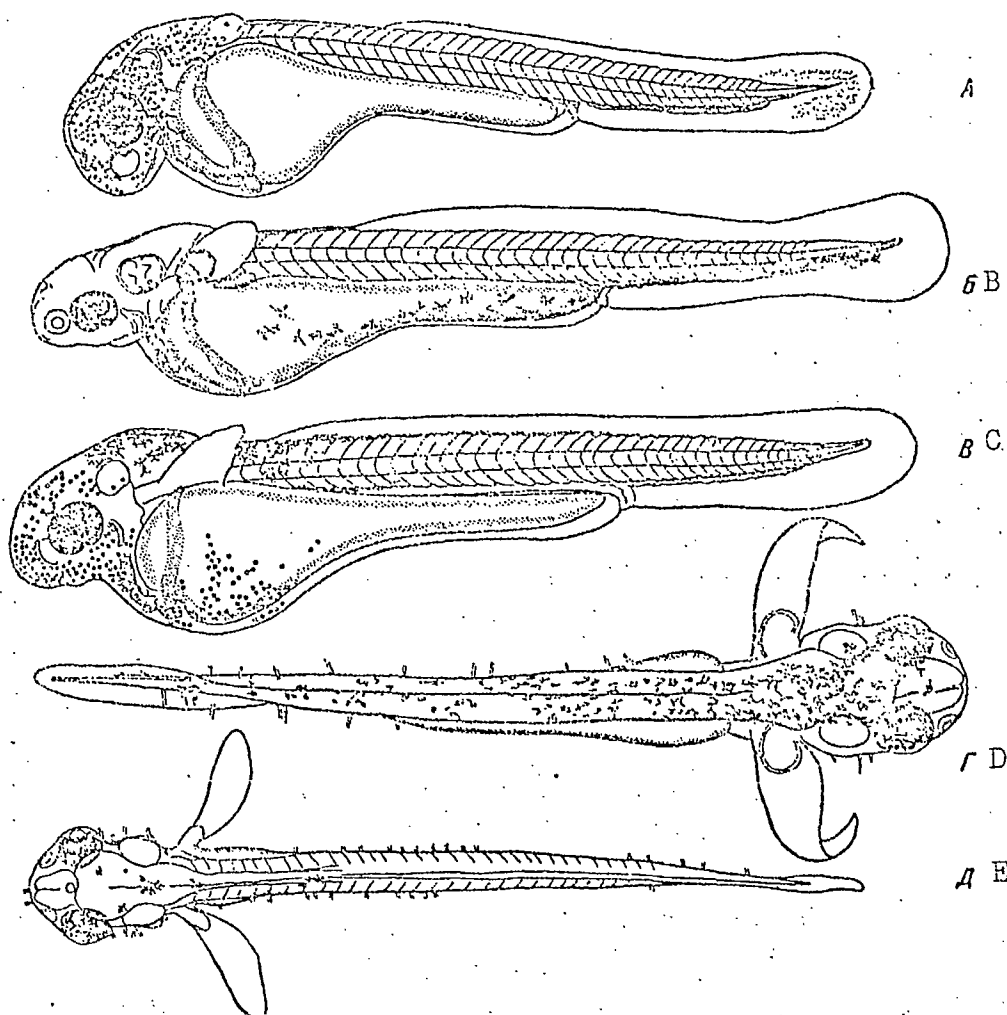


Рис. 88. Эмбрионы псаммофильных рыб.

А — *Gobio gobio*, извлеченный из оболочки. Зачатки грудных плавников увеличены; органами дыхания служат длинные кульеровы протоки (на желточном мешке) и отчасти — нижняя хвостовая вена. Б — он же, немного старше. Пигмент на нижней поверхности желточного мешка. Грудные плавники увеличены. В — соответственно развитой *Nemachilus dorsalis*, извлеченный из оболочки. Органы дыхания те же. Грудные плавники увеличены. Пигмент сверху. Г — *Nemachilus dorsalis* (сверху) в естественном положении. Увеличенные грудные плавники растопырены. Д — *Gobio gobio* с растопыренными грудными плавниками в естественном положении, видимый сверху.

Fig. 88. Embryos of psammophilous fish.

A-*Gobio gobio*, extracted from the membrane. The rudiments of pelvic fins are enlarged, the long ducts of Cuvier (on the yolk sac), and to some extent the lower caudal vein are used for respiration. B-same embryo--a little older. The surface of the lower part of the yolk sac is pigmented. The pectoral fins are enlarged. C-*Nemachilus dorsalis*, at the same stage of development, extracted from the membrane. Respiratory organs are the same. Pectoral fins are enlarged. The pigmentation is above. D-*Nemachilus dorsalis* (from above) in a natural position. The pectoral fins are spread out. E-*Gobio gobio* with the pectoral fins spread out, in a natural position, viewed from above.

The pigment first appears mainly in the integument covering the dorsal (and not the ventral) surface (Fig. 88C). The gills develop earlier than in gudgeons, at the beginning of the larval period and are irrigated by water from behind, through the gill slits which are opened wide and not through the mouth. Moreover, the larvae acquire, in addition to the gills, though quite insignificant, respiratory structures within the pectoral fins and the non-paired fin folds (Fig. 65). All these peculiarities in the development of Nemachilini are related to some as yet insufficiently studied peculiarities of their larval life which result from the fact that the Nemachilini inhabit mainly small, swiftly flowing brooks and mountain rivers. However in many other essential aspects of their development, they are very similar to the psammophilous gudgeons. Their hatched embryos also develop lying on a clean bottom. They are not photophobic and are unable to become attached to plants as they are not provided with adhesive organs. Their pectoral fins also appear early, grow exceptionally long and serve (in a flared position) as support on the bottom (Fig. 88B and D). The embryonic respiratory organs in Nemachilini are also poorly developed and are represented by temporarily elongated ducts of Cuvier and by a short nonconvoluted lower caudal vein (Fig. 88B). However, in contrast to the larvae of gudgeons, the pectoral and nonpaired fins of their larvae carry out a respiratory function: vessels appear within these fins (Fig. 65).

The psammophilous fish are distributed very widely: some of their species are present in almost every river and lake of the Union, except Kamchatka (Tables 84 and 85). But they are actually abundant in only two locations--in mountain rivers and lakes of Middle Asia (about 25 subspecies), and in the Far East (about 9 species). In Middle Asia the psammophilous stone loaches prevail--23 subspecies, as compared with only two gudgeon subspecies. In the Far East the psammophilous gudgeons rank first--for their 7 subspecies there are only 2 species of stone loaches.

4. Freshwater pelagophilous fish.

Fish which release their eggs within the water column where they float freely and continue to develop, and which have special adaptations for this, belong to the pelagophilous group.

At present in our freshwater fauna 20 cyprinid species which certainly belong to this group are known (Table 69). However with reasonable certainty one can assume that the number of our pelagophilous cyprinids is even higher. In addition to them, one species of the Serranidae (Siniperca) and two species of the Clupeidae (Clupeonella abrau and C. delicatula tscharchalensis) are known without considering the 6 to 8 species of anadromous clupeids which live in the sea and enter the rivers for the purpose of reproduction.

The pelagophilous fish inhabit only the rivers and lakes of the basins of the Black, Caspian, Aral and Baltic Seas, and the Amur River; they are absent in the basin of the Arctic Ocean (if one does not consider the semi-pelagophilous smelt).

In European freshwater reservoirs there are 9 to 11 species of pelagophilous fish, including the anadromous clupeids. Of this total, 8 to 10 belong to the Clupeidae and only one species belongs to the Cyprinidae (the chekhon). However these 9 species neither live nor reproduce together (Table 72). Only in the Volga River are there 4 species of pelagophilous fish, one of which is the chekhon. In the Don River 3 species ^{reproduce}, one of which is the chekhon, and in some bodies of water only one of these species reproduces (the chekhon in the Kuban River and sprat in Lake Abrau). The semi pelagophilous smelt meets the chekhon only in the Neva River; the smelt is absent in the southern rivers. Thus, if the European fresh water reservoirs are considered individually, it becomes apparent that they are lacking in pelagophilous fish. (258)

All European fresh water pelagophilous species are connected with the sea, either by their origin or by their way of life (Table 69). Two of them (the sprat of Lake Abrau and the clupeonella of Lake Charkhal) settled in lakes, after coming from the sea; one species (chekhon) is semi-anadromous and the other 6 species (of the genus Caspialosa)

are diadromous. There is not a single species among them with an undisputable fluvial origin (indications that the barbels of Lake Aral and the Kura River are pelagophilous, require verification). All these species belong to the Pontico-Caspian fauna.

In contrast to the European rivers, pelagophilous species are exceptionally abundant in the Amur River. At present the number of known species there approaches twenty, but apparently, it will rise higher. In addition to these species two species of semi-pelagophilous smelts also reproduce in the Amur River. Nineteen pelagophilous species belong to (259) the family Cyprinidae and only one species--Siniperca chuatsi--to the family Serranidae. Thus, in number of known pelagophilous cyprinids, the Amur River certainly ranks first among the rivers of our homeland. At present, except for the rivers of China, there is no other freshwater reservoir known to be as abundant in pelagophilous fish as the Amur River. From what is known of the great rivers of China, although they are little studied as yet, one can assert with confidence that they are at least as abundant in pelagophilous species as the Amur River, if not more so, because all the pelagophilous species of the Amur River originated in the rivers of China and still inhabit these rivers.

The systematic composition of fish of the Amur River and European rivers which undoubtedly belong to the pelagophilous group, is given in Table 69.

Table 69

1) Species of pelagophilous fish and their distribution

Таблица 69

1 Виды пелагофильных рыб и их распространение

2 Водоемы	3 Семейства и подсемейства	4 Происхождение их	5 Виды и роды
7 Амур	Gobionini	6 Пресноводные аборигены	1. <i>Paraleucogobio soldatovi</i> 2. <i>Sarcohilichthys sinensis lacustris</i> 3. <i>Armatogobio dabryi</i> 4. <i>Rostrogobio amurensis</i> 5. <i>Gobiobotia</i> sp. 1 6. <i>Gobiobotia</i> sp. 2
	Leuciscini " Cultrini	6 Пресноводные аборигены	7. <i>Hemiculter eigenmanni</i> 8. <i>Hemiculter leucisculus</i> 9. <i>Xenocypris macrolepis</i> 10. <i>Ctenopharyngodon idella</i> 11. <i>Hypophthalmichthys molitrix</i> 12. <i>Parabramis pekinensis</i> 13. <i>Megalobrama terminalis</i> 14. <i>Erythroculter erythropterus</i> 15. <i>Erythroculter mongolicus</i> 16. <i>Culter alburnus</i> (?) 17. <i>Elopichthys bambusa</i> 18. <i>Opsariichthys uncirostris</i> (?) 19. <i>Pseudaspius leptocephalus</i>
	Serranidae	8 Морские эмигранты	20. <i>Siniperca chuatsi</i>
12 Реки и озера Черно-морско-Каспийского бассейна	Leuciscini	9 Полупроходные	1. <i>Pelecus cultratus</i>
	Clupeidae	10 Морские реликты	2. <i>Clupeonella abraui</i> 3. <i>C. delicatula tsharchalensis</i>
		11 Проходные	4. <i>Caspialosa kessleri</i> 5. <i>C. caspia</i> 6. <i>C. volgensis</i> 7. <i>C. tznaiica</i>

2) bodies of water; 3) families and subfamilies; 4) their origin; 5) species and genera; 6) freshwater aborigines; 7) Amur River; 8) emigrants from the sea; 9) semi-migratory; 10) marine relicts; 11) migratory; 12) rivers and lakes of the Black Sea-Caspian Sea basin.

Table 70

1) Comparison of the absolute and relative numbers of Amur and Volga river fishes which are protecting their eggs, of the pelagophilous species, and other species which do not protect their eggs. (The relative number of species in the groups is expressed as a % of the total number of ecologically characterized species).

Таблица 70

1. Сравнение абсолютного и относительного количеств охраняющих, пелагофильных и прочих не охраняющих икры видов рыб Амура и Волги (относительные количества видов в группах выражены в % от общего количества экологически определенных видов)

2 Рекa	3 Охраняющие, причущие и т. п.		4 Не охраняющие						8 Неиз- вестные
			5 пелагофильные		6 псаммофильные		7 литофильные, фитофильные		
	абсолют- ное коли- чество	%	абсолют- ное коли- чество	%	абсолют- ное коли- чество	%	абсолют- ное коли- чество	%	абсо- лютное количе- ство
10Амур . . .	19	25.0	23	30.9	9	12	17	23.0	7
11Волга . . .	13	22.4	6	10.3	3	5.1	35	62.0	—

2) rivers; 3) protecting, hiding, etc. 4) not protecting
 5) pelagophilous and semi-pelagophilous; 6) psammophilous;
 7) lithophilous, phytophilous; 8) unknown; 9) absolute number; 10) Amur River; 11) Volga River.

As was already indicated, the pelagophilous species came to the Amur River from the rivers of China. They are all, except for the Siniperca, of freshwater origin and all their adaptations associated with development in a pelagic state evolved under the influence of conditions prevailing

in the rivers of south-eastern Asia. They all permanently inhabit rivers and never leave them to go to sea.

In the Amur River the known composition at present is about 27% pelagophilous fish species, 25% species which protect and hide their eggs and 35% psammophilous, lithophilous and phytophilous species which do not protect their eggs (Table 70). However, when all ecological groups are considered separately the largest, by number of species, is the pelagophilous group (probably more than 20 species), followed by the group of fish which protect their eggs (10 species), in third place--the lithophilous group (9 species) and then the psammophilous group, and others (Table 71).

Thus, in the Amur River and probably in the rivers of China, the pelagophilous species and the species which hide and protect their eggs dominate. In contrast, representatives of other ecological groups which do not protect their eggs, are relatively few (36.9%).

Such a species ratio within various ecological groups indicates that the environmental conditions in the Amur River (and in the rivers of China) are not favorable for reproduction of lithophilous and phytophilous fish species which do not protect their eggs. The lithophilous species are harmed by the abundance of gudgeons which destroy their eggs. In order to survive, one of them, the Chinese chebachok, is forced to deposit its eggs at lake effluents, in early spring, before the return of the gudgeons which

leave these areas for winter. Another species--the Lagovskii minnow, spawn in small, cold brooks not inhabited by gudgeons.

Table 71

(260)

1) Absolute numbers of species in the ecological groups which inhabit the Amur and Volga rivers.

Таблица 71

1 Абсолютные количества видов рыб в главных экологических группах Амура и Волги

4 Реки	2 Не охраняющие						3 Причущие		11	12	13
	5 литофиль- ные	6 фитофиль- ные	7 индифе- рентные	8 пелагофиль- ные	9 полупелаго- фильные	10 псаммофиль- ные	5 литофиль- ные	6 острано- фильные	Охраняющие	Вынашивающие	Неизвестные
14 Амур . . .	9	8	—	20	3	9	6	3	10	—	7
15 Волга . . .	18	14	4	4	2	3	3	1	9	1	—

2) do not protect; 3) hide; 4) rivers 5) lithophilous; 6) phytophilous; 7) indifferent; 8) pelagophilous; 9) semi-pelagophilous; 10) psammophilous; 11) with parental protection; 12) carry their offspring; 13) unknown; 14) Amur; 15) Volga.

Additional difficulties for the phytophilous species arise from insufficient flooding of meadows and from the peculiar inconsistency of spring flooding in the Amur River. In contrast to our other rivers, the spring floods in the Amur River are often so insignificant that they do not flood the grass and consequently the phytophilous species do not have places to spawn, and are forced to wait until the summer floods in June which are caused by rainfall. However,

according to M. M. Sleptsov's observations, in some years with little rain, the phytophilous species even have to wait until August, because only then does the water reach the necessary level. This inconsistency in spawning conditions makes the proliferation of phytophilous species very difficult because it upsets the process of ripening and the time of release of the sexual products. In these conditions our phytophilous fish species would become extinct because their sexual products are resorbed, if they are not released on time.

In the environment of the Amur River and rivers of south-eastern Asia, the creation of pelagic eggs and the adaptations associated with them, freed the fish from the destructive difficulties which beset the lithophilous and phytophilous species because for the most part, the pelagic eggs are not destroyed by any predators and their release is not dependent on the nature and variations of floods.

In contrast to the Amur River, the lithophils, phytophils and other fish which do not protect their eggs predominate in European rivers. In the Volga River which has the highest number of species, for instance, they represent 70% (not counting the pelagophilous fish). The species which protect or hide their eggs are second (22%) and the pelagophilous species occupy last place (6.8%) (Table 70). Among the ecological groups, the lithophilous group ranks first (18 species, Table 71) followed by the

phytophilous group (14 species) and others. The pelagophilous group is only in fourth place (4 species).

However, with the exception of the catfish which protects its eggs and the chekhon which deposits its eggs in the water column, both undoubtedly of freshwater origin, all other egg protecting species and river pelagophils (Syngnathiadae, Gobiidae, Cottidae, Clupeidae) have penetrated European rivers by coming from the sea. The pertinent adaptations associated with development were acquired by these species when they were still inhabitants of the sea where conditions favor the species which protect their eggs and pelagophilous species. After migration into fresh water they simply preserved the adaptations acquired in the sea. However, the environmental conditions in European rivers, unlike the conditions in the rivers of south-eastern Asia, are adequate for the lithophilous and phytophilous species which do not protect their eggs. Here they are not required to migrate into the pelagic zone for reproduction or to create more complex forms of care for their offspring. (261) One such favorable factor for the lithophilous fish is the absence of such dangerous predators as the gudgeons (the European rivers are not inhabited by more than one or two species of gudgeons); for the phytophilous species a favorable factor is the regular spring flooding which covers vast areas of meadows suitable for their reproduction. Therefore in European rivers, in contrast to the rivers of

south-eastern Asia, not a single pelagophilous species evolved. The chekhon, as was mentioned before, is a semi-diadromous fish and is not a typical river fish. Like the pelagophilous herrings it is also associated with the sea. Apparently this also determined the nature of its reproduction.

The differences in origin of the European and the south-east Asian pelagophilous species are shown in Tables 69 and 72.

Table 72

1) Faunal components of the freshwater group of pelagophilous (and semi-pelagophilous) fish species.

Таблица 72

1 Фаунистические компоненты групп пресноводных пелагофильных (и полупелагофильных) рыб

3 Водоемы	2 Фаунистические компоненты пелагофильной (и полупелагофильной) группы пресноводных рыб (абсолютное количество видов)				
	4 понто-каспийская чехонь	5 понто-каспийские Clupeidae	6 арктические Osmeridae	7 восточноазиатские	
				Cyprinidae	Serranidae
8 Нева	1	—	1	—	—
9 Волга	1	3	—	—	—
10 Дон	1	2	—	—	—
11 Днепр	1	2	—	—	—
12 Дунай	1	1	—	—	—
13 Кубань	1	—	—	—	—
14 Озера Абрау и Чархал	—	2	—	—	—
15 Европейские водоемы СССР, вместе взятые	1	8	1	—	—
16 Амур	—	—	2	19	1

2) faunal components of the pelagophilous (and semi-pelagophilous) group of freshwater fish species (absolute number of species); 3) bodies of water; 4) Ponto-Caspian chekhon; 5) Ponto-Caspian Clupeidae; 6) Arctic Osmeridae; 7) eastern China; 8) Neva River; 9) Volga River; 10) Don River; 11) Dniepr River; 12) Danube; 13) Kuban River, 14) Lakes Abrau and Charkhal; 15) European and U.S.S.R. bodies of water taken together; 16) Amur River.

The spawning of pelagophilous and semi-pelagophilous species, as was already stated, does not depend directly on the height of floods, but is linked to certain temperature conditions. The smelt, a fish of nordic origin which inhabits mainly northern water reservoirs, releases its eggs at the lowest temperatures. According to the observations of S. G. Soin, even in the warm Amur River the smelt spawns in spring (in April and May) when the temperature remains from 3 to 12C. In contrast to typical pelagophilous fish species, the smelt first attaches its eggs to stones and plants, like the lithophils do. A few days after spawning the eggs become detached from the stones and are carried by the current. Therefore, in the Amur River environment, the smelt, like the lithophilous Amur ide, releases its eggs only in early spring and in the sources of oxygen deficient lakes which are abandoned by the gudgeons during winter. The gudgeons return in spring but only when the water temperature is high enough. Apparently this association of Amur smelt with low temperatures and with definite spawning grounds saves its egg from destruction by predators. The attachment of the eggs for few days, which develop at a low temperature (development is greatly retarded), considerably shortens the distance that the embryos will float downstream (as compared with the distance they would float downstream if they developed in unattached eggs) and prevents them from being carried into the open sea prematurely (the currents of the Amur River can carry the eggs downstream 120 km or more in 24 hours).

The typical European pelagophilous fish species spawn at higher temperatures than the smelt; the chekhon and clupeids begin to spawn about mid-May, at a temperature of approximately 18 C. The spawning of the chekhon continues (262) for about 1.5 months. The spawning of some Volga clupeids extends to the beginning of July, when the water temperature reaches more than 20 C.

The Abrau sprat spawns in summer, at least until mid August, when the temperature is about 22 C.

The pelagophilous species of the Amur River reproduce at similar and even higher temperatures. Their spawning begins at the end of May (about May 24th) and lasts until the end of July. The water temperature during this period rises from 11 to 26 C. Most of the fish release their eggs when the temperature is from 18 to 24 C. The confinement of spawning to high temperatures considerably shortens the distance that the eggs and embryos travel ^{passively} downstream. Thus, for instance, the pelagophilous gudgeons, belonging to the group Armatogobionina, in three days, at a temperature of 24 C, reach the stage of development at which they are capable of reaching the bottom and resisting being carried further downstream by the current. During this period of time they may be carried downstream from the place of spawning for a distance of about 360 km. If development took place at 18 C, they would only reach a corresponding stage on about the sixth day and would already have been carried downstream for

some 720 km. At even lower temperatures the embryos would be carried downstream some 1,000 km or more. For the pelagophilous Amur fish, which do not go to sea, the shortening of the development period and the downstream drift of eggs, because of the confinement of spawning to a high temperature, results in the protection of the embryos from being carried out to sea and shortens the distance of the return migration of the young fish upstream.

The duration of the spawning periods vary with species. Some species (vostrobriushka, lazy gudgeon) spawn intermittently for 1.5 months, others (blackbelly) for only a few days. The principles which would explain these differences have not been developed as yet.

The locations where pelagophilous fish release their eggs are varied. The European pelagophilous fish forage in the sea and ascend the rivers ^{for} various distances: some spawn in the mouth of the river or somewhat higher (chekhon, Don River herring and others) while others, such as the Volga herrings, ascend the river for many hundreds of kilometers. The Amur River aboriginal fish species also perform upstream migrations, but the length of these migrations is not known as yet. Numerous species (vostrobriushka, Dabri gudgeon, lazy gudgeon and others) migrate only very short distances. Apparently however, even then their offspring, which have been carried downstream by the current, must ascend the river for hundreds of kilometers in order to return to the spawning area and the permanent habitat of adult fish. The lower spawning boundaries of pelagophilous fish in Amur River are not known.

Undoubtedly these places must be hundreds of kilometers above the mouth of the river. The lower limit of how far the eggs, embryos and larvae may be carried downstream, without being harmed, has not been established either.

The size of the eggs of pelagophilous fish species, and consequently their relative fecundity, is very varied. One of them, the eight whiskered gudgeon, releases eggs 0.55 mm in diameter, i.e. the smallest known among our freshwater fish in general; the other species (lazy gudgeon) release eggs which are three or four times larger, i.e. about 1.9 mm in diameter. The majority of the other species have eggs that vary in size from 0.9 to 1.2 mm. These differences in egg size reflect the varied fecundity of the pelagophilous fish species, i.e. indicates that some of these species are relatively and exceptionally productive while others, just the opposite, are four times less productive. The described variations in fecundity and egg size distinguish the pelagophilous fish from the fish of other ecological groups, the latter, in this respect, are very uniform. The low productive lazy gudgeon produces large eggs (up to 1.9 mm) and thus, in this respect, approaches the lithophilous Barbini; the moderately productive pelagophilous species with an egg size (263) of approximately 1.2 mm, correspond to the lithophilous Leuciscini; highly productive pelagophilous species, the egg size of which is from 0.9 to 1 mm, correspond to the phytophilous

fish species and the unusually productive species, like Gobiobotia, which have the smallest eggs are found exclusively in the pelagophilous group.

Such a great diversity in the egg sizes of pelagophilous fish species indicates, that few of their floating eggs are destroyed by predators and that mortality, which determines the differences in their productivity, occurs mainly in the larval and other, later stages of their life cycle.

The buoyancy of the eggs, i.e. their decreased specific gravity, compared to that of demersal eggs, is achieved by various differences in their structure. In the majority of pelagophilous cyprinids, large quantities of water penetrate through the membrane of the released eggs decreasing their specific gravity. At the same time the membrane becomes greatly distended, (its diameter, in some species, reaches 5 mm or more; Table 73), forming a very large perivitteline space (Fig. 89, A-B). If in the demersal eggs the relative perivitteline space is often completely absent or relatively small (Fig. 89 D) i.e. it is not larger than 1.5, then in the pelagic eggs, its relative size is from 2 to 4 (Table 73; the relative size of the perivitteline space is the ratio of the diameter of the egg membrane to the diameter of the yolk sac). In a few fish species (Paralencogobio, Gobiobotia) egg buoyancy is achieved by their extremely swollen, tender and watery mucous membrane.

Table 73

1) Comparison of pelagic and demersal eggs*).

Таблица 73

1 Сравнение пелагических и донных яиц

2 Название рыбы	3 Диаметр оболочки яйца	4 Толщина слизисто- го слоя оболочки	5 Диаметр яйца без оболочки	6 Относительный размер перивит- телино- вого про- странства	7 Жировая капля	8 Экологи- ческие группы
	9 (в миллиметрах)					
1. <i>Pelecus cultratus</i>	5.0	10 Нет	1.2—1.5	3.3	10 Нет	13 пелагофильные
2. <i>Sarcophilichthys sinensis lacustris</i>	5.3	»	1.8—2.0	2.65	»	
3. <i>Xenocypris macrolepis</i>	3.5—4.1	»	1.15—1.2	3.4	»	
4. <i>Hemiculter leucisculus</i>	2.9—3.0	»	0.9	3.3	»	
5. <i>Armatogobio dabryi</i>	2.3—2.9	»	0.9—1.0	2.9	»	
6. <i>Rostrogobio amurensis</i>	2.8—3.05	»	0.8 (?)	3.8	»	
7. <i>Paraleucogobio soldatovi</i>	3.4—4.25	0.6—1.15	Около 1	2.2	»	
8. <i>Gobiichthys</i> sp.	2.5—3.3	0.6—0.8	0.55—0.6	1.7	12 Имеется большая	
9. <i>Siniperca chuatsi</i>	2.05	10 Нет	?	11 Мало		
10. <i>Leuciscus waleckii</i>	2.15	»	1.4	1.5	10 Нет	14 Лито- фильные псаммо- фильные
11. <i>Gnathopogon ussuriensis</i>	1.2	»	0.8	1.5	»	

* Пелагические яйца отличаются от донных тем, что имеют большее перивиттелиновое пространство (№ 1—6), или толстый слизистый слой оболочки (№ 7—8), или большую жировую каплю (№ 9).

2) fish names; 3) diameter of the egg membrane; 4) thickness of the mucous membrane; 5) diameter of the egg without the membrane; 6) the relative size of the perivitteline space; 7) oil droplet; 8) ecological groups; 9) in millimeters; 10) absent; 11) little; 12) a large drop is present; 13) pelagophilous; 14) lithophilous, psammophilous.

*) The pelagic eggs differ from the demersal eggs in that they have a larger perivitteline space (No. 1 to 6), or a thick mucous layer on the membrane (No. 7 and 8), or a large droplet of oil (No. 9).

Consequently, in such cases, the perivitteline space is relatively small (Fig. 89, E-F). In addition to the modifications of the egg membranes just described, in pelagic

eggs of many fish species (vostrobriushka and others), the consistency of the egg yolk is modified: it is very transparent, i.e. it obviously contains more water, and therefore is lighter than the yolk of demersal eggs.

The yolk of pelagophilous clupeids is particularly watery: it contains more than 90% water (while the water content of the yolk of benthonic fish species is below 70%). For this reason the perivitteline space in their eggs is not as large as that in the pelagophilous cyprinids however it is larger than in clupeids which reproduce in the sea. The yolk sac of Siniperca contains a very large oil droplet, which decreases the specific gravity of the eggs, while the perivitteline space is correspondingly negligible (Fig. 89G). The eggs of smelt also contain a large amount of oil and in addition, when the egg detaches from the substratum the membrane slides off in such a manner that an auxiliary flotation surface is formed and makes surfacing of the eggs easier. The perivitteline space in these eggs therefore is also insignificant (Fig. 89H). (264) (265)

Lightened by one or other of the methods just described, the eggs nevertheless sink to the bottom in completely still water. However, they are lifted by the slightest current or ripple and become buoyant again .

The eggs of all pelagophilous fish, in contrast to the demersal eggs of other fish are usually either completely or almost devoid of pigment and are colorless. Because the

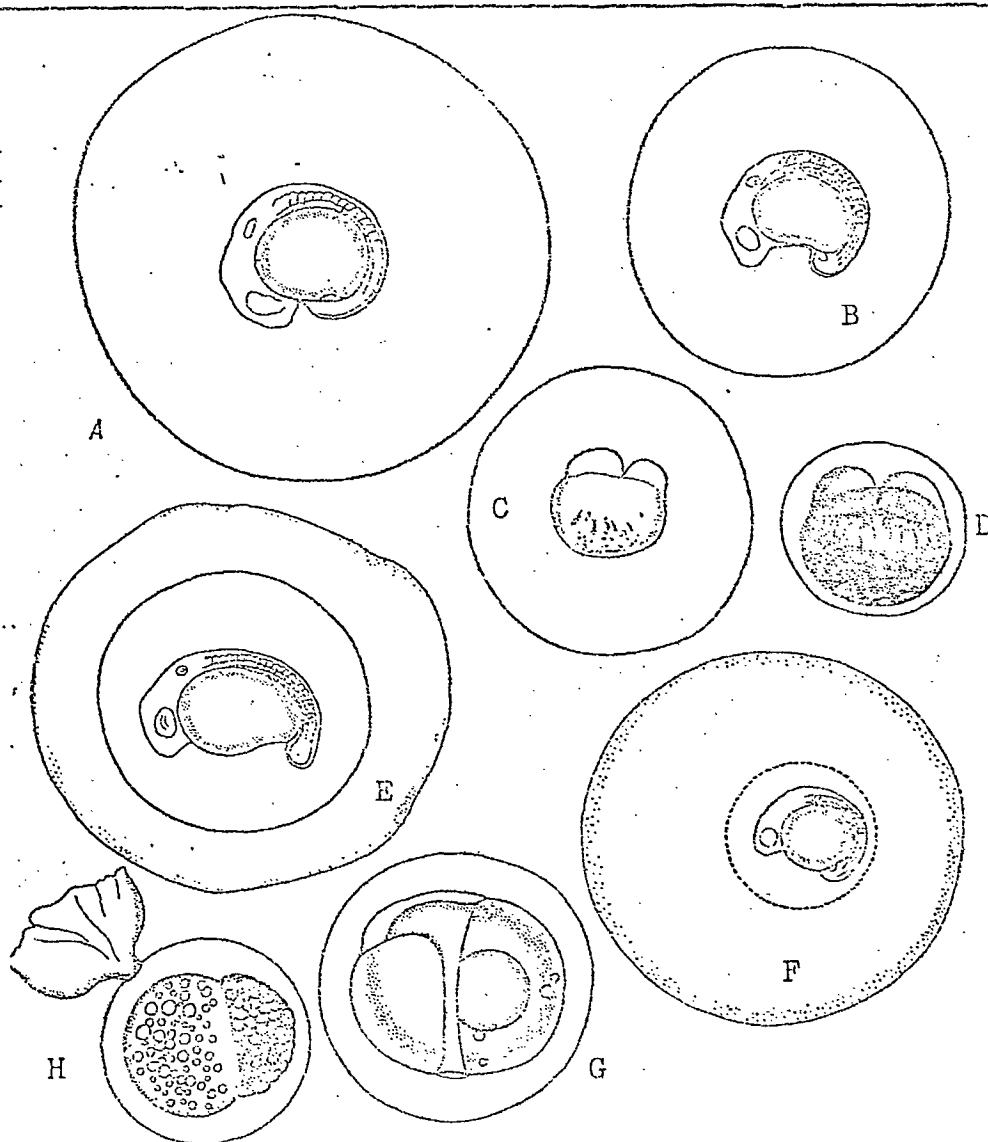


Рис. 89. Яйца пелагофильных и фитофильной (H) рыб в оболочках.

A — *Xenocypris macrolepis*, B — *Hemiculter leucisculus*, B — *Armatogobio dabryi*, Г — *Carassius carassius*, Д — *Paraleucogobio soldatovi*, E — *Gobiobotia* sp., Ж — *Siniperca chuatsi*. Пластушка поддерживается большой жировой каплей; перивителлиновая камера незначительная. З — *Hypomesus olidus*.

Fig. 89. Eggs of pelagophilous and phytophilous (D) fish with their membranes.

A- *Xenocypris macrolepis*; B-*Hemiculter leucisculus*;
C-*Armatogobio dabryi*; D-*Carassius carassius*;
E-*Paraleucogobio soldatovi*; F-*Gobiobotia* sp.;
G-*Siniperca chuatsi*; Buoyancy is maintained by a
large oil droplet; the perivitelline space is
negligible; H-*Hypomesus olidus*.

yellow and red pigments participate in the processes of oxidation, their regular absence in pelagic eggs reflects their basic physiological properties and apparently is explained by the fact that the eggs develop in the most favorable, and moreover, constant conditions of aeration.

The constancy of these conditions is explained by the fact that eggs carried by the current are not subjected to diurnal or any other fluctuations in the gaseous state which may appear because of the interruption of the photosynthetic activities of plants during the night and by other factors which often result in the complete disappearance of oxygen in stagnant waters, in densely overgrown areas and at the bottom.

The experiments performed by Loeb on the respiration of pelagic eggs of marine fish showed that physiologically they are so narrowly adapted to the most favorable conditions of aeration, that in cases of oxygen deficiency they perish considerably sooner than demersal eggs.

In contrast to the pelagic eggs, the demersal eggs are usually colored and their color becomes more intense with worsening of the external conditions of respiration in which they are developing. The eggs of phytophilous fish are usually deeper yellow than those of the lithophilous species; the eggs of the catfish which develop in small burrows made in the earth--are completely yellow. The eggs of salmonids, which are buried in the ground, are yellow-orange;

the eggs of blennies (Bleniidae), which develop under stones, are lilac in color.

The peculiar conditions of pelagic development described not only determine the absence of pigment in pelagic eggs but also strictly regulate their whole development by causing regular changes in the respiratory system and the organ systems linked with respiration.

These conditions are the ones that cause the gradual degeneration of the embryonic respiratory organs and retard the appearance of erythrocytes and gills. However, the intensity of the manifestation of these two processes, the degeneration and the retardation, varies with the species. The large eggs and large embryos emerging from them have relatively smaller external body surfaces for oxygen absorption than the small ones. Therefore, in the same water, the respiratory conditions are different for each of them; this environment is more favorable for the smaller organisms than it is for the large ones. For this reason the degree of degeneration of the embryonic respiratory organs and retardation of the appearance of erythrocytes and gills, increases with a decrease in the size of the eggs and embryos developing from them.

The embryos of pelagophilous cyprinids first use the ducts of Cuvier for respiration. Initially the ducts are, for a certain period of time, enlarged and have long vessels embracing the anterior part of the yolk sac (Fig. 90, A-B). To provide enough space for their length, the

anterior section of the yolk sac where they are located is usually very enlarged. In addition to the ducts, respiratory functions are also carried out temporarily by the lower caudal vein which descends into the anal fin fold where it forms convolutions thus enlarging its respiratory surface. Later the dorsal fin fold, in which seven segmentary vessels are formed is added to this system (Fig. 90 B); in the Barbini, besides these systems, subintestinal veins forming a respiratory network on the surface of the yolk sac also appear (Fig. 85 A). The vessels are filled with erythrocytes at an early stage and the embryonic respiratory system begins to function as soon as the process of body segmentation is completed or even before this.

In pelagophilous fish, such as the chekhon and the (266) lazy gudgeon, which develop from the largest eggs (the diameter of the chekhon egg is 1.2 to 1.3 mm and that of the lazy gudgeon is 1.6 to 1.9 mm) the embryonic respiratory organs are present and they are partially formed by the same vessels as those in the non-pelagophilous fish species, i.e. the ducts of Cuvier on the yolk sac, the lower caudal vein and the anal fin fold. However, in the chekhon, the ducts of Cuvier are not as long, and the anterior part of the yolk sac is accordingly less enlarged than in the non-pelagophilous species, while the lower caudal vein is narrow and not convoluted. The respiratory vascular network in the dorsal fin fold, which is so typical of the embryos of

non-pelagophilous species, is completely absent in the chekhon. The development of erythrocytes in the chekhon is retarded but not significantly. Thus, under the developmental conditions in the pelagic state, the chekhon has lost the respiratory network of the dorsal fin fold which is typically present in the related ^{non-}pelagophilous Leuciscini, and it has also reduced the respiratory surface of the ducts of Cuvier and lower caudal vein, as well as in the dorsal fin fold.

The lazy gudgeon, as stated previously, has embryonic respiratory organs identical to those of the chekhon. The development of erythrocytes in the chekhon may be slightly retarded, however in comparison with the related psammophilous gudgeons, the respiratory system in the lazy gudgeon has not suffered any modifications for the most part. Neglecting some assumed differences in the time of appearance of erythrocytes and the somewhat more accentuated convolution of the lower caudal vein, the respiratory system in all fish is identical. This is explained by the fact that the eggs and embryos of the lazy gudgeon are more than twice as large as those of the psammophilous gudgeons (the diameters of the gudgeon eggs are from 0.8 to 0.9 mm), and that the latter also develop in good conditions of aeration (in currents).

Only the lazy gudgeon and the chekhon, among all the pelagophilous species have changed, as described, so insignificantly. In all other pelagophilous cyprinids, and

in all other fish species, degeneration of the embryonic respiratory system has progressed much further. The degree of degeneration becomes more pronounced when the eggs become smaller. In some of the pelagophils (Paraleucogobio, Amatogobio), the ducts of Cuvier are so narrow that the erythrocytes can fit in the duct only in single file; moreover they are very shortened and therefore the anterior part of the yolk sac is hardly enlarged (Fig. 90 B). In other species (vostrobriushka, eight whiskered gudgeon), the ducts of Cuvier are completely displaced from the yolk sac and shortened to the limit, i.e. they are not visible on the yolk sac and do not have a respiratory function (Fig. 90 D, E). The lower caudal ^{which} vein is narrow, straight and barely descends into the anal fin fold, has also lost its respiratory function. The erythrocytes appear very late--one to three days after the process of body segmentation is completed. They appear in small numbers and for a long time they do not fill the vessels but pass through them one by one and with a large distance between (in the eight whiskered gudgeon, even at the end of the embryonic period). In non-pelagophilous fish species the vessels are filled with erythrocytes from the very beginning (compare Fig. 90 A and E).

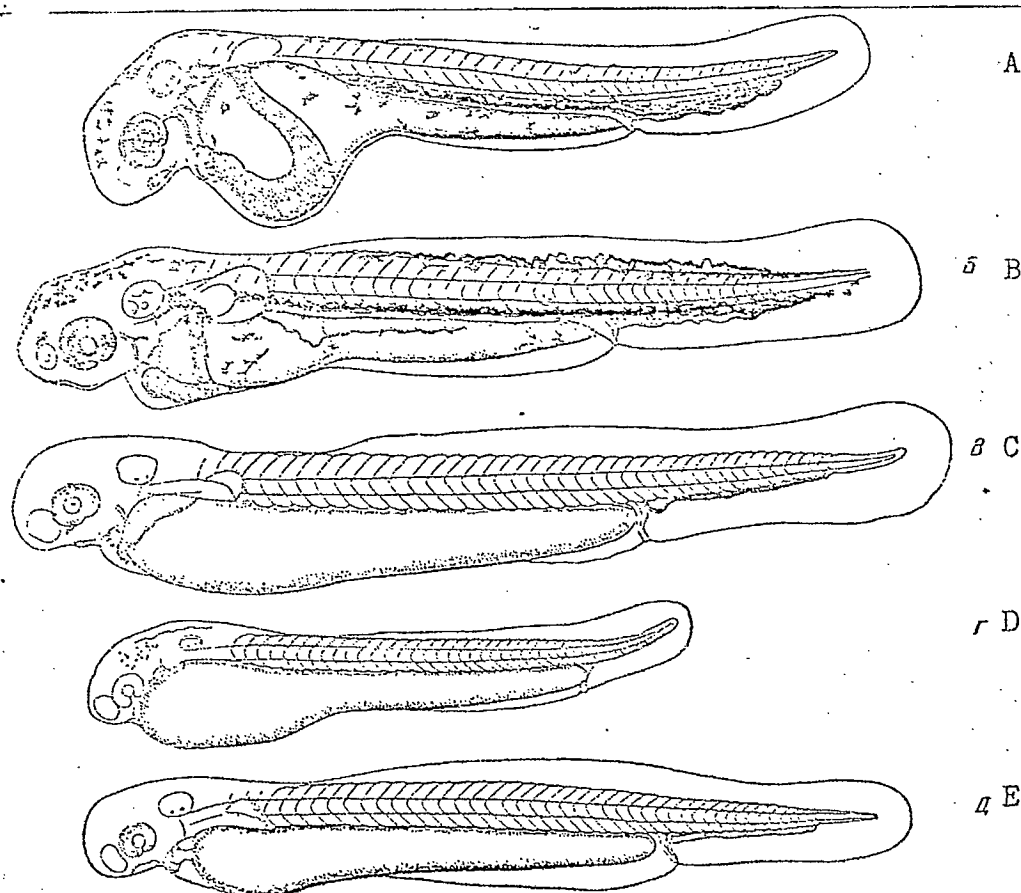
The development of gills is retarded in accordance with the described processes. While in the lazy gudgeon and the chekhon the rudiments of gill arches appear during the embryonic period (like in non-pelagophilous fish species),

in the *vostrobriushka*, which has completely lost its embryonic respiratory organs, and in *Paraleucogobio soldatovi*, the gill filaments are barely visible at the beginning of the larval period (Fig. 93 B) and in the eight-whiskered gudgeon and in other fish species at the same stages they are completely absent (Fig. 93, D-E).

In the pelagophilous herrings degeneration of the respiratory system has reached extreme limits. Not only do their embryos have no respiratory organs but also for a long time the larvae have no gill filaments (Fig 100, E, D), and erythrocytes are missing for even longer periods--the vessels (267) become filled with them only when the larvae reach a length of 30 mm (?). However in herring species in the early developmental stages, close to the completion of the segmentation process when the heart begins to beat, as is typical in non-pelagophilous species, the erythrocytes do appear but in small numbers and they soon disappear. A very long period of time elapses from the moment of their disappearance in the embryos to their second appearance at a late larval stage, when they again fill the vessels. The biological significance of this peculiar and interesting phenomenon, which differentiates the pelagophilous clupeids (all of them?) from the pelagophilous cyprinids and from the non-pelagophilous species is not understood as yet.

In the smelt species, like the clupeids, the embryonic respiratory system is completely absent and the development of gills and erythrocytes occurs very late. The larvae have

neither of them. It is not known if they have primary production of a few erythrocytes, such as is observed in clupeids.



Ггз. 90. Сравнение эмбриональных органов дыхания фитофильной (А—В) и пелагофильных рыб (В—Д).

А — эмбрион *Cyprinus carpio*. Кювьеровы протоки преобладают, длинные, широкие. Желточный мешок соответственно спереди расширен. В — он же, немного старше; большая дыхательная сеть в спинной и анальной плавничковых складках и на желточном мешке. В — *Paraleucogobio soldatovi*. Кювьеровы протоки очень узкие и короткие; других органов дыхания нет. Всплывших кровяных клеток мало. Г — Д — *Hemiculter leucisculus*. Кювьеровы протоки укорочены до предельно; их не видно сбоку желточного мешка. Эритроциты единичные. Желточный мешок спереди мало расширен.

Fig. 90. Comparison of the embryonic respiratory organs of phytophilous (A-B) and pelagophilous (C-D) fish species.

A-embryo of *Cyprinus carpio*. The ducts of Cuvier predominate, they are long and wide. The anterior part of the yolk sac is correspondingly enlarged. B-the same embryo, a little older; large respiratory network of vessels occur in the dorsal and anal fin folds and on the surface of the yolk sac.

C-*Paraleucogobio soldatovi*. The ducts of Cuvier are very narrow and short; there are no other respiratory organs. The vessels contain little blood.

D-E: *Hemiculter leucisculus*. The ducts of Cuvier are extremely short; they are not noticeable on the side of the yolk sac. Only single erythrocytes are observed. The anterior part of the yolk sac is only slightly enlarged.

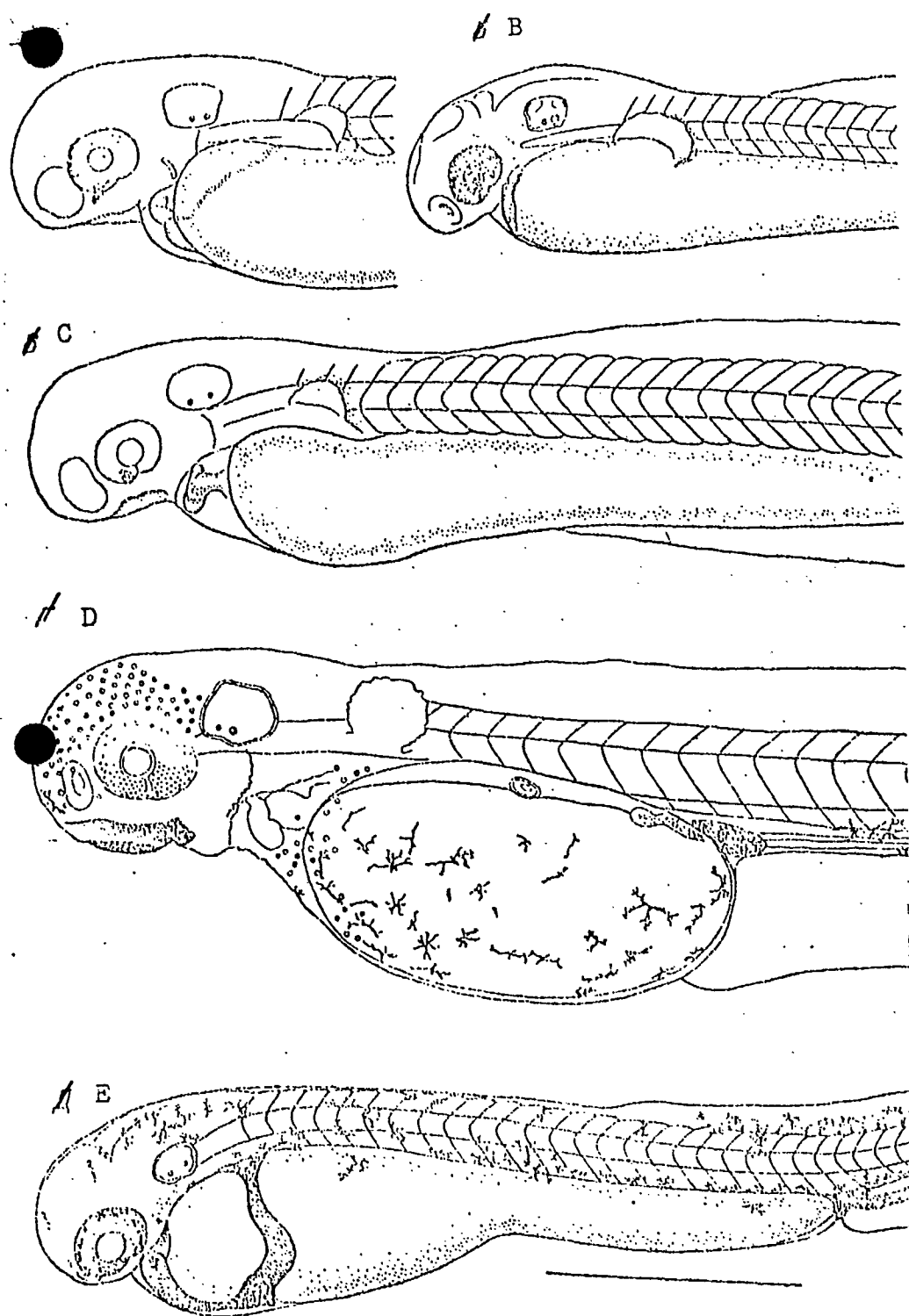


Рис. 91. Цветные пигменты в глазах и в области продолговатого мозга
 А — *Paraleucogobio soldatovi*, Б — *Rostrogobio amurensis* (по С. В. Соколову),
 В — *Hemiculler leucisculus*, Г — *Caspialosa volgensis*, Д — желтый пигмент на теле эмбриона фитофильной рыбы *Phoxinus*

Fig. 91. Colored pigments in the eyes and in the region of the medulla oblongata of pelagophilous fish embryos.

A-*Paraleucogobio soldatovi*; B-*Rostrogobio amurensis* (S.G. Sonin's data); C-*Hemiculler leucisculus*; D-*Caspialosa volgensis*; E-the yellow pigment on the body of the embryo of the phytophil *Phoxinus perenurus mantschuricus* (A. I. Smirnov's data).

The loss of the embryonic respiratory system and the (268) delayed appearance of erythrocytes, are accompanied by peculiar changes in pigment development in the eyes and head, but this is typical only of pelagophilous species. In all fish species, the embryos of which have respiratory organs and an early appearance of erythrocytes, the eyes become uniformly covered with black pigment only (Fig. 91, E); the guanine appears later. The pigment develops in the eyes of the chekhon and lazy gudgeon, the embryonic respiratory systems of which are only slightly weakened in this manner: their eyes become gradually and uniformly covered with melanin over the whole surface while guanine appears in the eyes later. In the eyes of all other pelagophilous cyprinids with very weak embryonic respiratory systems or which have lost them completely, the melanin appears first as a small black spot in the lower part of the eye, apparently in the region of the optic nerve (Fig. 91, A-B), then the amount of pigment increases, settling either in the anterior or ventral part of the eye. The melanin does not develop in the posterior part of the eye for a long time. However, almost simultaneously with the appearance of the black spot, a more or less intensive deposition of yellow pigment takes place in the remaining areas of the eye (vostrobriushka, clupeids; Fig. 91, B, D); in the blackbelly and eight whiskered gudgeon this pigment is brown and in the Paraleucogobio it is red (Fig. 91, A). Moreover, in some species (Gobiobotia, Rostrobio), the red pigment appears behind the eyes, in the region of the medulla oblongata (Fig. 91, B). Later, the eyes

of all these fish species are uniformly covered with black pigment and guanine. It is not known if the yellow and other pigments are also preserved. As yet it is not clear what the biological significance is for the initial spot-like distribution of the black pigment in a certain sector of the eye, the early appearance of the yellow, brown and red pigments in the eyes or the pigmentation in the region of the medulla oblongata. However it is beyond any doubt that all these peculiarities are characteristic only of the pelagophilous fish species and that they are linked to a certain degree of degeneration of the embryonic respiratory system and the delayed appearance of erythrocytes, and that they are linked to some functional requirements of the eyes, due to the described changes in the respiratory and blood circulatory systems.

The body pigmentation in pelagophilous species also develops in a somewhat different manner than in fish of other ecological groups. The differences concern mainly the time of the beginning of pigmentation, its intensity and its distribution. In the embryos and young larvae of pelagophilous fish, melanin is mainly distributed within a single band, stretching along the body cavity and in the tail--along the caudal vein (Fig. 93, A,B, and Fig. 100 E). Such a band exists in embryos of other ecological groups, however in this case the pigmentation is more intense. In pelagophilous fish, in contrast to other fish, for a long time there are no melanophores on the back or the sides or they are very scarce. The delayed appearance of melanin in these body parts is illustrated in Table 74.

The presence of a single ventral band of pigmentation, containing few melanophores, is typical for embryos of lithophilous and phytophilous fish groups (vostrobriushka, various gudgeons, clupeids, smelts; compare Figs. 87, 93 and 100). This indicates the ecological determination of the reduction of black pigmentation on the body of pelagophilous fish and its confinement, most often, to a single ventral band.

In contrast to all other pelagophilous fish, the clupeids at first acquire relatively abundant pigmentation on the yolk sac and the head (Fig. 91, D). However this pigmentation does not persist for a long period of time. For some time after its disappearance, the embryos and larvae of clupeids do not differ in any significant way from the embryos and larvae of pelagophilous cyprinids with respect to the location of the melanophores.

The cause of the peculiar pigmentation changes in clupeids is not known. (270)

The yellow body pigment in pelagophilous fish also appears considerably later than the body pigmentation in other species, particularly the phytophils (see Table 74). Moreover, the pigmentation of pelagophilous fish is considerably less intense than that of the embryos of phytophilous fish. The phytophils are conspicuously yellow while the embryos of pelagophils, at the same stage of development, are completely colorless (Fig. 91, B-E). This peculiarity of pelagophilous fish is possibly caused by the fact that they develop in the best possible conditions of aeration. Table 74 shows the main peculiarities of pigment development in pelagophilous fish which distinguish them from fish of other ecological groups.

Table 74

1) Time of appearance of pigment in the eyes and on the body of fish belonging to various ecological groups*).

Таблица 74

1 Сроки появления пигмента в глазах и на теле у рыб разных экологических групп *

2	8	9	14 Пигмент глаз			21 Пигмент тела						С
			15	16	17	22	23	24 меланофоры				С
								25	26	27	28	
Экологическая группа	Название рыбы	Крово-носная система	желтый	черное пятно	рассеянный черный	красный, позади глаз	желтый	дорзальный ряд	вентральный ряд	боковая линия	мозг	С
3	<i>Hemiculter leucisculus</i>	10 Редуцированная	18 3 1/2 суток	18 2 1/2 суток	18 4 суток	19 Нет	18 11 суток	18 7 суток	18 4 1/2 суток	29 Поздно	18 12 суток	20
	<i>Xenocypris macrolepis</i>	11 То же	3 »	2 »	4 »	»	Поздно 29	6 »	4 »	»	Поздно 29	20
	<i>Armatogobio dabryi</i>	»	3 »	2 »	4 »	»	4 суток 18	После 30	»	»	4 суток 18	—
	<i>Rostrigobio amurensis</i>	»	3 »	2 » (?)	3 »	2 суток 18	7 »	17 суток 18	»	»	4 » (?)	—
	<i>Gobiobotia sp.</i>	»	1 1/2 »	1 1/2 »	3 1/2 »	2 1/2 »	»	Поздно 28 1/2	»	»	После 30	—
	<i>Paraleucogobio soldatovi</i>	»	2 1/2 »	2 »	3 »	Нет 19	6 суток 18	(7 суток) 18	Поздно 28 1/2	»	7 суток 18	18
4	<i>Sarcochilichthys sinensis lucusiris</i>	12 Нормальная	19 Нет	19 Нет	3 »	»	Поздно 29	8 суток 18	4 »	»	8 суток 18	20
	<i>Acanthorhodeus asmusi</i>	13 Увеличенная	»	»	13 »	»	14 суток 18	14 »	14 »	Около 20	Поздно 29	22
5	<i>Carassius auratus gibelio</i>	То же 11	»	»	2 »	»	4 »	2 1/2 »	2 »	Поздно 29	»	22
	<i>Phoxinus phoxinus</i>	»	»	»	Около 20 4 суток 18	»	Около 20 4 суток 18	Около 20 4 суток 18	Около 20 4 суток 18	Около 20 5 суток 18	Около 20 5 суток 18	20
6	<i>Phoxinus lagowskii</i>	12 Нормальная	»	»	Около 20 6 суток 18	»	Около 20 9 суток 18	Около 20 6 суток 18	Около 20 5 суток 18	Около 20 5 суток 18	Около 20 5 суток 18	20
	<i>Hemibarbus maculatus</i>	11 То же	»	»	2 суток 18	»	6 суток 18	Поздно 29	4 суток 18	Поздно 29	5 суток 18	22

* Сроки указаны, считая с момента оплодотворения икры.

2) ecological groups; 3) pelagophilous; 4) ostracophilous; 5) phytophilous; 6) lithophilous; 7) psammophilous; 8) fish names; 9) blood circulatory system; 10) reduced; 11) same; 12) normal; 13) enlarged; 14) pigment in the eyes; 15) yellow; 16) black spot; 17) scattered, black; 18) days (24 hours); 19) none; 20) about; 21) body pigments; 22) red, behind the eyes; 23) yellow; 24) melanophores; 25) dorsal band; 26) ventral band; 27) lateral line; 28) brain; 29) late; 30) after.

*) The times are indicated from the moment of fertilization of the egg.

The rate of development of pelagophils is different in various ways from that in fish of other ecological groups. When developing at identical temperatures with fish of other ecological groups, most of them, apparently, finish the process of segmentation and formation of the body sooner. The yolk sac is resorbed sooner (this is probably due to its lesser density) and therefore the transition to larval period occurs sooner (Table 75; compare the *vostrobriushka* with fish of other ecological groups). Independent of their classification, a similar, accelerated rate of development is typical of pelagophils which develop from small eggs. In the chekhon and lazy gudgeon, which develop from larger eggs, the accelerated rate of development is not observed. In numerous pelagophilous fish the development of the swim bladder is retarded: in *vostrobriushka*, undermouth, clupeids and other species it becomes filled with air not at the beginning of the larval period of life, which begins like in all other fish slightly before the disappearance of the yolk, but a few days after its disappearance. Moreover, as indicated previously, in an overwhelming majority of pelagophils the appearance and development of body pigments, gills, erythrocytes and also the segmental vessels is greatly retarded.

Pelagophilous fish emerge from the egg membranes at various stages of development (Fig. 92). Some of them (*vostrobriushka*) emerge as soon as body segmentation is completed, i.e. at a very early stage--at an age of 24 hours; the majority of other species emerge considerably later--at

an age of 48 to 60 hours when the embryos already have large fin rudiments and pigment spots in their eyes. Finally, the lazy gudgeon emerges later than any other fish--at an age of 3 days. At this time its eyes are already black, there is pigmentation on the body, the pectoral fins are vertical etc. It is difficult to say exactly what causes these variations in the hatching time.

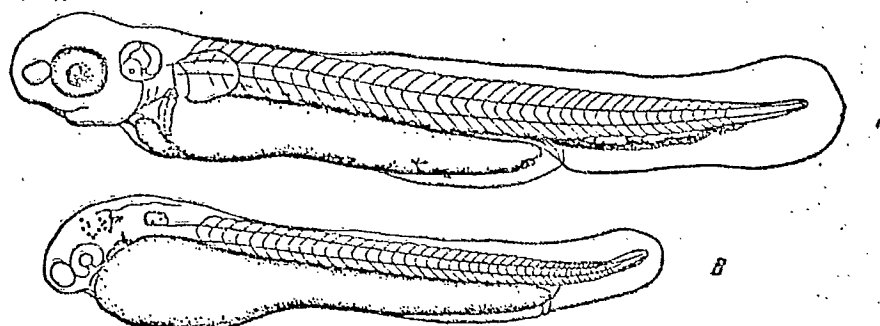


Рис. 92. Стадии вылупления пелагофильных рыб.
 А — *Sarcochilichthys sinensis lacustris*. Б — *Hemiculter leucisculus*

Fig. 92. Stages at which pelagophilous fish emerge from egg membranes.

A-*Sarcochilichtys sinensis lacustris*.
 B-*Hemiculter leucisculus*.

The very delayed hatching of the lazy gudgeon can apparently be explained because of the circumstance that its poorly developed embryos, burdened by a large quantity of yolk, would have greater difficulties in maintaining their buoyancy, than the early hatching, small embryos of other fish which easily maintain their buoyancy. The early hatching of the latter may possibly be explained by the necessity of ridding

I) Rate of development of fish belonging to various ecological groups.*)

Таблица 75

I Скорость развития рыб разных экологических групп

1 Экологические группы	5 Название рыбы	6 Величина яйца без оболочки (в мм)	7 Выклев из оболочки	8 Начинают плавать	9 Начало самостоятельного питания	10 Исчезновение всего желтка	11 Начало сегментации	12 Окончание сегментации	13 Начало кровообращения	14 Замещение грудных плавников	15 Появление желтого пигмента	16 Появление метаморфоз		19 Первые зачатки жаберных лепестков	20 Жаберная крышка закрывает жаберы	21 Наполнение водным пузырем
												17 в глазах	18 в покровах тела			
2 Псаммофильные	1. <i>Hemibarbus maculatus</i>	1.0	22 суток	22	22	22	22	22	22	22	22	22	22	22	22	22
3 Оптофильные	2. <i>Carassius auratus gibelio</i>	0.9	4-5 »	8 »	9 »	10 »	1 сутки 4 часа	2 »	2 »	3 »	4 »	2 »	2 »	6 »	9 »	8 »
4 Пелагофильные	3. <i>Hemiculter leuciscus</i>	0.9	22 1 сутки 4 часа	22 1 сутки 1 час	22 4 1/2 суток	22 4 1/2 суток	23 13 час. 30 мин.	22 1 сутки 1 час	(2 »)	2 »	(3 1/2 »)	(1 1/2 »)	(2 1/2 »)	(3 1/2 »)	25 После 11 суток	25 После 11 суток
			23	23			24	23							22	22

* Сроки указаны, считая от начала дробления. Развитие происходило приблизительно при одинаковой температуре — 22°. Жирными цифрами обозначены (подчеркнуты) ускоренно проходимые стадии развития, в скобках — замедленные.

1) ecological groups;
 2) psammophilous; 3) phytophilous; 4) pelagophilous; 5) fish names;
 6) egg size, without membrane (mm); 7) time of emergence from the membrane; 8) begin to swim; 9) beginning active feeding; 10) total disappearance of yolk; 11) beginning of segmentation; 12) end of segmentation; 13) beginning of blood circulation; 14) anlage of pectoral fins; 15) appearance of yellow pigment; 16) appearance of melanin; 17) in the eyes; 18) in the body integuments; 19) first rudiments of gill fringes; 20) covering the gills with the opercle; 21) filling of the swim bladder with air; 22) days (24 hours); 23) hours; 24) minutes; 25) after.

*) The times indicated are from the beginning of blastula formation. Development took place at approximately identical temperatures: 22 C; the bold figures are used to underline the accelerated developmental stages, in parenthesis--the retarded stages of development.

themselves of the unfavorable effects of the membrane on the respiratory process, which is already made difficult by the absence of respiratory organs and erythrocytes. The correctness of this assumption is indirectly confirmed by the behavior of pelagophilous embryos within the membrane. Even at very early developmental stages they begin to roll extremely energetically and frequently. The lazy gudgeon, for instance, at a stage of development when body segmentation is just completed (26 segments), but the tail bud is still completely unsegmented, completes about 107 turns per minute. Later, but still long before hatching, the embryos begin to struggle (272) very vigorously, calming only for short moments (embryos of fish of other ecological groups, possessing well developed respiratory systems turn within the membrane, but much less frequently, and they do not struggle.

After emerging from the egg membrane, the embryos of pelagophilous fish still remain extremely restless for a long time (a couple of days). They constantly swim towards the surface and if they again sink to the bottom, they immediately make a new attempt to surface. The embryos are photophilic and therefore, once emerged from their egg membranes, they do not remain on the bottom for any length of time but strive to be carried by the current, up to such time as they reach a stage of development which allows them to change this behavior. The embryos of cyprinids of the other ecological groups remain quiet after hatching. The lithophils are photophobic and lie on the bottom wedged

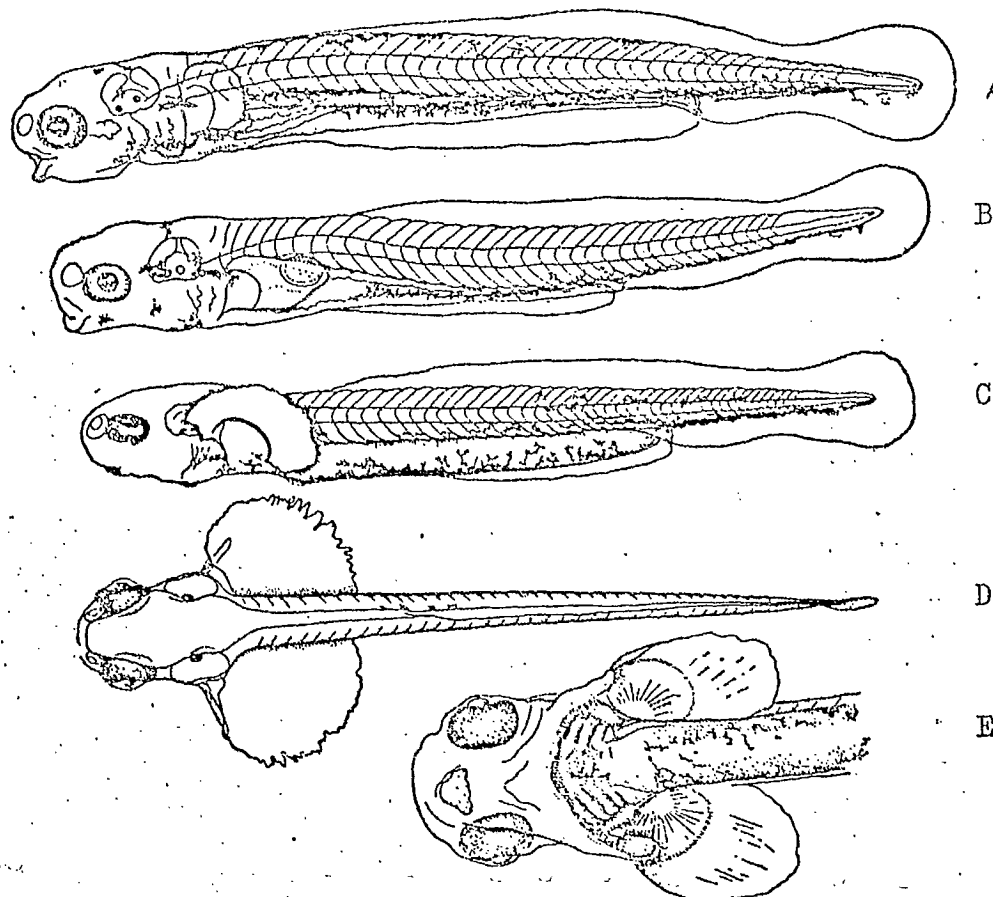


Рис. 93. Личинки пелагофильных рыб.

A — *Xenocypris macrolepis*. Б — *Paraleucogobio soldatovi*. В — *Armatogobio dabryi*. Г — *Rostrogobio amurensis* (сверху). Д — *Gobiobotia* sp. (снизу). Грудные плавники и жаберные крышки образуют присасывательную воронку

Fig. 93. Larvae of pelagophilous fish.

A--*Xenocypris microlepis*; B--*Paraleucogobio soldatovi*; C--*Armatogobio dabryi*; D--*Rostrogobio amurensis*, dorsal view; E--*Gobiobotia* sp. (ventral view); Pectoral fins and gill opercles form a suction funnel for attachment.

under stones; the phytophils are not photophobic and remain suspended and attached to plants or other objects.

With the transition to the larval period of life (or sometimes earlier), the pelagophilous fish undergo differentiation corresponding to the various ecological requirements. Many of them (Cultrinae, Fig. 93, A; Clupeidae,

Fig. 100 E), continue their typical pelagic way of life. Provided with a long, light body, they do not need the swim bladder for a long time and for this reason it remains unfilled with air for this period. The lazy gudgeon, whose body is short and heavy, fills its swim bladder with air long before resorption of the yolk sac is complete and remains close to the bottom among water plants.

The pelagophilous gudgeons begin their benthonic way of life even during the embryonic stage. Only one among them, the Paraleucogobio, is comparable with psammophilous gudgeons. It has long, narrow, vertically directed pectoral fins, which can be spread and used for support (Fig. 93, B). Armatogobina settle on the bottom and remain there using their huge gill opercles and wing like horizontal pectoral fins as a suction cup (Fig. 93, B-E). In contrast to larvae of other fish, the mouth of their larvae serves only for probing for food while water flows to the gills from behind, through the widely opened gill slits (Fig. 93, D).

On the whole, the group of fresh water pelagophilous fish is heterogeneous, as is the marine group. It is formed by representatives of various orders which have developed similar adaptations independent of each other. However, the pelagophilous clupeids and the semi pelagophilous smelt, within the limits of their families, are undoubtedly homogeneous. There is no doubt, that the Black Sea-Caspian Sea clupeids are so closely related that any assumption of parallel evolution of their basic, general, developmental adaptations

is excluded. The same holds for the smelts. In contrast, the pelagophilous cyprinids are extremely heterogeneous. There is no doubt that the chekhon evolved its adaptations independent of the Amur River cyprinids. Even within the latter, some subfamilies, groups and subgroups evolved pelagophilous species independently and parallelly. Thus, the adaptations of the pelagophilous vostrobriushka, grass carp and silver carp, not only have evolved independent of the adaptations of the gudgeons, but also even their own adaptations have no common origin. Within the subfamily of gudgeons, and even within one of its subgroups--the Armatogobionina, the individual pelagophilous forms also evolved parallel to each other: the lazy gudgeon became pelagophilous independent of the Armatogobionina; the Gobiobotia, which in many essential features of development is similar to the pelagophilous Armatogobio, became pelagophilous independent of the latter. This is indicated by differences in the means by which buoyancy of the eggs of these species is achieved (in some there is a large perivitelline space, in others, a thick mucous coating) and, inversely, by the similarity, in this regard, between the Gobiobotia and the distantly related Paraleucogobio. The abundance of parallelisms, i.e. the extraordinary heterogeneity of the pelagophilous cyprinid group in the Far East, for which there is no similar variety in any other family of fish nor in other bodies of water in the world, characterize the ecological peculiarity of the rivers in Far East Asia, which we have mentioned previously.

5. Ostracophilous group.

The bitterlings are the only members of this group and thus, genetically in contrast to all other groups, this is a completely homogeneous group. The species of this group (about 19) mainly inhabit the rivers of Korea and China. Three or four species (Rhodeus sericeus, Pseudoperilampus (?) sp., Archilognatus chankaensis and Acanthorhodeus asmusi) live in the Amur River while in European rivers there is only one--Rodeus amarus.

These fish lay their eggs in the mantle cavity of bivalves and their whole development is adapted to the life conditions in such a peculiar environment.

Bitterlings spawn in summer. In the Amur River (274) spawning lasts from mid May to mid July (maybe even longer) at temperatures from 12 to 24 C. The molluscs in which the eggs are deposited, provide reliable protection from all fish that prey on eggs (mainly gudgeons) thus insuring a high survival rate for the eggs. Consequently the fecundity of ostracophilous fish, in contrast to other species, is very low. Most of them probably deposit about 100 eggs or even less, and only one of them--the spiny bitterling--deposits about 300 eggs. The egg size varies with the species--from 1.1 to 2 mm in diameter, i.e. even the largest eggs are not larger than those of the lithophilous Barbini. However, unlike the Barbini and all other cyprinids, their eggs are either meso- or oligoplasmatic and not polyplasmatic,

i.e. the longest diameter of their eggs is 3 to 4.2 times longer than the height of the blastodisc, while in other fish this ratio equals 1 to 1.5 (see Table 21 and Fig. 19). This means that the eggs of the bitterlings contain 3 to 4 times more yolk, in relation to the plasmatic material, than the eggs of other cyprinids. Moreover the yolk of their eggs is so much more concentrated that at an identical egg size it lasts for almost twice as long a period of development (for 22 days, while in other fish only 10 to 13 days; see Table 21). This concentration of yolk prolonged for 10 to 12 days the embryonic period of life of bitterlings under the protection of mollusks and at the same time made it possible for them to begin their independent activities outside the mollusks at a considerably more advanced stage of development when compared with other fish species. If the latter begin to hunt for food at an age of 9 to 11 days, having only one section of the swim bladder, non differentiated, non paired fin folds devoid of skeletal rays, weak mouths etc., then the bitterlings at the beginning of their larval period, at an age of 23 days, have both sections of the swim bladder, the considerably differentiated fins have rays, the mouth is strong and the gill apparatus is developed etc. This difference in development from the very beginning puts the larvae of bitterlings into an advantageous position, because in hunting for food and avoiding enemies they are able to perform more varied and swifter movements. These advantages arising from development under the protection of the mollusc, predetermined

the previously mentioned low fecundity which distinguishes bitterlings from other cyprinids.

The high yolk concentration explains why the bitterling begins its independent life at such an advanced stage of development; it has also made organs of the early larval period (typically present in other species) superfluous in bitterlings and has influenced all stages of the bitterling's development.

Other fish species, as mentioned, begin their larval period of life at an age of 9 to 11 days, having only one chamber of the swim bladder filled with air (Figs. 87 and 93) and the large dorsal, anal and pre-anal unpaired fin folds are still without skeletons and muscular tissues which would perform locomotory functions. The pectoral fins are functional, the black eyes can distinguish objects, pigmentation of the integument is present, etc. Bitterlings at the same age still have very large amounts of yolk (Fig. 21, 25), are well protected by the molluscs and therefore do not require all these organs: the swim bladder fills with air only at an age of 23 days when it already has two chambers (Table 21); the pre-anal fin fold is still rudimentary (it will grow large only at an age of 22 days i.e. at the moment when the larvae emerge from the mollusc), while other fin folds are large only because they have respiratory functions; the pectoral fins are still very small (they appear only at an age of 14 days), the body integuments are not pigmented, there are no gill filaments etc., (see Table 21, which shows (275)

the variations in the length of the periods of development of ostracophilous fish in comparison with the periods of development of fish of other ecological groups).

In addition to these peculiar features of development, caused by the high concentration of yolk and late beginning of independant life, the bitterlings are characterized by a very peculiar adaptation to life within molluscs. Their eggs are not round like those of other fish but are elongated and oval shaped (Fig. 19), the previtteline space is almost completely missing or there are only insignificant spaces on the poles, which correspond to the compressed position of eggs between the gill filaments of molluscs. Since in this environment the respiratory conditions are much less favorable than in the clear water outside the molluscs, the eggs and embryos of the bitterlings are adapted physiologically and morphologically to the oxygen deficiency of the water in which they develop. These adaptations, by the way, become evident when they survive up to 12 hours at 22 C without harm either in a live mollusc taken out of water and containing a small amount of water contaminated by the warm water excreted by the host, or in an excised, dead and decomposing gill, i.e. in an environment in which, evidently, oxygen is completely absent. Apparently, due to the adaptation to a lack of oxygen, the early stages of bitterling development are slower than in other fish (Table 21): their periods of blastula formation and gastrulation are more protracted, the process of body segmentation begins and ends later and

circulation begins three times later. Such a rate of development is a consequence of adaptation to the bad conditions of aeration. Improved conditions of aeration do not accelerate the process of development, but rather are harmful, because by extracting the bitterling eggs from the mollusc and placing them into clear water, the described slow process of development is not made faster, but a considerable portion of the eggs die.

After the circulatory system is formed, an exceptionally powerful embryonic respiratory system appears in the bitterlings. It consists of a densely branched subintestinal vein on the yolk sac and even more dense vascular network within the dorsal and anal fin folds (Fig. 16-25). Another peculiarity of this system consists of the fact, that it persists for a very long time--up to the emergence of the larvae from the mollusc, i.e. up to the developmental stage at which there are two chambers in the swim bladder and the non paired fins have skeletons (at an age of about 24 days). In other cyprinids the embryonic respiratory system is much less powerful and disappears at an early stage: at the beginning of the larval period of life (at an age of about 10 days). The described peculiarities of the embryonic respiratory system in bitterlings, apparently, also reflect adaptation to the poor conditions of aeration.

After the appearance of eye pigmentation the embryos of bitterlings become very photophobic, which apparently prevents them from leaving the mollusc's shell prematurely.

Otherwise the bitterlings of the two systematic groups--Rhodeina and Acanthorhodeina--have different adaptations for life within molluscs.

The spiny bitterlings Acanthorhodeina are larger than other bitterlings and their fecundity is considerably higher: they are the ones which deposit up to 300 eggs in one spawning period. The eggs are smaller than those of other bitterlings, almost round (diameter 1.1 to 1.07 mm, Fig. 19, C), layed in a cluster, all together, probably only once in a season. Several females may use the same mollusc, so that clusters may be found which contain up to 600 eggs, or even more. Eggs deposited in a cluster cannot be well irrigated and impede each other's respiration in an environment in which the respiratory conditions are already extremely difficult. For this reason extremely peculiar adaptations appear in the development of spiny bitterlings aimed at overcoming these difficulties. Their embryos emerge from the membranes at an unusually early stage of development--when only some 15 body segments are formed, i.e. earlier than any other fish in general; they become covered with small epidermal scales with the apexes bent towards the tail, and acquire a worm-like appearance (Fig. 24, A). The rudiments of their eyes, brain and head, on the whole are of an exceptionally reduced size (3 to 5 times smaller than in embryos of other fish, Fig. 22 and 23; Table 63), they are closely pressed to the yolk sac and are not visible; in contrast, the segments are enlarged (Table 76) and partially

embrace the yolk sac. Segments begin to shrink more or less rhythmically and are able to communicate worm-like movements to the whole body. Due to the very streamlined form of their body, the reduced size of the head, and the scales with their apices bent backwards, soon after hatching the embryos gradually begin to scatter out of the cluster and occupy the gills of the mollusc entirely, thus moving into better conditions of aeration. The small scales grow larger with development of the embryos which begin to look worm-like even more (Fig. 24, B). They perform even more energetic worm-like movements and resemble some kind of parasite more than fish embryos. After some period of time following the resettlement of the embryos over the whole gill area, the described form of their body and their behavior lose their purpose. The head and its organs: eyes, otic vesicle and brain; begin to grow intensively--considerably faster than in embryos of other fish (Table 63), finally reaching a normal size (Fig. 25, B-C). The little scales persist for a long time, almost to the point where the larvae leave the mollusc. The embryonic respiratory system is built like in other bitterlings, however the corresponding vascular networks in the fin folds are less strongly developed. This could be explained by the smaller size of the spiny bitterling embryos.

The spiny bitterling begins its larval period of life when it has reached a length of 6.5 mm, i.e. at a smaller body size than other bitterlings (the initial larval length of the latter is 7.5 mm, because of the larger size of the

eggs). This difference in the initial size of the two groups of fish, for some reason, results in a higher mortality of the larvae of spiny bitterlings in comparison with the mortality of other bitterlings. The adult bitterlings compensate for this mortality by higher fecundity.

The adult spiny bitterlings are twice as big as the other species of bitterlings. If the latter had conserved the egg size and manner of development of the spiny bitterlings, then their fecundity would be almost only one half of the present fecundity and they would be doomed to extinction. Actually, by changing the size of their body, they also completely changed the manner of their development, in spite of the fact that they deposit their eggs in the same molluscs that are used by the spiny bitterlings. They have also increased the size of their eggs almost twofold--up to 2mm, thus creating oligoplasmatic eggs, with a relative yolk amount of 4.2 (Table 63 and Fig. 19, C-D). Although this has further lowered their fecundity, the body size of their larvae, at the moment of emergence from the mollusc, is thus increased providing the larvae with vital advantages over the smaller larvae of the spiny bitterlings and compensating for the extraordinarily decreased fecundity.

The fecundity of *Rhodeina* is not known with certitude. Apparently they deposit less than 100 eggs in one season. The eggs are released repeatedly (how many times it is not known) in very small portions consisting of 5 to 7, and seldom 10 eggs into one mollusc. These small portions are not

deposited in a cluster but singly. Due to this kind of egg release, the eggs do not hinder each other's respiration and development. Accordingly there is no need for the same adaptations as occur in the case of the spiny bitterling. The embryos emerge from the egg membranes at a later stage than those of the spiny bitterling, when the process of body segmentation is nearing completion, but still considerably earlier than in other fish. This could apparently be explained (277) by the lack of space for the embryos under the membrane (as described, the eggs of bitterlings do not have a perivitelline space or it is very limited) and also by unfavorable conditions of respiration.

The newly hatched embryos are not crowded and do not have to crawl. Therefore their bodies are devoid of scales, the body myotomes are not enlarged, i.e. they are smaller than those of the spiny bitterling (Table 76) and do not embrace the yolk sac; the size of the head and its organs--eyes, otic vesicle and brain--are not very reduced (however they are smaller than in other fish); these embryos do not resemble worms, do not wiggle like worms and are unable to crawl. On the anterior part of their yolk sac, two bulges which are bordered with glandular tissue appear at an early stage. In some species they are very large and resemble some appendages (Fig. 20). Judging from Uchida's drawings only the Achilogathus does not have such outgrowths. The outgrowths approach the gill filaments of the mollusc very closely, holding the embryos in place up to a late stage of development.

The head and eyes of the embryos also become covered with glands and this covering is unusually dense. The significance of this phenomenon is not yet understood.

Table 76

- 1) Increase in size of the body myotomes and the head of fish.
- 2) (measurements of the largest myotomes are given).

Таблица 76

- 1 Изменение размеров туловищных миотомов и головы рыб
- 2 (указаны размеры самых больших миотомов)

3 Название рыбы	4 Ширина туловищного миотома (в мм)			5 Длина головы личинки	
	6 в момент закладки	7 в возрасте 3 суток	8 в возрасте 10 суток	9 в миотомах	10 в % к длине тела
<i>Acanthorhodeus asmusi</i>	0.09	0.14	0.13	10	22
<i>Rhodeus sericeus</i>	0.08	0.11	0.16	10	21.6
<i>Hemibarbus maculatus</i>	0.08	0.10	0.11	11	20
<i>Pseudobagrus fulvidraco</i>	0.10	0.09	0.11	13.9	25
<i>Silurus glanis</i>	0.10	0.12	0.13	13.5	20
<i>Hoplosternum</i> sp.	0.08	0.20	0.20	6	17.6

- 3) fish names; 4) width of the body myotome (in mm);
- 5) length of larva's head; 6) at the moment of anlage appearance; 7) at an age of 3 days; 8) at an age of 10 days; 9) in number of myotomes;
- 10) in % of the body length.

Apparently the adaptation to unfavorable respiratory conditions within the molluscs, in common bitterlings is generally the same as in the spiny bitterling. However, the embryonic respiratory organs, formed by identical vessels are better developed in the common bitterlings (Fig. 16). This is due to the larger size of their embryos which adds to the respiratory difficulties.

As it can be seen, the biological differences between adult *Rhodeina* and *Acanthorhodeina* resulted in differences in fecundity, which in turn, determined different environments for their development and created two sharply different types of development. The species and genera of bitterlings also differ in their features of development, although not so substantially. Their eggs differ in size, relative amount of yolk, and structure of the membrane (Fig. 19, C-D). Their embryos differ in the position of the head on the yolk sac, the form and size of their lateral appendages etc. Considering that some bitterling species deposit their eggs in only one species of mollusc (*Pseudoperilampus* (?) sp.---only in *Unio*) while others use molluscs of various species (*Rhodeus* in *Unio* and *Anodonta*), then these differences in environment determine, to a certain degree, differences in their development. However this alone is not sufficient for the understanding of all the evolutionary varieties in bitterlings, for this a knowledge of all the stages of their life cycle is necessary.

Obviously, the differences in bitterling development (278) are not directly determined by the environment in which they develop (if that includes only the water and the molluscs, etc., which are identical for all of them), but rather they are directly determined by the differences in fecundity, i.e. in the constitution and biology of the adult forms. As mentioned, the spiny bitterling is about twice as large as any of the others thus allowing them to produce considerably more eggs, approaching, in this respect, the cyprinids which

develop outside molluscs, and from which they actually evolved. Since, in reality, the environment for the eggs and embryos, and generally, for the organisms as well, includes themselves in addition to all other factors, then the spiny bitterling itself, as an environmental factor, predetermines the necessity of all previously described and extremely peculiar adaptations connected with development; these adaptations--hatching at an early developmental stage, the epidermal scales covering the body, and all other peculiar structures that help the embryos to crawl around on mollusc gills--are predetermined by the high fecundity of the spiny bitterling and consequently by the fact that it is impossible for all the individual eggs to develop, for any length of time, within a single egg cluster.

Other adult bitterlings are considerably smaller than the spiny bitterling. This is justified by their ecological peculiarities: food requirements are lower and of a different kind, etc. However, the smaller body size, i.e. the ecology of adult organisms, does not allow them to produce eggs comparable in quantity, size and adaptability to those of the spiny bitterling. They are compelled to reduce their fecundity sharply and to deposit the eggs, all other conditions being equal, in unfavorable conditions where they could not possibly survive. In order to survive, they must find a way out of this situation, i.e. having a body of smaller size they have to create a new type of development which would eliminate the disadvantages of the forcibly

acquired lowered fecundity. Apparently the conditions for the development of eggs within molluscs are not propitious for the elimination of this disadvantage through the creation of a very small egg, which would increase the fecundity again. The evolution of the small bitterlings proceeded in the opposite direction -- they lowered their fecundity below that which would be proportional to their size: instead of hundreds of eggs they began to release only tens of eggs, but at the same time they increased the size of their eggs considerably. This provided the eggs with vital advantages over the smaller eggs of the spiny bitterling, and eliminated the disadvantages of the extremely reduced fecundity. The very low fecundity allows them to deposit the eggs singly and over a very widely spaced area. Thus the individual eggs, as environmental factors, lost their detrimental effects on each other, a problem which plagues the clustered eggs of the spiny bitterling. Now the newly hatched embryos do not have to crawl around on the mollusc's gill in search of more favorable conditions for development. Consequently they are not provided with scales and other adaptations necessary for crawling, but have instead outgrowths on the yolk sac which help them to remain in one place; the rudiments of the head, eyes etc. are reduced to a lesser degree, they do not have a worm-like appearance, etc.

Development of the bitterlings shows convincingly that the evolutionary organismic changes are infinite, but not definite, as is so often and erroneously assumed. These

changes always embrace not only isolated but also all stages of development, since a change in any one of them inevitably affects all others. For this reason changes in the adult organism are always accompanied by changes in the whole process of development (i.e. by changes in the eggs, embryos and larvae). Moreover such a thing as a "practical" conservatism in the early stages of development, expounded up to the present, does not exist.

It is also evident that the only correct interpretation (279) of Sechenov's notion of an organism, which stipulates that "in a scientific definition of an organism the environment affecting it, must also be included"--also has the inverse meaning: a scientific definition of an environment, affecting an organism, must also include this organism. Therefore, the interpretation of an "ecological niche" must also include both--the environmental factors and the organisms, never omitting the latter. This point of view has been advanced for a long time, persistently and very convincingly by V.V. Vasnetsov. Moreover, in modern biology the "external environment" and "ecological niche" are understood to include the external factors of an environment, disconnected from the specifics of the organism, and therefore they are abstract and totally inoperative. With such theoretical concepts, enforced by a faith in "practical" conservatism in the early stages of development and in the finite character of the evolutionary changes of organisms, it is completely impossible to understand the sense of the evolutionary changes

in bitterlings. For such a theory, their whole evolution appears like screaming "biological nonsense" and lawlessness.

6. Egg protecting psammophilous Cyprinidae.

Pseudogobio rivularis as yet is the only known cyprinid in our ichthyofauna which guards its eggs. This gudgeon inhabits the rivers of China, and the Ussuri and Amur rivers. According to the observations of V. D. Lebedev, Pseudogobio rivularis reproduces throughout the whole month of June and up to the first days of July. It deposits the eggs in small excavations (up to 5.5 cm deep and 25 cm in diameter) made in the bottom on shoals in lakes, oxbow-lakes and puddles (Fig. 94). Up to 1711 eggs have been found in these nests and the water temperature there may reach 30 C. Numerous sand grains stick to the chorion rendering the eggs virtually invisible. Each deposit is guarded by the male. The latter ensures that the eggs lie in a small heap at the bottom of the excavation and that they are not carried away by currents. From time to time, the male moves the eggs using his mouth or fans them with his pectoral fins thus improving the respiratory conditions. Moreover the male chases predators (small fish) away from the nest. Small schools of these predators wait around the nest ready to attack and destroy the eggs if the guardian male is chased away. After hatching the embryos develop lying on the sandy bottom.

According to the data of S. G. Soin, their respiratory system,
According to the data of S. G. Soin, their respiratory system,

similar to that of the psammophilous gudgeons, is poorly developed and consists only of the ducts of Cuvier and the lower caudal vein which, at a later date, are replaced by gills. The newly hatched embryos do not avoid light but remain on the bottom, using their very large paddle-like pectoral fins as support. The fins are spread out like fish belonging to the *Armatogobionina* group. At the edges of the fins there are long finger-like appendages, typical only of the fish of this group. Like the latter, the larvae of Pseudogobio have a very small swim bladder which remains unfilled with air for a long time. It can be seen from the biology of the embryos and larvae that the Pseudogobio must be grouped with psammophilous fish. However it differs from the psammophilous gudgeons and stone loaches which do not protect their eggs, not only in the fact that it guards its eggs, but also in the peculiarities of the construction and use of the pectoral fins and swim bladder. These peculiarities make it similar to the fish of the *Armatogobionina* group indicating that it is not only related to this group but also has identical biological features: the larvae of *Armatogobionina* also live on the bottom, supported by their very large, paddle-like, horizontally situated pectoral fins with finger like appendages and for a long time they do not have a swim bladder.

7. Ecological groups of the Cobitidae.

As previously mentioned, among the loaches, all *Nemachilini* apparently belong to the psammophilous group

whereas all Cobitini and in any case the loaches and "shchipovki" (Cobitis) are phytophilous fish.



Рис. 94. Два гнезда *Pseudogobio rivularis*. Темное пятно в каждом гнезде — самец, охраняющий кладку икры (фото В. Д. Лебедева)

Fig. 94. Two nests of *Pseudogobio rivularis*. The dark spot in each of the nests is the male, protecting the clutch. (Photo V. D. Lebedev).

(280)

The adaptations of the latter are generally similar to the adaptations of phytophilous cyprinids. They reproduce at the end of spring and in summer when the water is warm (temperature 17 C or higher). The eggs are small (1.17 mm or smaller), which indicates a high fecundity. The eggs adhere to plants. The hatched embryos are provided with adhesive organs, so that they can suspend themselves from plants and develop for some time immobile and in a suspended

position; they are not photophobic, avoiding only direct sunlight.

The main peculiarities distinguishing phytophilous loaches from cyprinids are that the former have barbels, which appear at a very early stage of development and which partially serve as adhesive organs and that their embryonic respiratory organs consist of external filamentous gills which are typical only of the Cobitini (Fig. 95, A). The phytophilous group of loaches, like the psammophilous group, is homogeneous from a systematic point of view.

The group consists of only 8 species, i.e. about one third of the psammophilous group (the latter consists of 23 species; Table 1). In contrast to the psammophilous group, most of its species are inhabitants of flatland rivers and only two species of the genus Cobitis inhabit mountain rivers. According to the observations of S. K. Troitskii, the latter release their eggs on rocky bars.

In our fauna Leptobotia has not been studied.

3. Ecological groups of the Siluroidei.

(281)

The Siluroidae and probably some of the Bagridae (Liocassis brashnikovi) are phytophilous. They lay their eggs in grass during the summer when the water temperature is from 18 to 24 C. Spawning lasts up to three months. However, in contrast to the carps and loaches, their bodies are very short while their tails are very long (twice as long as those of cyprinids). Consequently, their embryos

are provided with a very active respiratory mechanism, which alters all the other typical relations between the phytophilous cyprinids and the environment.

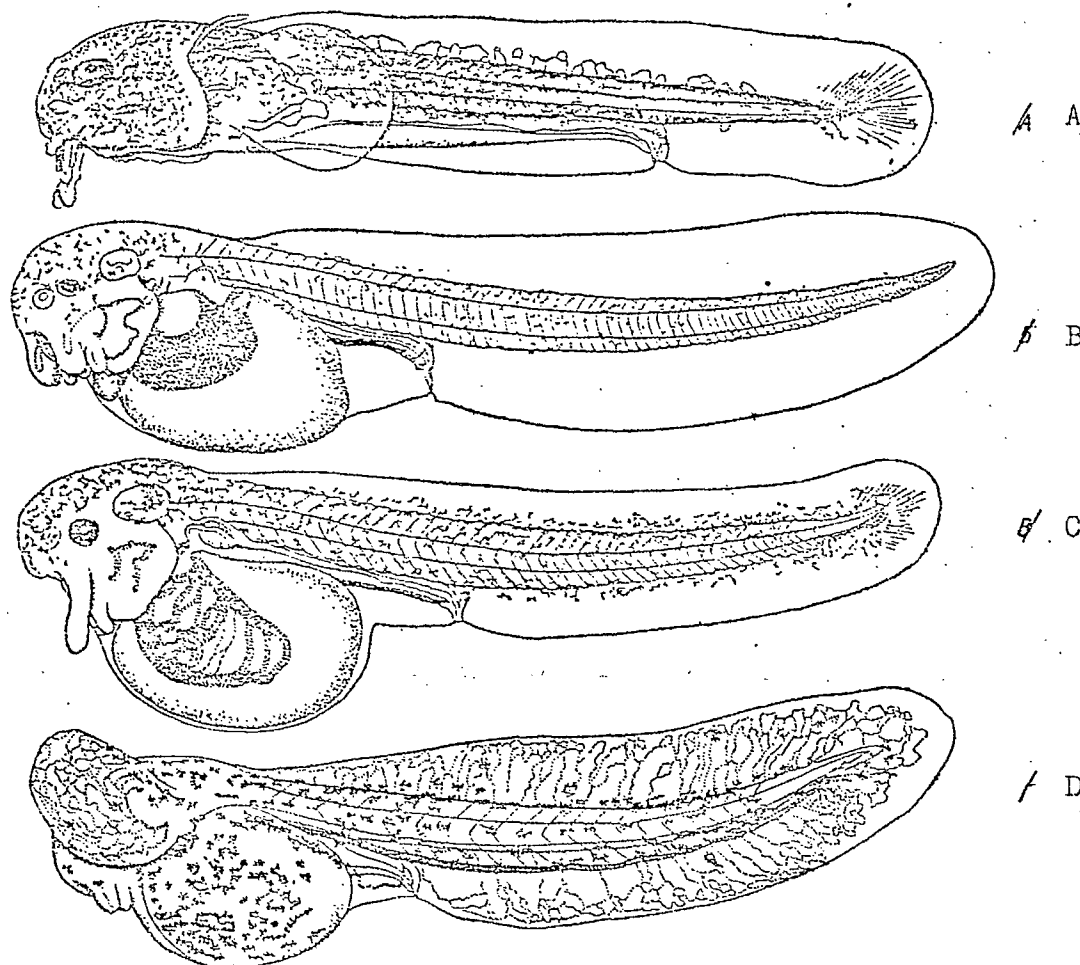


Рис. 95. Органы дыхания фитофильных Cobitidae и Siluroidei.

А — *Misgurnus fossilis*. Начало личиночного периода. Дышит наружными жабрами и плавниками. Б — *Silurus glanis*. Середина эмбрионального периода. Дышит кювьеровыми протоками и жаберной крышкой; притоняет к ним воду движениями хвоста. В — эмбрион *Pseudobagrus fulvidraco*. Дышит кювьеровыми протоками и жаберной крышкой, как сом; разгребается в норках. Г — эмбрион *Callichthys* sp. Дышит грудными и непарными плавниками.

Fig. 95. Respiratory organs of the phytophilous Cobitidae and Siluroidei.

A-*Misgurnus fossilis*. Beginning of the larval stage. External gills and fins are used for respiration. B-*Silurus glanis*. Middle stage of the embryonic period. Ducts of Cuvier and gill opercle used for respiration; tail movements are used to force water to these organs. C-embryo of *Pseudobagrus fulvidraco*. Respiration, like the catfish is by the ducts of Cuvier and gill opercle; develops in small burrows. D-embryo of *Callichthys* sp. Respiration by the pectoral and non paired fins.

Table 77

1) Summary of the characteristics of the ecological groups.

Таблица 77

1 Суммарная характеристика экологических групп

2 Экологические группы	3 Диаметр яйца (в мм)		11 Относительный размер первичного ядра	12 Длительность развития в оболочке	15 Длина вышедшего эмбриона (в мм)	16 Длительность развития эмбриона вне оболочки	17 Начало личиночного периода	18 Начальная длина личинки (в мм)	19 Интенсивность питания	20 Длительность нереста	21 Плодовитость (в тыс.)
	9 с оболочкой	10 без оболочки									
Литофилы 3 Barbin	2.97—3.90	1.95—2.34	1.45—1.66	13 5 суток 14 2 часа—8 суток	7.28—9.36	13 10—13 суток	15—23 суток	10.59—14.25	12—17	2—5 мес. 22	8—52.5
Литофилы 3 Leuciscini	1.60—2.27	1.15—1.56	1.2—1.62	13 2 суток 14 5 часов—22 суток	4.40—7.28	5—13	11 суток—16 суток 13 20 час. (22 суток)	6.7—10.2	3—24	Несколько дней—1 1/2 мес. (5 мес.) 23	1—193
Фитофилы 4 Cyprinidae и Cobitidae	1.20—1.76	0.84—1.3	1.2—1.9	13 2 суток 14 20 часов—9 суток	4.27—6.20	13 1 сутки—7 суток 14 10 час. 14	6—12 суток	5.75—7.00	15—24	Несколько дней—2 мес. 22	10—1664
Фитофилы 4 Siluroidei	3.5	1.4—1.9	1.17	2—6 суток	6.7—7.4	13 1 сутки—4 суток	6—7	12.0	18—24	До 3 мес. 24	?
Псамофилы 5	1.27—2.30	0.8—1.2	1.3—1.6(2)	3—13	4.35—4.61	13 5 суток 14 12 час.—12 суток	7—14 (25 суток)	6.23	10—20	Несколько дней—3 мес. 22	3 и больше 26
Пелагофилы 6	2.00—6.00	0.55—1.9	2—4	13 1 сутки 14 4 часа—3 суток	3.3—7.6	3—4 суток	4.5—8 суток	4.0—8.5	11—26	От 1/2 до 1 1/2 мес. 25	?
Остракофилы 7	1.6—2.1	1.1—1.95	1.07—1.08	2—2 1/2 суток	2.0—2.5	21—22 суток	23—24	6.7—8.0	12—24	2—3 мес. 22	0.1—0.3

27 * Отношение диаметра яйцевой оболочки к диаметру желточного мешка.

2) ecological group; 3) lithophilous; 4) phytophilous; 5) psammophilous; 6) pelagophilous; 7) ostracophilous; 8) diameter of the egg (in mm); 9) with the membrane; 10) without the membrane; 11) relative dimension of the perivitelline space; 12) duration of development within the membrane; 13) days; 14) hours; 15) length of the newly hatched embryo (in mm); 16) duration of development of the embryo outside the membrane; 17) beginning of the larval period of life; 18) initial length of the larva (in mm); 19) water temperature during spawning (in °C); 20) duration of spawning; 21) fecundity (in thousands); 22) months; 23) few days; 24) up to 3 months; 25) from 0.5 to 1.5 months; 26) and more; 27* ratio of the diameter of the egg membrane to the diameter of the yolk sac.

The newly hatched catfish embryos are restless and perform continuous wave-like movements with their tails thus moving fresh water towards the yolk sac and gill opercle which are the main respiratory organs (Fig. 95, B-D). This mechanism of active respiration makes it unnecessary for the embryos to suspend themselves from plants in the upper water layers and allows them to seek refuge on the bottom in vegetal detritus, where, although the conditions of aeration are poorer than at the surface, the defence conditions against enemies are better. Due to this manner of defence, most of (282) the embryos of phytophilous catfish, in contrast to the embryos of other phytophilous fish, are extremely photophobic: their negative reaction to light is even much more pronounced than in the photophobic embryos of lithophilous fish.

The concealed way of life of the embryos and larvae on the bottom predetermined a lower mortality for catfish compared to other phytophilous fish. For this reason their fecundity is comparatively much lower than that of other phytophils. The eggs are almost twice as large (1.9 mm) thus resembling the lithophilous Barbini in this respect.

The Amur catfish (Parasilurus) scatters its eggs in grass and does not guard them. Brazhnikov's catfish (Liocassis brashnikovi) sticks its eggs to the roots of grass and probably does not care for them. The European catfish lays its eggs in clusters in grass which it flattens, i.e. it prepares some kind of a primitive nest and stands guard over the eggs until the embryos emerge from the egg membranes (at about two days).

The banded catfish (Pseudobagrus fulvidraco) differs from phytophilous catfish in its habit of laying eggs in small burrows dug in soil (Fig. 74) and guarding the spawn throughout the whole period of embryonic development, i.e. about 7 days. This complex care for offspring is only possible because of the activities of the embryos which create a flow of fresh water for themselves using their long tails. The aeration conditions in the burrows are so unfavorable that immobile embryos with passive respiration, like the embryos of cyprinids, would not be able to survive. They respire mainly through the vascular network of the yolk sac (Fig. 95, B,C).

Since the catfish are very little studied as yet, it is difficult to state with certainty to what extent their phytophilous group is heterogeneous.

Among our catfish, perhaps only the Turkestan little catfish which lives in mountain rivers, does not belong to the phytophilous group. This fish has not yet been studied. The majority of other catfish inhabit tropical countries. Except for the "kallikht" catfish their developmental patterns for the most part have not been studied as yet. For this reason, it is not possible to give an overall eco-morphological description of these fish at the present time. The "kallikht" is a phytophilous fish adapted to very poor conditions of aeration. It uses its unpaired fin fold and pectoral fins for respiration (Fig. 95 D). A summary description of the ecological groups of the Ostariophysii is given in Table 77.

9. A short ecological description of the families
of other orders of our freshwater fish.

1. Acipenseridae--typical lithophilous fish. They release their eggs from the end of spring until fall, in swift currents of large rivers, on rocky banks. The eggs become fastened to stones. The diameter of the eggs varies from 2 to 3 mm, i.e. they are like the eggs of the lithophilous Barbini, or even larger. Development within the egg membrane lasts about 5 days (at a water temperature of 17 to 18 C). The embryos emerge at approximately the same stage of development as the lithophilous Barbini (Fig. 96, A). They have a very large supply of yolk, the pectoral fins are rudimentary, the head is weakly differentiated; the yolk sac is covered with ramifications of the sub-intestinal vein which serves the embryo as a respiratory organ. The body is edged by a fairly broad non paired fin fold. Due to the large amount of yolk and the lack of pectoral fins the embryos are unable to swim for long periods of time. They continuously perform vertical leaps, i.e. they swim towards the surface and then sink to the bottom. Because of these activities the newly hatched embryos do not lie in one place for a long time but are continuously caught and carried downstream by the current. After the eyes become pigmented (24 hours after hatching) the embryos of the stellate sturgeon become photophilic which stimulates them to strive upwards and thus helps them to be carried downstream (these are indications that the embryos

might be photophobic, but these assumptions must be verified). Later, when the ability to swim directionally is acquired, the behavior of the embryos changes.

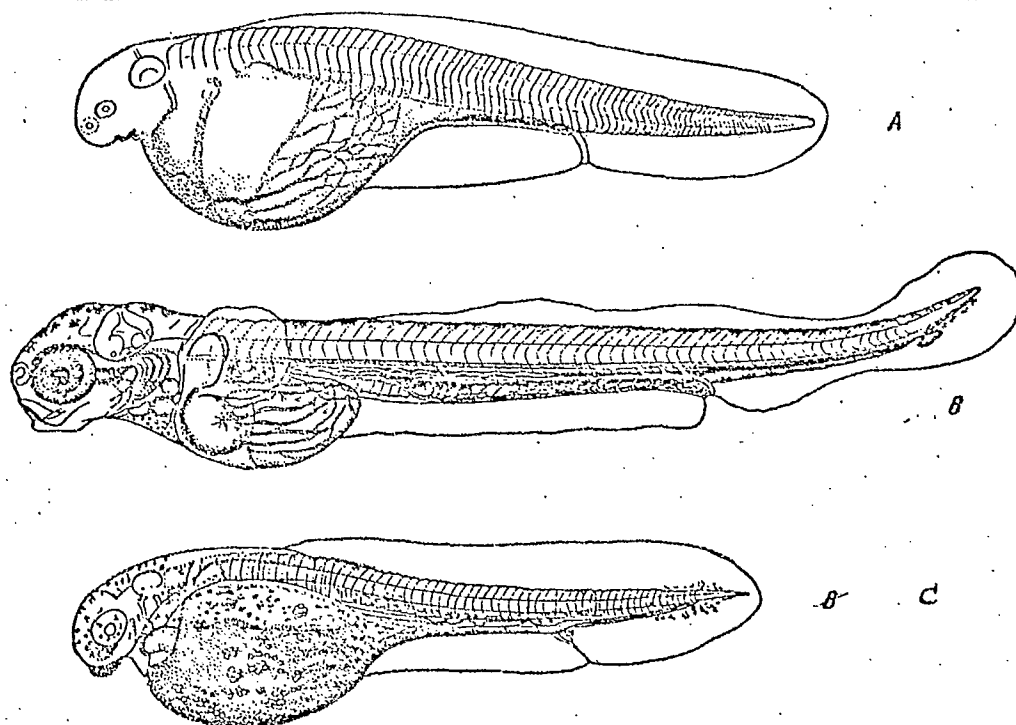


Рис. 96.

А — *Acipenser stellatus*. Вскоре после вылупления из оболочки. Всплывает, затем падает на дно; безразличен к свету. Возраст около 5 суток (по Н. Н. Дислер). Б — *Stenodus leucichthys*. Постоянно плавает. Поддерживается большой жировой каплей и грудными плавниками. Светолюбив. Возраст 75 суток (по С. Г. Соин). В — *Esox lucius* вылупившийся из оболочки. Имеет железы прилипания на голове. Подвешивается к растениям, не боится света

Fig. 96. A-*Acipenser stellatus*. Soon after hatching. Swims up and sinks to the bottom; indifferent to light. Age about 5 days (data of N. N. Disler). B-*Stenodus leucichthys*. Swims continuously. Held in a floating position by a large oil drop and the pectoral fins. Photophilic. Age 75 days (S. G. Soin's data). C-*Esox lucius*. Newly hatched. Has adhesive glands on its head. Suspends itself from plants; not photophobic.

It is obvious that the acipenserids, being lithophilous fish, differ from the lithophilous cyprinids in that they

do not hide under rocks after hatching but continuously swim upwards, striving towards the light. By doing so they are carried downstream.

In contrast to the cyprinid family the acipenserid family, in ecological terms, is uniform and homogeneous. (285)

2. All Clupeidae, except for the northern herring, as was already pointed out, are typical pelagophilous fish (Fig. 100, D, E). In ecological terms this family is also uniform and homogeneous.

3. The Coregonidae belong to the lithophilous group of fish. In contrast to the majority of other fish, they spawn in late fall and develop in winter at a very low temperature (3 C and lower). The eggs are scattered on the rocky-sandy bottoms of rivers or clear water lakes. The eggs roll under the rocks but do not adhere to them. The eggs are of approximately the same size as those of the Barbini, i.e. about 2 mm in diameter. Hatching takes place in early spring. The newly hatched embryos have a broad, unpaired fin fold and large, broad pectoral fins. The yolk sac is already considerably reduced, containing a large amount of oil which is in the form of ^a large drop. This oil reduces the specific gravity of the embryo considerably (Fig. 96, B). Due to these structures, the embryo begins to swim immediately and thus begins a pelagic way of life. They do not sink to the bottom and are independent of the living conditions there. The embryos are not photophobic, but to what degree they are photophilic is not yet known. The main differences between the whitefish

and the lithophilous cyprinids is that the former develop in winter and not during the spring and that after hatching they do not hide on the bottom but enter the pelagic zone.

From an ecological point of view the whitefish are uniform and homogeneous.

4. The Salmonidae are lithophilous fish and as such they deposit their eggs in redds excavated in a sandy-gravelly bottom. This makes them very exacting in regard to the conditions of aeration and forces them to deposit their eggs only in very clear and cold rivers or lakes. Spawning takes place mainly in fall, in places where there are spring fed brooks. The survival rate of the hidden eggs is high and therefore the fecundity of these fish is relatively the lowest. The eggs are very large--up to 5 mm in diameter. The embryos are provided with a very large respiratory network which covers the whole surface of the yolk sac. This arrangement is related to the difficult conditions of aeration in the redd. The embryos emerge from the membranes early, with a very large amount of yolk. They are totally unable to float but they are able to move along the bottom. At this time they are photophobic. For this reason the newly hatched embryos become somewhat scattered and actively seek cover under the rocks. The scattering of embryos from the redd, in which one portion of the eggs (the unfertilized ones) perish and undergo decomposition thus aggravating the conditions for respiration*.

* Translator's note: Although this sentence is incomplete in the original the author presumably means:...respiration, improves the survival rate.

Due to the large amount of yolk, the supply is sufficient for development of the fry, which at the time of disappearance of the yolk resembles the adult fish in its general appearance.

5. Thymallidae. In contrast to the salmonids, the Thymallidae reproduce mainly in spring. Their eggs are considerably smaller than those of salmonids (the diameter with the membrane is 3.5 to 4 mm, that of the yolk sac: 2.5 mm). At the moment of absorption of yolk larvae are formed (not fry). They are edged by an unpaired fin fold and provided with other larval organs. The biology and development of graylings has not been studied sufficiently. According to a communication from F. V. Krogus they also bury their eggs.

Salmons, like the graylings, are uniform and homogeneous in ecological terms.

6. The Osmeridae, as stated previously, belong to the semi-pelagophilous group of fish. They attach their eggs to stones as well as to plants and reproduce not only in rivers and large lakes but also in lakes in the tundra which are unfit for habitation by other fish. Thus, for instance in a tundra lake isolated from the Tym' River (on Sakhalin), according to Tarants (1937), only the stickleback lives next to the smelt.

7. The Catostomidae, with respect to reproduction (286) and development, have not been studied at all. It may be assumed that the representatives of the only species of this family, which inhabits our waters, are lithophilous fish.

8. Umbridae in our fauna is represented by only one species which certainly belongs to the phytophilous group of fish. They are very poorly studied. There are indications that the eggs are guarded.

9. Esocidae in our fauna is represented by two phytophilous species. The common pike begins to spawn at the beginning of the spring spate, i.e. earlier than most of the lithophilous Leuciscini, at a water temperature of about 3 C or higher. The eggs are large, like those of the lithophilous Barbini, about 2 mm in diameter. In the middle zone the spawning period is short but in the deltas of such large rivers as the Volga it is long, lasting about two months. To deposit its eggs, the pike moves out onto the flooded meadows and scatters its eggs in last year's grass. The eggs sink to the bottom. The newly hatched embryos are provided with a large amount of yolk, they are heavy, poorly developed and unable to swim directionally. They can only swim upwards from time to time. In front of their eyes, there are adhesive organs (Fig. 96, C) with which they become attached to grass and for some period of time they develop in a suspended position, like the embryos of phytophilous cyprinids. The surface of the yolk sac serves as a respiratory organ. The embryos are not photophobic. The pike differs from the phytophilous cyprinids by reproducing at a considerably earlier time, in much colder water and also by the size of its eggs which are almost twice as large. All these features make the pike resemble the lithophilous cyprinids.

In general, the Amur pike, according to the observations of S. G. Soin, has the same adaptations as the common pike. Its main peculiarity is that it often releases its eggs a long time after the beginning of spring spate--in mid May or even at the end of this month. This is explained by the peculiarity of the aquatic conditions of the Amur River, where the coastal grasslands become flooded at later dates.

10. Dallia pectoralis (the only species of the family Dalliidae) which inhabits small brooks, lakes and sphagnum bogs of the tundra of the Chukhotskii Peninsula and Alaska, is probably a phytophilous fish. There is a complete lack of information concerning its development..

11. The genera of the family Percidae which have been studied, such as the perches, ruffs and pike perches, are grouped into a single group of indifferent fish because they are more or less indifferent to the substratum available for egg deposition. However, among them only the perch is a truly indifferent fish in all respects. It deposits ribbons of eggs on grasses, growing or dead, on submerged branches, roots, sticks and stones-avoiding only, like all other fish in general, the silty bottoms. Embryos remain within the membrane for a long period of time and emerge only after having reached an advanced stage of development (Fig. 97, B). Their supply of yolk is small, the non paired fin fold is broad and long, the pectoral fins are also broad and large. The yolk sac contains a very large oil drop which lowers the specific gravity considerably. Due to these structures the

newly hatched embryos are able to begin a pelagic way of life. They do not sink to the bottom and are independent of the conditions prevailing there.

The described manner of egg deposition, the late emergence from the egg membrane and the pelagic way of life of newly hatched embryos makes the perch indifferent to the nature of the bodies of water, i.e. it is able to reproduce in densely overgrown water reservoirs, which are suitable only for phytophilous fish, as well as in rivers and large clear-water lakes which are suitable only for lithophilous fish (for instance in Lake Baikal, according to the data of D. N. Taliev).

The other Percidae--ruffs and pike-perches--are more dependent on the nature of the bottom conditions of the water reservoirs in which they reproduce, than the perches. (287) They can also scatter their eggs on plants as well as on stones, however their embryos emerge from the egg membranes considerably earlier than embryos of the perch and they are less developed (Fig. 97A). At the moment of hatching they still have a large supply of yolk, the pectoral fins are rudimentary and therefore they are unable to swim. After hatching, the embryos sink to the bottom and for some time they even develop laying there, only occasionally swimming to the surface and then sinking again to the bottom. Only 2 to 3 days after hatching do they reach the developmental stage at which they leave the bottom and begin, like the perch, a pelagic way of life. These peculiarities of

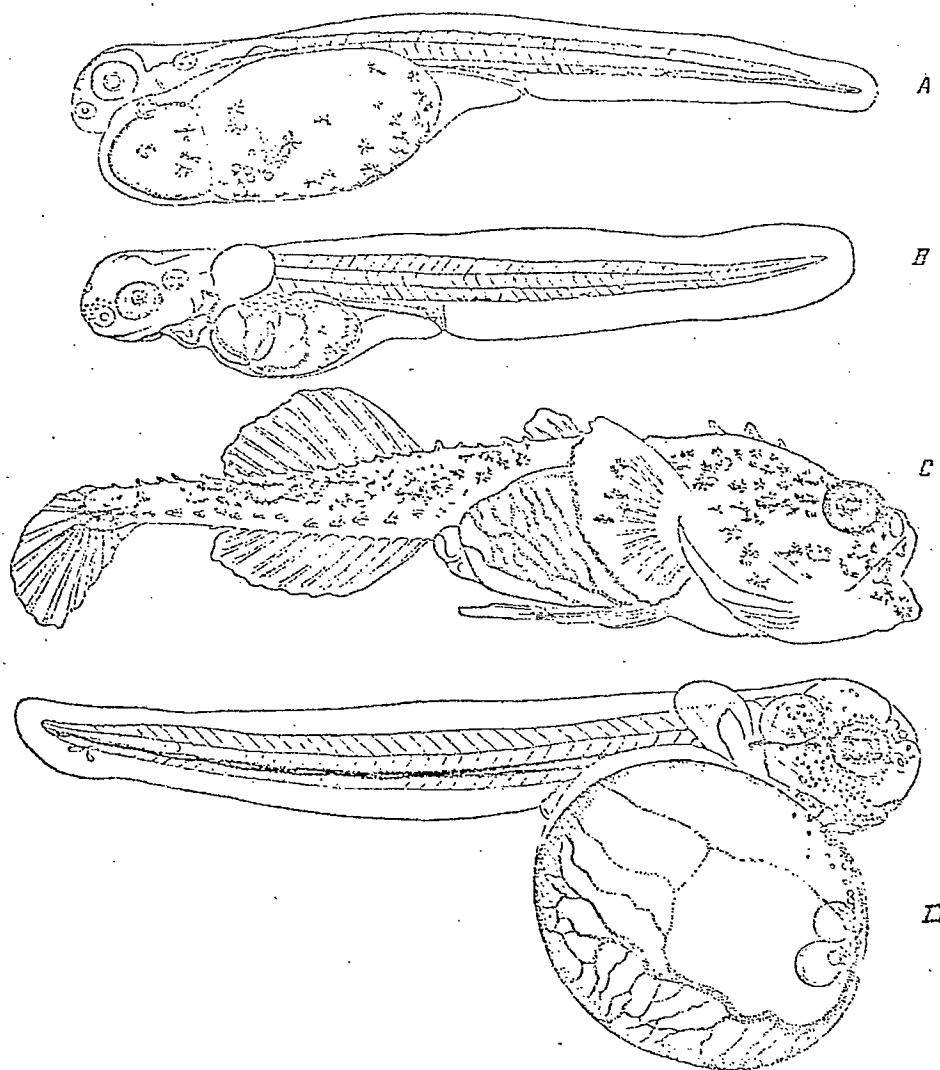


Рис. 97. Вылупившиеся эмбрионы.

А — *Lucio-perca lucio-perca*. Лежит на дне; по временам всплывает. Б — *Perca fluviatilis*. Все время плавает. В — *Benthophilus* sp. Сидит на дне. Д — *Cottus kessleri*. Извлечен из оболочки задолго до вылупления.

Fig. 97. Hatched embryos.

A-*Lucio-perca lucio-perca*. Rests on the bottom, occasionally swims to the surface. B-*Perca fluviatilis*. Swims continuously. C-*Benthophilus* sp. Rests on the bottom. D-*Cottus kessleri*--extracted from the egg membrane long before hatching.

development make the pike-perches and ruffs dependent on bottom conditions, i.e. they are forced to deposit their bottom conditions, i.e. they are forced to deposit their

eggs, in running river water or in lakes over a clean sandy bottom and makes it impossible for them to live in densely overgrown bodies of water, which can be inhabited by perches and phytophilous fish. Further studies of the development of the genera Aspro and Percarina, will certainly provide the possibility of devising a more accurate ecological (288) description of the family, and will possibly allow us to detect two ecological groups within this family.

12. Siniperca chuatsi--is the only representative of the freshwater family Serranidae in our fauna. As mentioned--it is a pelagophilous fish which reproduces in the Amur River during the summer season.

13. The snakehead (see Ophicephalidae) builds a nest of vegetal material in which it deposits floating eggs which it protects. A cursory study of the development of this fish was made by Uchida and Fujimoto (1935). This species inhabits the Amur River.

14. Eleotridae in our far-eastern ichthyo-fauna is represented by one species only--Percottus glehni. This fish--locally called rotan--prefers stagnant waters and even boggy lakes. It is found together with the phytophilous lake minnow (Phoxinus phoxinus mantschuricus). However, it is not adapted in the same manner as the phytophilous cyprinids. The eggs are deposited mainly on the strong, round stems of plants or on broad leaves closer to the surface (Fig. 98,A). The individual eggs are layed in a continuous layer, close
The individual eggs are layed in a continuous layer, close

to each other in order to save space. For this reason the shape of ^{the} eggs is elongated, like those of the Gobiidae. The free end of the eggs is rounded and the opposite end, which becomes fastened to the plant, is slightly flattened. Only this end is provided with a tuft of sticky villi (Fig. 98, B).

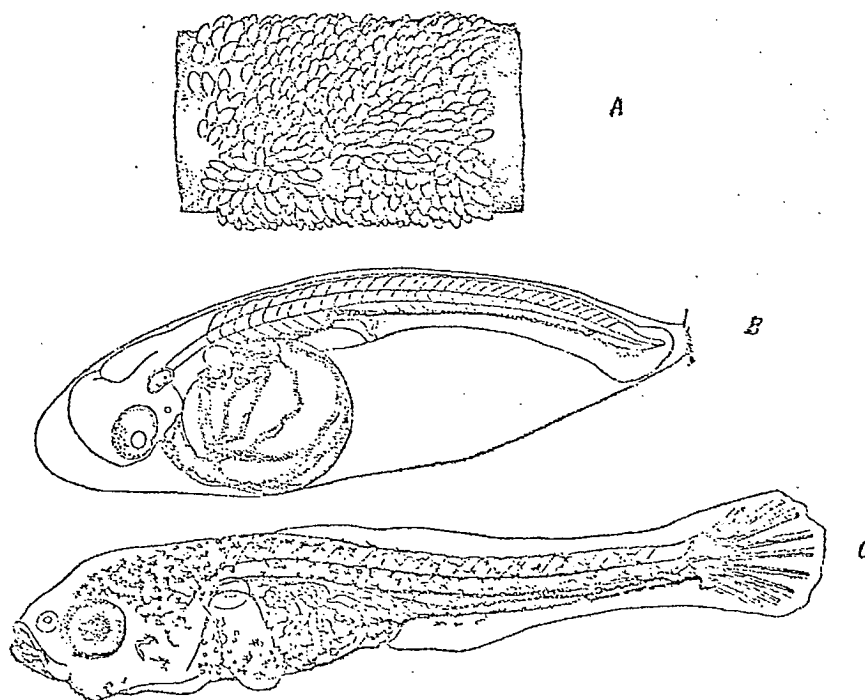


Рис. 98. *Percottus glehni*.

А — кладка икры на ветке. Б — зародок в оболочке. В — личинка вскоре после вылупления икры

Fig. 98. *Percottus glehni*.
A-spawn fastened to a branch. B-embryo within the membrane. C-larvae soon after hatching.

The egg clutches are probably guarded by males. Development within the egg membrane takes a very long time--up to the time when practically all the yolk is used up. The hatchlings time when practically all the yolk is used up. The hatchlings

are larvae (without ventral fins) provided with an already air filled swim bladder. The larvae immediately begin a mobile, pelagic way of life (Fig. 98, C). Later, they acquire the typical features of adult fish. The deposition of eggs on plants near the surface, the late emergence from the egg membrane and the pelagic way of life of the hatched larvae free this fish from the effects of the conditions prevailing on the bottom, and as mentioned before, these adaptations allow it to reproduce even in boggy lakes which are suitable for only the typically phytophilous fish. In some of its adaptations, the rotan is similar to the phytophilous verkhovka (Leucaspius delineatus). The latter also deposits its eggs near the surface and attaches the eggs to each other; the embryo develops within the egg membrane for a long time and the hatchlings are highly developed. They do not attach themselves but are pelagic. The combination of the rotan's adaptations apparently does not prevent it from also depositing its eggs on stones and from reproducing, like lithophilous fish, in small clear-water brooks, without dense vegetation, on the condition that there are no predators which would destroy the eggs. However, it is actually not definite that they reproduce in such waters.

15. Gobiidae is mainly a family of the southern seas. Their freshwater representatives evolved from marine forms and all their adaptations were acquired when they were still in the sea. After immigration into freshwater, they changed little, because their inherited adaptations were quite

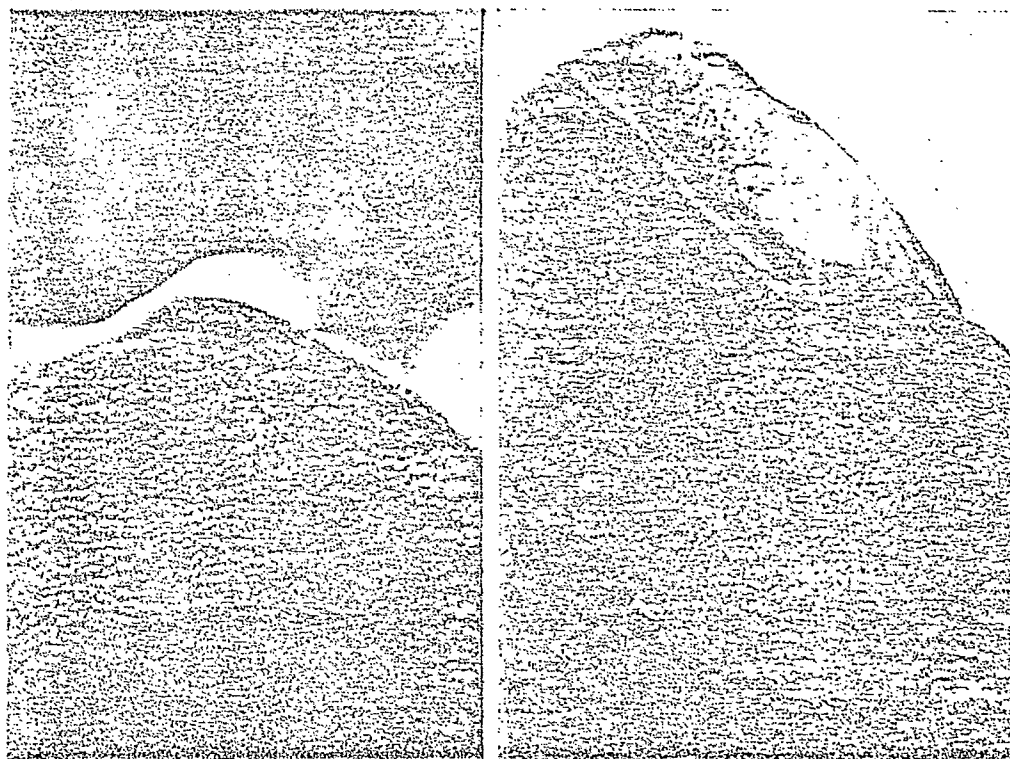
satisfactory for the living conditions in these waters. Gobies are lithophilous fish which guard their eggs. The eggs are deposited on the lower surfaces of stones, frequently in depressions where the guardian male can also find shelter. The eggs are spread over the surface of the stone in a continuous layer in which the individual eggs are layed very close together (Fig. 99, A). Their membrane forms a large perivitteline space, but the shape of the membrane is not rounded but elongated like that of Eleotridae. Only the free end is rounded. The opposite end, which becomes attached, is provided with a tuft of sticky villi. This form of membrane results in a considerable saving of area on which the eggs are deposited and greatly facilitates protection of the eggs. The gobies of the subfamily Eichwalidiinae, which mainly invaded the rivers of the Black Sea-Caspian Sea basin, have large eggs--about 2 mm in diameter--with very dense yolk. Development proceeds under the protection of the male and is very protracted; it lasts until the yolk is consumed almost completely. The emerging hatchlings resemble the adult fish in their principal features--they have ventral fins like sucking discs etc. (Fig. 97, B) and like the adult fish they adopt a diurnal way of life, hiding under stones.

The eggs of the members of the subfamily Gobiini are very small--up to 0.5 mm in diameter. From these emerge small larvae which do not resemble the adult fish at all, and which for some period of time are pelagic. They also immigrated into freshwater. Our Far East freshwater gobies

(Rhinogobius similis) also belong to this subfamily (S. G. Sonin's data).

The described manner of egg laying and their protection explains why the gobies can reproduce only in the currents of rivers. Only in such an environment are their eggs well irrigated and not suffocated. In still lakes, even if the bottom is rocky and the water clear and suitable for the existence of lithophilous cyprinids, such as in Lake Abro where the lithophilous Kolkhidean minnow lives, the gobies cannot reproduce.

16. Cottidae like Gobiidae is mainly a northern marine family. Its freshwater representatives have also preserved the basic adaptations developed by their ancestors in the sea. The underrock gobies are lithophilous fish, which protect their eggs. In contrast to the southern gobies, they do not spread their eggs in a single layer on the surface of a stone, but deposit the clutch under stones in a densely packed cluster in which the eggs are cemented to each other. The egg membrane is rounded, almost without a perivitteline space, which is an advantage when the clutch is compact. The eggs are relatively large, in some species over 2 mm in diameter, with dense yolk and a large quantity of oil. The eggs are of a yellowish or yellow-orange color. (290) Development within the membrane is very long, but it is not known at what stage hatching occurs (an embryo extracted from the egg membrane is shown in Fig. 102, D). from the egg membrane is shown in Fig. 102, D).



A

B

Рис. 99. Кладки икры литофильных рыб.
 А — *Eichwaldia melanosiomus*. Б — *Blennius* sp.

Fig. 99. Egg clutches of lithophilous fish.
 A-*Eichwaldia melanosiomus*. B-*Blennius* sp.

The yolk supply is sufficient for development of hatchlings which resemble adult fish in general features and which are adapted to a benthonic way of life. The deposition of eggs in clusters under stones, makes them even more exacting than the southern gobies with regard to the aeration conditions for their eggs. They reproduce only in cold water (at a temperature of about 7 C) on stony shoals in very clear brooks or near the shores of clear, cold water lakes, such as Lake Baikal, which are constantly washed by waves.

17. The Cottocomephoridae are direct descendants of the Cottidae. In general, their adaptations are the same as those of the Cottidae. They are lithophilous fish which protect their eggs which are deposited in clusters under stones near the shore line. They inhabit Lake Baikal. The Cottocomephoridae have been studied very little and therefore the specific peculiarities of their development are not known.

18. The Comephoridae are the only viviparous fish in our freshwater fauna. They are endemic to Lake Baikal and are related to the Cottocomephoridae. The adult fish (291) are pelagic and live far from shore in very deep water. For these reasons their modifications are so profound (they are very tender and in order to breathe they must be in constant motion), that they are unable to approach the shore to deposit and protect their eggs, as is done by the less modified pelagic Cottocomephoridae. Viviparity made them totally independant of the bottom and shore conditions and allowed them to become truly pelagic, deep-water fish. Their eggs are smaller than those of the non-viviparous related fish (about 1 mm in diameter), and this means that their fecundity is considerably higher than the latter. In their development there is a larval stage. The females release small larvae which lead a pelagic way of life.

The golomanka*, as far as is known, is the only pelagic viviparous fish. Its increased fecundity and the inclusion of a larval stage in its development, together

* Translitterated Russian name.

with its transition to viviparous reproduction, are features that distinguish it from all other viviparous fish in general. The fecundity of other viviparous fish is very low and the egg size is large--much larger than those of their non-viviparous relatives. Moreover, their relatives have lost the larval stage in their life cycle. The offspring released are large like the adult fish^{and}, lead a benthonic way of life. The peculiarities of golomanka development, i.e. the increased fecundity and the inclusion of larval features together with the viviparity, indicate that in the conditions prevailing in Lake Baikal, mortality in the pelagic zone is so elevated compared to the mortality at the bottom, that it is necessary not only to increase the fecundity but also to change to viviparity which increases the survival rate during the early stages of the life cycle. According to the observations of D. N. Taliev, under the conditions in Lake Baikal, the fish of other, related families, which only partially adapt themselves to the pelagic zone, also increase their fecundity in comparison with their benthonic relatives.

The development of golomanka has not yet been studied. Only their larvae have been described by Korotnev.

19. Casterosteidae build nests using slime and fragments of plants as building materials. The eggs are deposited in these nests and protected. These fish are of marine origin.

20. Cadidae is a marine family of typically pelagic fish. Only the burbot lives and reproduces in fresh water.

It has partially preserved the adaptations of its arctic marine ancestors and partially modified them according to the living conditions in fresh water. The burbot is a semi-pelagophilous fish. It spawns in winter like most of the marine gadoids do (during the coldest season, when water temperatures on the spawning grounds reach 0.5 to 0.6 C). Spawning takes place in shallow water areas on pure sand bottoms. Development within the membrane takes place throughout the winter and the embryos emerge at the beginning of spring. The eggs are about 1 mm in diameter, with a very large oil droplet and a slightly sticky transparent membrane which forms an insignificant perivitelline space. In spite of the presence of a large oil droplet, the eggs sink and develop on the bottom in still water (in lakes). Within river currents the eggs may float. When emerging from the membranes, the embryos are structured like typical pelagophils (Fig. 100, A). They do not have respiratory organs and the erythrocytes appear late. The gills also appear late, during the larval stage. The front end of the dorsal fin fold is expanded forming a cavity which enhances the buoyancy of embryos and larvae. The large oil droplet is resorbed late in the larval stage, after resorption of the yolk. The droplet fulfills the role of a swim bladder, i.e. it reduces the specific gravity of the embryos, allowing them to swim upwards after hatching and to remain floating thus avoiding the bottom. Black pigmentation covers the body quite densely. Like all gadoids, the vent opens on the side of the unpaired fin fold, not dividing it into anal and pre-anal (294)

parts. The marine gadoids differ from the burbot in that their pelagic eggs are smaller and are completely without an oil drop (cod) or the oil droplet is very small (hake, Fig. 100, B).

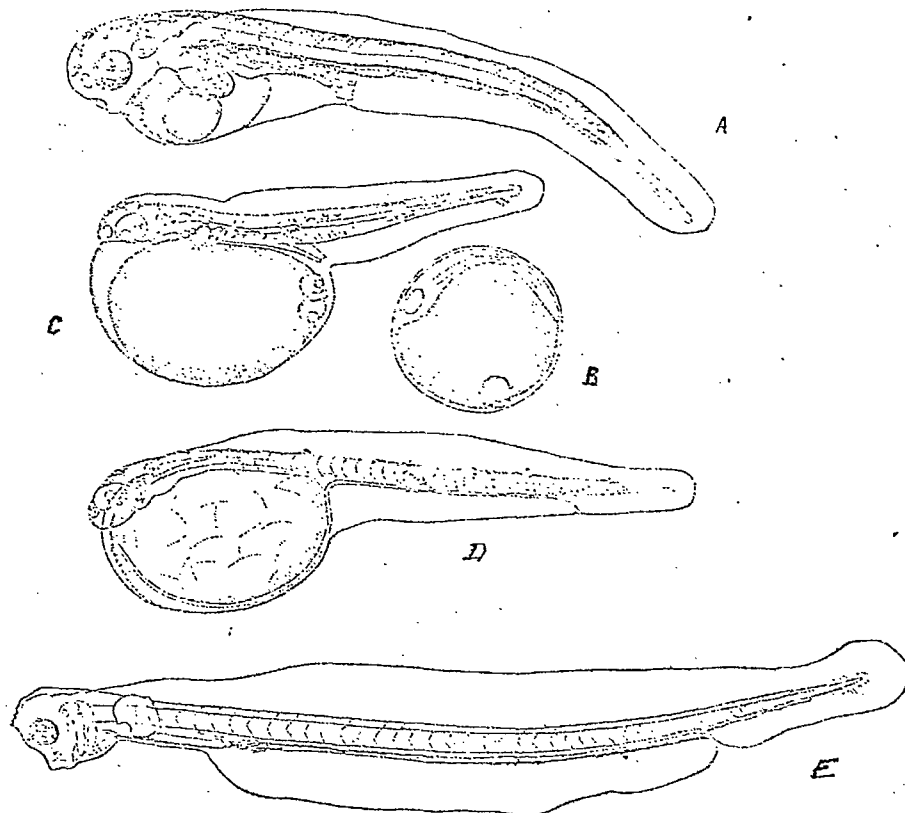


Рис. 100.

A — *Lota lota*, выплывший из оболочки. Большая жировая капля помогает всплывать. B — *Caidropsarus tricirratus* в яичной оболочке. B — она же после вылупления. Жировая капля мала. Эмбрионы и личинки pelagические. D и E — *Sprattus sprattus*. Pelagический эмбрион (D) и личинка (E) без жировой капли.

Fig. 100.

A-*Lota lota*, newly hatched. Large oil droplet helps to swim upwards. B-*Caidropsarus tricirratus* within the egg membrane. C-the same after hatching. The oil droplet is small. The embryos and larvae are pelagic. D and E-*Sprattus sprattus*. Pelagic embryo (D) and larva (E)-without oil droplet.

This is explained by the simplicity of conditions insuring the buoyancy of eggs and embryos in the dense sea water,

where flotation is possible even without the oil droplet (Fig. 100, D-E). Black pigment does not cover the embryo's body very densely because they live near the water surface, far from the bottom (embryos and larvae of burbot remain a short distance from the bottom and later settle on the bottom permanently).

21. Syngnathidae are marine fish. The males carry the eggs either on the surface of the belly (Nerophis) or on the tail in special pouches (the other Syngnathidae). Species which have penetrated freshwater reservoirs have preserved all principal adaptations of their marine ancestors.

A short ecological description of our freshwater fish families is given in Table 78.

10. On the specificity of ecological groups.

In an ecological sense, orders, families and lower systematic categories of fish are specific. Among all fish in general, the cyprinids, in an ecological sense, are apparently noted for their great abundance of variety. In our ichthyofauna they are represented by seven ecological groups (Table 78); most of the other orders are represented by only one ecological group. Among the families of our freshwater ichthyofauna, the cyprinids are the leaders (six ecological groups), with respect to ecological behavior, followed by the catfishes and loaches (each represented by two ecological groups). All other families, from an ecological point of view, are homogeneous. (295)

(292)

Table 78

(293)

Table 78

1) Ecological description of freshwater fish families (families and the number of species are mainly according to L. S. Berg, 1932-1933).

2) families; 3) number of species (or subspecies) in families or groups; 4) scatter their eggs; 5) hide; 6) protect; 7) lithophilous; 8) indifferent; 9) phytophilous; 10) pelagophilous; 11) semi-pelagophilous; 12) psammophilous; 13) ostracophilous; 14) eggs layed in layers; 15) eggs layed in clusters; 16) build nests; 17) in soil; 18) on the surface; 19) carry the eggs; 20) viviparous; 21) unknown; 22) total number of species in groups; 23) absolute number; 24) in % of the total number of species.

Among the ecological groups of our cyprinids the largest is the lithophilous group (89 species and subspecies; Table 64 and 1); it is followed by the phytophilous group (25 species) and others; the ostracophils with 3 species rank last. Among the loaches, first place belongs to the psammophilous group (23 species), followed by the phytophilous group. Among the catfishes, the forms which in one way or another protect their eggs apparently dominate.

Among the ecological groups of cyprinids the ostracophils do not have analogues in other families, i.e. this group is absolutely specific; the psammophilous group has its analogue only in the related family of loaches. Although the other groups (lithophilous, phytophilous and pelagophilous) do have analogues in many other, non related families, they

nevertheless also have their specificity. Thus the lithophilous cyprinids, among other things, differ from other lithophils in their habit of hiding themselves, after hatching, under stones where they lie on the ground and are photophobic, whereas the lithophilous acipenserids (the stellate sturgeon) are not photophobic, do not rest on the bottom but swim to the surface, etc. The phytophilous cyprinids, after emerging from the egg remain quietly suspended in daylight; the phytophilous catfishes hide on the bottom, breathe actively and are photophobic; the phytophilous Eleotridae lead a pelagic way of life etc.

Ecologically, the subfamilies, groups and subgroups of cyprinids are also specific (Table 79). The Barbini are mainly characterized by the lithophilous (mountain) and ostracophilous forms, the Gobionini--by the psammophilous and pelagophilous groups; the Leuciscini--by the lithophilous (flatland) and phytophilous groups.

Ecologically, the cyprinid subfamilies, like the whole family, are diversified: the Barbini are represented by three ecological groups; the Gobionini probably by four, etc. In contrast, the systematic groups and subgroups, Leuciscini excepted, are not only specific in an ecological sense but ^{are} also entirely homogeneous (Table 79). Thus, all the Barbina are exclusively lithophilous fish, Cyprinina--phytophilous, Rhodeina--ostracophilous, etc. However, the Leuciscina group differs from all other groups by its diversified ecological relations: its subgroup Leuciscinae

is represented by three ecological groups--lithophilous, phytophilous and pelagophilous, and even its genera--Abramis and Phoxinus--are each represented by two ecological groups, the lithophilous and phytophilous, while the genera of all other systematic groups are uniform.

The ecological groups of all families, except the Cyprinidae, are completely homogeneous from a systematic point of view; the species forming them are linked by direct relationships and there is no parallelism within them. Thus all the Acipenseridae and all the Coregonidae are lithophilous fish; the Clupeidae, with only one exception, are pelagophils, etc. Among the loaches, all Nemachilini are psammophilous fish while all Cobitini are phytophilous, etc. In contrast, among the Cyprinidae there are only two groups, the psammophilous and the ostracophilous, as well as one subgroup of the lithophilous Barbini, which are entirely homogeneous; the pelagophilous and phytophilous groups and the subgroup of lithophilous Leuciscini are heterogeneous, i.e. they are formed by species which have developed parallelly and are not directly related. The heterogeneity and parallelism of ecological groups are shown in Table 80. Evidently the (296) phytophilous group is heterogeneous because it is formed of species which are not directly related and belonging to the subfamilies Barbini, Leuciscini and Danionini, as well as to Cobitini. As mentioned previously, the most heterogeneous group is the group of pelagophilous cyprinids: in every one of the subfamilies which form this group, most of the species

Table 79

1) Ecological description of the systematic groups and subgroups of cyprinids.

Таблица 79

1 Экологическая характеристика систематических групп и подгрупп карповых рыб

2 Подсемейства	3 Систематические группы	4 Систематические подгруппы	5 Экологические группы
Barbini	Barbina	Barbinae Schizothoracinae	6 Литофильные горные »
	?	«Barbus» phutunio	7 Фитофильные
	Cyprinina		»
	Rhodeina	Rhodeinae Acanthorhodeinae	8 Остракофильные »
Gobionini	Gobionina	Gobioninae Paraleucogobioninae(?)	9 Псаммофильные 1 Пелагофильные
	Sarcochilichthyna		»
	Armatogobionina	Armatogobioninae Gobiobotinae	» »
	Pseudogobionina		11 Защищающие псаммофильные
Leuciscini	Leuciscina	Leuciscinae	12 Литофильные равнинные 7 Фитофильные 10 Пелагофильные
		Pelicinae	»
		Cultrinae	»
	Tincica		7 Фитофильные
Danionini	Danionina		»

2) subfamilies; 3) systematic groups; 4) systematic subgroups; 5) ecological groups; 6) mountain lithophils; 7) phytophilous; 8) ostracophilous; 9) psammophilous; 10) pelagophilous; 11) protecting, psammophilous; 12) flatland lithophils.

have even evolved parallelly; for instance the pealgophilous chekhon evolved parallel to the vostrobriushka, etc. Less evident is the heterogeneity of the lithophilous Leuciscini. However the heterogeneity is certain because some of its species have direct relatives among the phytophilous fish (the breams, minnows, bleaks). (297)

The homogeneity of some groups and the heterogeneity of others also reveal their faunic components (complexes, according to G. V. Nikol'skii, Table 81). The heterogeneous, lithophilous Leuciscini are recruited from boreal, subalpine, Ponto-Caspian freshwater, tertiary flatland and Fore-Asian components; the phytophilous cyprinids come from boreal flatland, Ponto-Caspian freshwater, tertiary flatland and Turkestan flatland components; the pelagophilous cyprinid group is formed from Ponto-Caspian freshwater and Chinese flatland components.

The homogeneous groups are represented by uniform faunic components. Thus the lithophilous Barbini are represented by the related Fore-Asian and Asiatic mountain components; the acipenserids--mainly by tertiary flatland; the coregonids--by Arctic freshwater components, etc.

11. The patterns of distribution of ecological groups by water bodies.

1. General ecological description of the freshwater ichthyofauna.

In our freshwater reservoirs fish which do not protect, but scatter their eggs predominate. They represent 74.5% of all species forming the ichthyofauna (Table 90). By excluding Lake Baikal and the Amur River--very peculiar water bodies, differing from other water reservoirs by their abundance of egg protecting and hiding fish--the number of fish species which are present in our ichthyofauna and which disperse their eggs, would rise to 76.2 %. The remaining 23.8% represent fish species which hide and protect their eggs.

In order to indicate their significance, the ecological groups are arranged in decreasing order of number of species, as is shown in Table 82. The lithophilous group of fish which do not protect their eggs ranks first (37%), followed by the psammophilous (11%) and phytophilous (10.5%) groups and by the lithophilous group of egg hiding fish (8.5%). These four groups together constitute the typical basis of our freshwater ichthyofauna (67.22%). The pelagophilous group of fish, followed by two groups of egg protecting fish occupy an intermediate position, each taken separately comprising from 8.36 to 4.15%, but together 18.54%. The remaining 8 groups altogether contain only 12.6% of the species, individually containing from 1.6 to 0.28%.

(298)

Table 80

Distribution of studied species of Cyprinidae and Cobitidae families among the ecological groups.

Table 80

Таблица 80

Распределение изученных видов семейства Cyprinidae и Cobitidae по экологическим группам

Экологические группы Ecological groups		Family Семейство Cyprinidae				Family Семейство Cobitidae	
группы groups	подгруппы subgrps	подсемейство Barbini subgroup	подсемейство Leuciscini subgroup	подсемейство Cobitini subgroup	подсемейство Barbioidi subgroup	подсемейство Nemacheilini subgroup	подсемейство Cobitini subgroup
Lithophilous каменистые	Barbini	<i>Barbus goktschaticus</i> <i>Varicorhinus capota seiangi</i> <i>Diplocheilus dybowskii</i> <i>Schizothorax pseudaksuensis</i>					
	Leuciscini		<i>Leuciscus schmidtii</i> " <i>danilevskii</i> " <i>cephalus</i> " <i>aphipsi</i> " <i>waleckii</i> <i>Aspius aspius</i> <i>Phoxinus phoxinus</i> " <i>colchicus</i> " <i>lagovskii</i> <i>Abramis sapa</i> <i>Vimba vimba n. carinata</i> <i>Chalchaburnus chalcoides</i> <i>Okondrostoma borysheni-cula</i>				
Intermediate промежуточные			<i>Leuciscus leuciscus?</i> <i>Leuciscus idus</i>				

Фитофильные Phyto- philous	<i>Barbus phutu- nio</i> <i>Cyprinus carpio</i> <i>Carassius caras- sius</i> <i>Carassius auratus gibelio</i>	<i>Phoxinus phoxinus</i> <i>Tinca tinca</i> <i>Scardinius erythro- phthalmus</i> <i>Rutilus rutilus</i> <i>Rutilus rutilus caspius</i> <i>Abramis brama</i> <i>Blicca bjoerkne</i> <i>Leucaspis delineatus</i> <i>Alburnus alburnus</i>		<i>Danio malabaricus</i> (по Н. С. Марошню)	I. S. Lagoiko's data	<i>Alisgornus fos- silis</i> <i>Cobitis taenia</i>
Псаммофильные Psammo- philous			<i>Gobio gobio</i> <i>Gnathopogon us- suriensis</i> <i>Hemibarbus macu- latus</i>			<i>Nemachilus bar- batulus</i> <i>Nemachilus steli- czkai</i> <i>Nemachilus dor- salis</i> <i>Nemachilus stru- achi</i> <i>Lefua esata</i> (по Учиды)
Пелагофильные Pelago- philous		<i>Pelteus cultratus</i> <i>Ctenopharyngodon idella</i> <i>Hypophthalmichthys molitrix</i> <i>Hemiculter leucisculus</i> <i>Xenocypris macrolepis</i> и другие <i>Cultrini</i>	<i>Sarmachilichthys sinensis lacustris</i> <i>Paraleucogobio soldatovi</i> <i>Armatogobio da- bryi</i> <i>Rostrigobio amu- rensis</i> <i>Gobiobotia</i> sp.			Uchida's data
Остракофильные Ostraco- philous	<i>Rhodeus amarus</i> » <i>sericus</i> <i>Pseudoperilampus</i> (?) sp. <i>Alcanthorhodcus asmussi</i>					
Охраняющие псаммо- фильные Protecting, Psammophilous			<i>Pseudogobio riu- laris</i>			

1) Faunic components of the ecological groups and subgroups.

Digits indicate the number of species (compiled from G. V. Nikol'skii's data).

1 Фаунистические компоненты экологических групп и подгрупп
Цифры указывают количества видов. (Составлено по данным Г. В. Никольского)

Таблица 81

2		3		4 Фаунистические компоненты													
Экологические группы, подгруппы и т. д.		Семейства и подсемейства		арктиче-ские пре-свод-ные	арктиче-ские мор-ские	бореаль-ные пред-горья	бореаль-ные рав-нинные	понтон-каспийские пресво-дные	понтон-каспийские морские	терети-ные рав-нинные	китай-ские рав-нинные	тузем-ские рав-нинные	передне-азий-ские	кавказ-ские	индо-азиат-ские		
не прилежные и не ограниченные	18 литофильные	Leuciscini Barbini Acipenseridae Coregonidae	1 — — 6	— — — —	3 — — —	— — — —	— — — —	8 2(?) — —	— — — —	3 — 7 —	— — — —	— — — —	3 1 — —	— — 3 —	— — — —		
	19 промежуточные	Leuciscini	—	—	—	2	—	—	—	—	—	—	—	—	—		
	20 индифферентные	Percidae	—	—	—	2	2	—	—	—	—	—	—	—	—		
	21 фитофильные	Cyprinidae Cobitidae Siluroidei Pisocidae	— — — —	— — — —	— — — —	4 1 — —	5 — — —	— — — —	— 1 1 1	— — — —	2(?) — — —	— — — —	1 — — —	— — — —	— — — —		
	22 пелагофильные и полупелаго-фильные	Cyprinidae Clupeidae Serranidae Osmeridae и Cladidae	— — — 2	— — — —	— — — —	— — — —	1 — — —	— 4 — —	— — — —	— — 1 —	19 — — —	— — — —	— — 1 —	— — — —	— — — —		
	23 псаммофильные	Cyprinidae Cobitidae	— —	— —	— 1	— —	— —	— —	— —	4 —	5 1	— 2	— 4	— 2	— —		
	24 остракофильные	Cyprinidae	—	—	—	—	—	—	—	—	4	—	—	—	—		
	25 литофильные	Salamandridae и Thymallidae	3	—	2	—	—	—	—	—	—	—	—	—	—		
	ограниченные	26 литофильные	Cobitidae Cottidae	— —	— 1	2	—	—	— 6	— —	— —	— —	— —	— —	— —	— —	
		27 фитофильные	Siluroidei	—	—	—	—	—	—	—	1	—	—	—	—	3(?)	
28 гнездящиеся		Gasterosteidae Bagridae Ophecephalidae	— — —	— — —	— — —	— — —	— — —	— — —	1 — —	— — —	— — —	— — —	— — —	— — —	1(?) 1		
29 планктоникающие		Syngnathidae	—	—	—	—	—	—	4	—	—	—	—	—	—		

- 2) ecological groups; 3) families and subfamilies; 4) faunic components;
 5) arctic, freshwater; 6) arctic, marine; 7) boreal, subalpine;
 8) boreal, flatland; 9) Ponto-Caspian, freshwater; 10) Ponto-Caspian
 marine; 11) tertiary, flatland; 12) China, flatland; 13) Turkestan,
 flatland; 14) Fore-Asian; 15) mountain, Asiatic; 16) Indo-African;
 17) not hiding, not guarding; 18) lithophilous; 19) intermediate;
 20) indifferent; 21) phytophilous; 22) pelagophilous and semi-pelagophilous;
 23) psammophilous; 24) ostracophilous; 25) hiding; 26) lithophilous;
 27) phytophilous; 28) guarding; 29) nest-building; 30) carrying.

1) Arrangement of ecological groups of freshwater fish in order of their numerical significance.

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Распределение экологических групп пресноводных рыб в порядке их значимости

Таблица 82

№ п. п.	2 Экологические группы		Количество видов в группе (в % от общего количества видов) 3	Происхождение группы 4	Морские аналоги пресноводных групп 5	
1 2 3	Разбрасывающие 6	Литофильные . . 7 . . Псаммофильные . . 8 . . Фитофильные . . 9 . .	37.12 11.08 10.52	10 Пресноводные	11 Нет :	
4	Прячущие 12	Литофильные 7	8.5	10 Пресноводные	11 Нет	
5	Разбрасывающие 6	Пелагофильные 13	8.3	14 Смешанные	—	
6	15 Охраняющие	16 Откладывающие кучей	Литофильные . . 7 . .	6.019	17 Морские	—
7		18 Распластывающие	Литофильные . . 7 . .	4.15	17 Морские	—
8	Разбрасывающие 6	Индиферентные 19	1.4	10 Пресноводные	11 Нет	
9		Полупелагофильные 20	1.08	17 Морские	—	
10	Строящие гнезда на поверхности 21		1.68	14 Смешанные	—	
11	Охраняющие 15	Фитофильные 9 . . .	1.5 (?)	10 Пресноводные	11 Нет (?)	
12	Прячущие 12	Остракофильные 22	1.12	10 Пресноводные	11 Нет (?)	
13	Охраняющие 15	Вынашивающие 23	1.12	17 Морские	—	
14		Живородящие 24 . .	0.54	10 Пресноводные	26 Имеется	
15	Строящие гнезда в земле 25		0.54	10 Пресноводные	11 Нет	

2) ecological groups; 3) number of species in one group (in % of the total number of species); 4) origin of a group; 5) marine analogs of freshwater groups; 6) dispersing; 7) lithophilous; 8) psammophilous; 9) phytophilous; 10) freshwater; 11) none; 12) hiding; 13) pelagophilous; 14) mixed; 15) protecting; 16) depositing in clusters; 17) marine; 18) depositing in a layer; 19) indifferent; 20) semipelagophilous; 21) building nests on surface; 22) ostracophilous; 23) carrying; 24) viviparous; 25) building nests in ground; 26) exist.

All groups of fish, which do not protect their eggs, except the pelagophilous and semipelagophilous groups, i.e. the lithophilous, psammophilous, phytophilous and indifferent (No. 1, 2, 3 and 8 in Table 82), by their origin, are entirely of freshwater origin. The lithophilous and ostracophilous fish that hide, but do not guard, their eggs are also of freshwater origin. Among the egg-protecting fish of freshwater origin, are the phytophilous and viviparous groups which build their nests in the bottom soil.

The pelagophilous fish groups that build nests on the surface of the bottom (No. 6 and 9) are of mixed origin: they are composed of species which have begun their existence parallelly, partly in freshwater and partly in the sea. Among the pelagophilous fish, the herrings and sea basses (2.52%) are of marine origin and cyprinids of freshwater origin (3.08%). Among the nest builders of marine origin are the sticklebacks (1.4%) and of freshwater origin--the snakeheads. The groups of semi-pelagophilous fish and the egg-protecting fish of the lithophilous group, which either spread their eggs or deposit them in clusters (12.48%) are also of marine origin. However, they evolved progressively in freshwater and created not only (302) new species but also a new, strictly freshwater family--Cottocomephoridae, which has preserved the basic adaptations of its group. The group of fish which carries its eggs (Syngnathide) is entirely marine; this group partly penetrated freshwater but did not produce anything new there (1.12%). On the whole, about 17% of the fish species in the various

ecological groups of our freshwater ichthyofauna are of marine origin. All typically freshwater groups, except the group of viviparous fish, i.e. eight out of nine, do not have analogs in the marine ichthyofauna and they reflect the peculiarities of the freshwater environment. This indicates that in our freshwater, in contrast to the seas, the conditions are particularly favorable for fish which do not protect but disperse their eggs on the bottom, i.e. for the lithophilous, psammophilous, phytophilous, and indifferent fish, as well as for the fish which hide their eggs in the ground. For the former such favorable conditions consist of a low abundance of egg predators (gobies, crabs, etc.) and spring floods which create the necessary conditions; for the second category the favorable conditions are--the absence of wave action i.e. the immobility of shore ground and the presence of spring brooks, indispensable for the preservation and aeration of the buried eggs.

The viviparous group (golomankas) by convention has its analogs among marine fish. However, essentially it is entirely original. As mentioned, the golomankas are the only viviparous fish which, in contrast to the others, have increased their fecundity and have acquired, in their development, larval features associated with viviparity, and predetermined by the specific environmental conditions of Lake Baikal.

The historical analysis of the ichthyofauna of some of our rivers (Volga, Amur, Pechora, Amu-Darya and Murgaba), of our rivers (Volga, Amur, Pechora, Amu-Darya and Murgaba), performed by G. V. Nikol'skii (1947), shows that it represents

a heterogeneous complex of species, derived from at least twelve faunas of various antiquities and distributions. The modern species of each of these faunas can be grouped into corresponding faunal groups (called complexes by G. V. Nikol'skii and other authors). These faunal groups have not only species but also ecological specificity and provide an idea about the origin of ecological groups. Of course, the ecological description of modern faunal groups cannot be faultless until a flawless historical analysis of the whole freshwater ichthyofauna has been performed.

The ecological characteristics of the twelve faunal groups established for the above mentioned rivers are shown in Table 83.

In contrast to the others, only the arctic freshwater fauna has produced lithophilous salmonids, which hide their eggs in the ground and non-hiding lithophilous coregonids. Among the modern representatives of this group the phytophils are completely absent as are all other fish. The boreal subalpine fauna produced the lithophilous graylings, close relatives of the salmon. In addition to these fish, the lithophilous ^{cyprinids (Leuciscini)} psammophilous loaches and the egg protecting underrock goby belong to this group but they are not originals.

The boreal flatland fauna consists of only phytophilous fish of three families (besides the catfishes) and their close relatives--the intermediate and indifferent fish. In this group the phytophilous cyprinids dominate; the lithophilous this group the phytophilous cyprinids dominate; the lithophilous and all other fish are absent.

Pechora.

Таблица 83

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Фрагментические группы

1) Arctic; 2) boreal, subalpine; 3) boreal, flatland; 4) Ponto-Caspian; 5) tertiary, flatland; 6) Turkestan, flatland; 7) Fore-Asian; 8) Asian, mountain; 9) China, flatland; 10) Indo-African; 11) Arctic; 12) Ponto-Caspian; 13) faunal groups; 14) freshwater; 15) marine; 16) non protecting; 17) hiding; 18) protecting; 19) lithophilous; 20) intermediate; 21) indifferent; 22) phytophilous; 23) pelagophilous; 24) semi-pelagophilous; 25) psammophilous; 26) ostracophilous; 27) nest builders; 28) carrying; 29) depositing in one layer; 30) depositing in clusters.

In the Ponto-Caspian freshwater fauna, in contrast to other faunas, the lithophilous Leuciscini (8 species) which originated there predominate. This fauna has also produced the only European pelagophilous carp--the chekhon; the phytophilous cyprinids here are more numerous than in any other group but there are no phytophilous fish of other families. Moreover it also produced the indifferent perches. The lithophilous (304) Barbini found here are not originals: their origin is linked to the Asiatic fauna. No other fish are found in this group.

The tertiary flatland group is the most varied in ecological terms. Its modern group is represented, in contrast to the others, by all four phytophilous families (by one species of each), i.e. also by the phytophilous catfish. In this group the psammophilous gudgeons and the lithophilous salmonids appeared; the lithophilous Leuciscini are also present, but in much lesser abundance than in the Ponto-Caspian fauna. Besides all these fish which do not protect their eggs, the egg guarding phytophilous catfish and the egg hiding species of ostracophilous cyprinids appeared in this group. The latter is not an original--it originates from the ostracophilous bitterlings from the China flatland fauna.

The Asiatic faunal groups--the Turkestan, the Fore-Asian and the Asian-alpine--produced the psammophilous loaches. They are particularly abundant in the Fore-Asian faunal group. The Asian-alpine group differs from the other groups group. The Asian-alpine group differs from the other groups in its abundance of original lithophilous Barbini, adapted to

life conditions in high-mountain rivers and in the absence of other fish, except the psammophilous loaches.

The faunal group of China's flatlands differs from the other groups in the extraordinary abundance of original pelagophilous and ostracophilous cyprinids, in the great numbers of psammophilous cyprinids and in the total absence of lithophils, phytophils and also egg protecting fish.

The Indo-African group differs from the other freshwater groups in the prevalence of nest building and egg protecting fish. Fish which do not protect or hide their eggs are completely absent.

The marine faunal groups--the Arctic and Ponto-Caspian--like the Indo-African group, differ from other freshwater groups in the prevalence of fish which protect their eggs (of the species which do not protect their eggs, only the pelagophilous fish are present among the members of the Ponto-Caspian fauna). Moreover, these two groups differ from each other mainly in the peculiarities of the egg protecting lithophilous fish: the Ponto-Caspian forms (Gobiidae) deposit their eggs on stones in a dense layer while the Arctic forms (Cottidae) deposit their eggs in clusters. This, at first glance an insignificant difference, actually reflects some important ecological peculiarities of the nordic fauna and of the southern seas because this difference regularly extends to the other marine fish families which protect their eggs.

2. Rivers.

In ecological terms, the ichthyofauna of large rivers is more diversified than those of the lakes and seas into which the rivers flow. In part this can be explained by the greater length of the rivers, by the variations of their level depending on spring flooding and other factors which create a variety of conditions favorable for the reproduction of fish.

Rivers which have many common features in their ichthyofaunas, at the same time differ in ecological groups and the quantitative ratio of their species. These differences, as well as the similarities, depend on the nature of the whole ecological condition of the river; therefore the variations in the composition of ecological groups have a regular pattern, which becomes clearly evident when the ichthyofaunas of various basins are compared.

All ecological groups of fish present in our rivers, and their quantitative composition by species, are shown in Tables 84 and 85. The percentage ratios of the quantitative compositions of the leading ecological groups are shown in Table 87. (305)

When rivers of northern basins are compared, it becomes evident that the rivers of the Baltic Sea basin differ sharply from rivers of the Arctic Ocean basin. Only in the former are there pelagophilous and ostracophilous cyprinids, lithophilous barbels and phytophilous catfish; the phytophilous lithophilous barbels and phytophilous catfish; the phytophilous

1) Ecological groups of fish of the Volga River, the rivers of northern Europe, Siberia and the Far East.

(the Amur River is shown twice for convenience of comparison with other rivers).

Таблица 84

1) Экологические группы рыб Волги, рек Северной Европы, Сибири и Дальнего Востока

(Амур указан дважды для удобства сравнения его с другими реками)

16	2	Река	3 Абсолютное количество видов в группах																														
			4 не охраняющие										5 привлекающие		6 охраняющие			15 мипа- наево- щие															
			7 митофильные				8 инди- фе- рент- ные	9 фитофильные				10 пелаго- фильные		12 пела- мо- филь- ные	13 мито- филь- ные	14 остра- но- филь- ные	7 мито- филь- ные		9 фито- филь- ные	14 различно группую- щиеся													
			Leuciscini	Barbini	Acipenseridae	Coregonidae		Percidae	Cyprinidae	Cobitidae	Siluridae	Esocidae	Cyprinidae								Clupeidae	Serranidae	Osmorhizidae	Lota	Cyprinidae	Cobitidae	Salmonidae и Thymallidae	Cyprinidae	Gobiidae	Cottidae	Siluridae и Bagridae	Eleotridae	Gasterosteidae
17	18	Амур	5	—	2	2	—	3	2	2	1	19	—	1	2	1	7	2	6	9	1	5	2	1	1	2	2	1	—	—			
		Волга	11	1	4	2	4	11	2	—	1	1	3	—	1	1	1	2	1	3	1	5	1	1	—	1	—	—	—	1			
		Висла	10	2	1	2	3	9	2	—	1	1	—	—	1	1	1	1	3	1	—	2	1	—	2	—	—	—	—	1			
		Западная Двина	7	—	1	2	3	9	2	—	1	1	—	—	1	1	1	1	3	1	—	—	1	—	2	—	—	—	—	—			
19	20	21	22	Нева	7	—	1	4	3	8	2	—	1	1	—	—	1	1	1	4	—	—	3	1	—	2	—	—	—	—			
				Северная Двина	7	—	—	3	2	6	—	—	1	—	—	—	1	1	1	1	3	—	—	2	—	—	—	—	—	—	—		
				Печора	4	—	1	5	2	2	—	—	1	—	—	—	1	1	1	1	2	—	—	2	—	—	—	—	—	—	—		
				Обь	8	—	2	7	2	5	1	—	1	—	—	(1)	1	1	1	1	4	—	—	3	—	—	—	—	—	—	—		
23	24	25	26	27	28	29	Енисей	6	—	2	3	2	5	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—			
							Лена	3	—	1	9	2	5	1	—	1	—	—	—	1	1	1	1	5	—	—	6	—	—	—	—	—	—
							Колыма	4	—	2	9	2	5	1	—	1	—	—	—	1	1	1	1	6	—	—	3	—	—	—	—	—	—
							Тюмень	4	—	2	9	2	5	1	—	1	—	—	—	1	1	1	1	5	—	—	2	—	—	—	—	—	—
30	31	32	33	34	Амур	1	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
					Камчатка	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
					Тыма	2	—	1	—	—	2	—	—	1	—	—	—	2	1	—	1	7	—	—	1	—	—	—	—	—	—		
					Амур	5	—	2	2	—	3	2	2	1	19	—	1	2	1	7	2	6	3	1	1	2	1	1	2	2	1	—	

2) rivers; 3) total number of species in groups; 4) non protecting;
 5) hiding; 6) protecting; 7) lithophilous; 8) indifferent;
 9) phytophilous; 10) pelagophilous; 11) semi-pelagophilous;
 12) psammophilous; 13) ostracophilous; 14) various nest builders;
 15) carrying; 16) basins; 17) Amur; 18) Volga; 19) Baltic; 20) Visla;
 21) Daugava; 22) Neva; 23) Arctic Ocean; 24) Severnaya Dvina; 25) Pechora;
 26) Ob; 27) Enisei; 28) Lena; 29) Kolyma; 30) Pacific Ocean; 31) Anadyr;
 32) Kamchatka; 33) Tym; 34) Amur.

loaches there are also more abundant (Table 84). Regardless of these and other differences the northern rivers of Europe and Asia are characterized by a certain identical quantitative ratio between the fish species that care for their eggs and those which do not care for their eggs. The relative abundance of the former, within the area from the Visla River to the Ob River, varies within an insignificant range--from 21 to 24% and that of the other group from 76 to 80% (Tables 86 and 87). Only from the Enisey River to the Kolyma River does the ratio of fish that protect their eggs increase slightly (up to 30%) and the ratio of the non-protecting fish decrease correspondingly (to 70%). However, the leading ecological groups of both types of fish vary regularly in a direction from west to east. Among the ecological groups of fish which do not protect their eggs, the number of species in the phytophilous group gradually decreases from the Visla River to the Kolyma River: in the former they represent 27% whereas they represent only 6% in the latter; conversely, in the lithophilous (unified) group the number of species correspondingly increases from west to east--from 34 to 50%. However the relative importance of families in the ecological groups varies irregularly: the number of lithophilous acipenserids, living in all rivers, varies insignificantly--within the limits of 7 to 13%. Beyond the Visla River, the lithophilous barbels abruptly fall out of the composition of the ichthyofauna completely. The lithophilous Leuciscini which, in European rivers up to the Severnaya Dvina (inclusive),

Table 85

1) Ecological groups of fish in rivers of Black-Azov and Aral-Caspian Sea basins.

Таблица 85

1 Экологические группы рыб рек Черноморско-Азовского и Аральско-Каспийского бассейнов

6 Бассейн	7 Река	2 Абсолютное количество видов в группах														
		3 не охраняющие					4 охраняющие					5 охраняющие				
		8			9			10			11			12		
		лево- береж- ный	лево- береж- ный	лево- береж- ный	лево- береж- ный	лево- береж- ный	лево- береж- ный	лево- береж- ный	лево- береж- ный	лево- береж- ный	лево- береж- ный	лево- береж- ный	лево- береж- ный	лево- береж- ный	лево- береж- ный	лево- береж- ный
16 Черно- морский	Дунай . . . 17.	10	2	5	—	—	7	10	3	1	1	1	1	1	1	1
	Днепр . . . 18.	11	1	4	—	—	6	12	2	1	1	1	1	1	1	1
	Дон . . . 19.	12	1	4	—	—	6	11	2	1	1	1	1	1	1	1
	Кубань . . . 20.	13	1	3	—	—	4	9	2	1	1	1	1	1	1	1
	Илансукхо . . . 21.	14	1	—	—	—	—	12	2	1	1	1	1	1	1	1
24 Каспий- ский	Мезень . . . 22.	15	1	—	—	—	—	12	2	1	1	1	1	1	1	1
	Рейс Западнорус- ский . . . 23.	16	1	—	—	—	—	12	2	1	1	1	1	1	1	1
	Западнорус- ский . . . 24.	17	1	—	—	—	—	12	2	1	1	1	1	1	1	1
	Волга . . . 25.	18	1	4	—	—	4	11	2	1	1	1	1	1	1	1
	Терек . . . 26.	19	2	3	—	—	2	10	1	1	1	1	1	1	1	1
28 Араль- ский	Кур . . . 27.	20	6	4	—	—	2	8	1	1	1	1	1	1	1	1
	Сыр-Дарья . . . 28.	21	2	2	—	—	—	4	1	1	1	1	1	1	1	1
	Аму-Дарья . . . 29.	22	6	3	—	—	3	6	1	1	1	1	1	1	1	1
	Зеравшан . . . 30.	23	4	3	—	—	—	2	1	1	1	1	1	1	1	1
	Рейс Туркмен- ский . . . 31.	24	2	2	—	—	—	—	1	1	1	1	1	1	1	1

2) total number of species in each group; 3) not protecting; 4) hiding;
 5) protecting; 6) basins; 7) rivers; 8) lithophilous; 9) indifferent;
 10) phytophilous; 11) pelagophilous; 12) semi-pelagophilous; 13) psammophilous;
 14) ostracophilous; 15) nest builders and egg-carriers; 16) Black Sea;
 17) Danube; 18) Dniepr; 19) Don; 20) Kuban'; 21) Shansukho; 22) Mezyb';
 23) Rivers of West Trans Caucasus; 24) Caspian; 25) Volga; 26) Terek;
 27) Kura; 28) Aral; 29) Syr-Dar'ya; 30) Amu-Dar'ya; 31) Zeravshan;
 32) Rivers of Turkmenia.

predominate over the other lithophilous fish, representing from 58 to 70% of their composition by species, lose their predominant position beginning with the Pechora River. In the Enisey River and then in the Kolyma River their abundance has already decreased to 26%, i.e. a decrease of more than half. In conjunction with this variation in the lithophilous group of cyprinids, the group of whitefishes varies in the opposite direction, i.e. its importance gradually increases.

In the Visla River its relative importance is very low--only about 13%. In the Neva River it reaches 33% and in the Enisey River and other eastern rivers with 60% or more, it becomes the predominant group. Thus, the previously mentioned increase in the number of lithophilous fish in a west to east direction results exclusively from the increase in coregonids: they are the fish which gradually replace not only the lithophilous cyprinids but also the phytophilous fish in general. These variations in the nature and composition of ecological groups indicate that in an eastward direction those fish species which reproduce in spring and summer decrease, but those which spawn in fall and winter (white fishes) increase; the largest decrease is suffered by the phytophils, i.e. fish which prefer warm water and spawn in late spring and summer. The lithophilous Leuciscini, which are less inclined to warm waters and spawn in early spring, decrease somewhat less. These variations correspond to the changes in general ecological conditions of the rivers and in some way reflect the differences in climate. Among the

remaining groups of fish which do not protect their eggs, the pelagophilous group (in the north represented only by the chikhon), as mentioned, exist only in the rivers of the Baltic Sea basin. Farther east it is absent. The semi-pelagophilous and psammophilous fish are present in small, almost equal numbers, in all rivers of Europe and Asia. For these rivers, in comparison with the southern rivers, the very small number of psammophilous fish is typical.

In the group of fish which hide their eggs the (308) lithophilous salmonids and graylings gradually increase in abundance in a west to east direction: from .6.%^{in Visla River} to 16% in the Kolyma River. Of the lithophilous fish which protect their eggs only the underrock gobies are present in the northern rivers. They reach their maximum in the Enisey River (15%), ranking even above the salmonids. In other rivers they are less numerous (6 to 8%) and they are particularly scarce in the Daugava (Dvina) and Visla Rivers (2 to 3%).

In the northern rivers of the Pacific Ocean basin, in contrast to the rivers of the Arctic basin and of the Baltic Sea, the importance of fish which hide and guard their eggs increases sharply: in the Anadyr River it increases about three times reaching 63% (instead of the 16% in the Kolyma River), and in the Kamchatka River they reach the maximum in our rivers--85%. The major proportion among these fish belongs to salmonids: their relative abundance

* Translator's note: the digit is missing in the original.

in the Anadyr River is twice as high as that in the Kolyma River (36% instead of 16%), while in the Kamchatka River their number is twice as high as in the Anadyr River (71%).

In conjunction with these changes, the number of fish species that do not protect their eggs decreases sharply reaching their minimum in those rivers. Of these fish, only the lithophils (not counting the semi-pelagophilous smelt) remain in the Anadyr River, being two times (and by absolute numbers three times) less numerous than in the Kolyma River. Among them the coregonids acquire the primary position (80%) because of the dropout of the lithophilous acipenserids. Besides the coregonids, only the lithophilous cyprinids remain in small quantities (only one species). The other fish species that do not guard their eggs--the phytophils and psammophils--which are still present in the Kolyma River are absent in the Anadyr River.

In the rivers of Kamchatka there are no more lithophilous fish and the egg hiding salmonids predominate (with the egg guarding sticklebacks).

The absolute predominance of egg hiding (and protecting) fish species (85%), i.e. the absence of all fish which do not protect their eggs (except the semi-pelagophilous), distinguishes the Kamchatka rivers from the southern rivers of the Pacific Ocean basin and from the rivers of other basins as well.

In rivers south of Kamchatka, the number of ecological groups of fish increases again. In the Tym River, (on

Sakhalin Peninsula), the lithophilous, phytophilous and psammophilous fish species that do not protect their eggs appear again. In conjunction with this, the number of egg hiding and egg protecting fish decreases. The Gobiidae, which are absent in the northern rivers of Europe and Asia, and the ostracophilous cyprinids as well appear among them.

In the Amur River all leading ecological groups are already present, but their mutual ratio and their faunal composition are completely peculiar.

In the Amur River, the egg hiding and egg protecting species represent 26%, i.e. slightly more than in the large rivers of Europe and northern Asia. However, in contrast to the latter, there are only 9% phytophilous fish in the Amur River (Table 86), i.e. they are not very numerous--almost as many as in the impoverished Kolyma River, while in European rivers they represent about 25%. Lithophilous fish are also very scarce in the Amur River--only 12% (while in the Volga River they represent 31%). In contrast, the psammophilous cyprinids are more abundant in the Amur River than in European rivers. The Amur River is particularly rich in pelagophilous fish: at present 20 species are known, representing 27% of the whole composition of the Amur River ichthyofauna (actually they are certainly more numerous). Thus, among the ecological groups of fish which do not protect their eggs, the pelagophilous group ranks first in number of species, while in European rivers it is last. The second peculiarity of the pelagophilous group in the Amur River

consists of the fact that it is formed of cyprinid species exclusively, i.e. of typically freshwater fish (not considering one species of Serranidae), while the pelagophilous group in European rivers consists mainly of clupeids, i.e. marine fish, and has only one species of the Cyprinidae.

Among the egg hiding fish, the ostracophilous group (309) of bitterlings has its maximum in the Amur River, where it is represented by three species. It is completely absent in the rivers of Siberia while there is only one species in the European rivers. The egg protecting group in the Amur River is represented not only by families which inhabit the European and Siberian rivers (Gobiidae, Cottidae and Gasterosteidae), but also by families which are not encountered in our other rivers (Eleotridae, Bagridae and Ophicephalidae). Only the lithophilous Barbini, the indifferent perches and the pelagic herrings, characteristic of European rivers, are missing in the ichthyofauna of the Amur River.

All pelagophilous, ostracophilous, and partly the psammophilous fish, which distinguish the Amur River from all our other rivers, are related to the ichthyofauna of China's flatland. The egg protecting catfish and snakeheads are related to the Indo-African ichthyofauna. They have both penetrated the Amur River, coming from the rivers of China. The origin of Eleotridae is not yet known with certainty, probably it is of Indo-African origin (according to G. V. Nikol'skii).

The predominance of fish which protect their eggs in various ways (26%) and of the pelagophilous species (27%) as well as the small numbers of other fish which do not protect their eggs, i.e. the phytophilous and lithophilous fish, indicates that the Amur River environment is not suitable for the latter. The abundance of gudgeon species is detrimental to the lithophilous fish because gudgeons are egg predators; the peculiar inconsistency of spring flooding in the Amur River, which does not depend so much on the melting of snow in spring as on the summer rain fall, makes the conditions unacceptable to phytophilous fish, because of the insufficient grassland areas that become flooded. Of course, these conditions alone do not fully explain the ecological peculiarities of the ichthyofauna of the Amur River.

In the rivers of southern basins, moving from west to east and southeast, the general nature of the ecological groups varies in a manner opposite to that of the variations in the ecological groups of the northern basins (Table 85). Passing from the Azov-Black sea basin to the Caspian and Lake Aral basins, a decrease in the abundance of egg protecting and egg hiding species is observed. Simultaneously, an increase in the abundance in fish species which do not protect their eggs is observed; they reach their maximum in the farthest southeastern area--in the area of Zeravshan and in the rivers of Turkmen. These rivers are inhabited exclusively by fish species which do not protect their eggs.

The relative number of egg protecting and egg hiding species decreases from 23% in the Danube to 14% in the Syr-Dar and falls to zero % in the rivers of Turkmen. The number of non-protecting fish increases from 77% in the Danube River to 86% in the Syr-Dar River and to 100% in the rivers of Turkmen (Table 86). However, the various ecological groups of the fish species that do not protect their eggs do not vary uniformly. The pelagophilous group of fish, which reaches 8% in the basin of the Black Sea, loses its importance because of the dropout of clupeids, and is represented by only one species---the chekhon. It then disappears completely from the composition of the ichthyofauna. The group of phytophilous fish also decreases in importance---from 23% in the Danube River to 12% in the rivers of Turkmen, i.e. strictly speaking, like the pelagophilous group, it varies almost in the same manner as in the northern rivers. The unified group of lithophilous fish increases numerically from 26% in the Danube River to 50% in the Kura River and in the rivers of Turkmen, but does not rise above this level, i.e. actually, ^{the} change is not very significant and is completely identical to its changes in the northern rivers: from the Severnaya Dvina up to the Kolyma River. However the relative number of species of which this group is composed, varies in a different manner than in the northern rivers. The coregonids, which in the northern rivers acquire greater significance in a west to east direction, are completely absent in all southern rivers (except the Volga River). The acipenserids

in southern rivers occupy a much more important position than they do in the northern rivers, but in the south-eastern area they are not present in the ichthyofauna. The lithophilous Leuciscini in the northern rivers lose their significance (312) sharply and regularly in a west to east direction (from 70 to 20%), whereas in the southern rivers they suffer only an insignificant decrease (from 58 to 75% in the rivers of the Black and Caspian seas, and from 44 to 57% in the rivers of the Aral Sea). However the unified lithophilous group of southern rivers also includes the lithophilous Barbini, which are absent in the north (except in the Visla River). Progressing from the northern rivers of the Black Sea basin, where their number is insignificant (5 to 10%), in southeasterly and easterly directions, their proportion within the lithophilous group increases continuously (reaching 50% in the rivers of Turkmenistan) thus rising to the leading position. This regular change in the importance of lithophilous Barbini in the southern rivers is similar to the regular variations in the significance of the lithophilous Coregonidae in northern rivers (Table 26).

When faunal compositions of the unified lithophilous group in major rivers of all basins are compared, it becomes evident that there is not only parallelism of the numerical variations of Coregonidae and Barbini, but also a reciprocal replacement of each other taking place, i.e. a vicarious relation exists between these groups of fish.

(311)

Table 86

(312)

1. Соотношение между экологическими группами рыб в реках разных бассейнов *

2	3	4	5		6										7	8			
			Охраняющие и прилегающие		и о з р а н я ю щ и е											При- чущие	Охраняющего		
			9	%	10	11	12		14	15				15			15		19
							псаммофиль- ные			литофильные							лито- филь- ные	литофильные	
Бассейны	Р е к и	Абсолютное количество видов всех групп	абсолютное количество видов		всего (н %)	пелагофильные (н %)	всего (н %)	Nemachilini (н %)	фигофильные (н %)	всего (н %)	16	Corygoni- dae	Barbini	Leuciscini	Asipensae- ridae	Salmonidae и Thymallidae (н %)	разнотелые иные Gobulidae (н %)	отличающиеся мелкие Cottidae (н %)	прочие (иначе с о с т р а н о ж е н н ы м и) (н %)
20		21	22																
Балтий- ский	(Волга)	58	13	22	78	6	5	1	24	31	11	5	61	32	5	8	1	6	
	Волга	44	9	24	75	13	4	2	27	34	13	13	66	7	6	0	3	9	
	Западная Двина	33	8	21	79	2	5	2.5	31	25	20	0	70	9	7	0	2	10	
	Нева	41	10	24	76	12	5	2.5	26	26	33	0	58	8	9	0	7	7	
25		26	27																
Ледови- тоокеан- ский	Северная Двина	30	7	23	77	0	6	3	25	33	30	0	70	0	10	0	6	6	
	Печора	24	5	20	80	0	8	4	12	41	50	0	40	10	8	0	8	4	
	Обь	38	8	21	79	0	5	2.5	18	44	41	0	47	11	10	0	7	2	
	Енисей	40	12	30	70	0	5	2.5	17	37	60	0	26	13	12	0	15	2	
	Лена	36	10	27	73	0	5	2.5	16	41	60	0	33	6	15	0	8	2	
Колыма	30	8	26	74	0	6	3	6	50	60	0	26	13	16	0	6	3		
32		33	34																
Тихо- океан- ский	Амур	19	12	53	37	0	0	0	0	26	80	0	20	0	35	0	15	10	
	Камчатка	14	12	85	15	0	0	0	0	0	0	0	0	0	71	0	0	14	
	Тысь	23	13	56	44	0	4	4	13	13	0	0	66	33	30	4	4	17	
	Амур	75	19	25	64	27	12	2.7	11	12	22	0	55	22	8	1	2	15	
37		38	39																
Черно- морский	(Волга)	58	13	22	78	6	5	1	24	31	11	5	61	32	5	8	1	6	
	Дунай	63	15	23	77	6	6	1.5	23	26	0	11	58	30	6	8	3	6	
	Днепр	50	16	26	74	5	5	1.5	23	26	0	6	68	25	1	13	1	10	
	Дон	56	13	23	77	5	5	1.5	25	28	0	0	75	24	0	13	1	8	
	Кубань	49	13	26	71	8	8	4	24	24	0	8	66	25	2	18	0	6	
	Мезень	10	4	40	60	0	10	10	10?	40	0	0	100	0	0	40	0	0	
	Реки Западного Закавказья	44	13	29	71	4	4	2	22	34	0	20	53	26	2	18	0	9	
45		38	45																
Каспий- ский	Волга	58	13	22	78	6	5	1	24	31	11	5	61	32	5	8	1	6	
	Терек	37	6	16	84	2	10	5	32	32	0	16	58	25	2	8	0	5	
	Кура	50	8	16	84	2	8	6	20	50	0	20	60	20	6	4	0	6	
48		49	50																
Араль- ский	Сыр-Дарья	21	3	14	85	4	14	10	28	38	0	25	50	25	4	0	9	0	
	Аму-Дарья	35	2	6	91	2	14	11	20	45	0	37	44	18	2	0	0	2	
	Зеравшан	16	1	6	91	0	31	20	18	43	0	42	57	0	0	0	0	6	
	Река Туркменья	8	0	0	100	0	37	25	12	50	0	50	50	0	0	0	0	0	

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* Количество видов в группах выражено в процентах от общего количества видов в реке; в скобках Волга указана для сравнения.

Table 86

1) Ratio of ecological groups of fish in the rivers of various basins.

2) basins; 3) rivers; 4) total number of species of all groups; 5) protecting and hiding; 6) not protecting; 7) hiding; 8) protecting; 9) total number of species; 10) total (in %); 11) pelagophilous, (in %); 12) psammophilous; 14) phytophilous; 15) lithophilous; 16) relative significance of families within the group (in % of the total number of species in the group); 17) deposit eggs in a layer, Gobiidae (in %); 18) deposit eggs in clusters, Cottidae (in %); 19) others; together with ostracophilous), (in %); Baltic; 21) (Volga); 22) Visla; 23) Daugava; 24) Neva; 25) Arctic Ocean; 26) Severnaya Dvina; 27) Pechora; 28) Ob; 29) Enisei; 30) Lena; 31) Kolyma; 32) Pacific Ocean; 33) Anadyr; 34) Kamchatka; 35) Tym; 36) Amur; 37) Black Sea; 38) (Volga); 39) Danube; 40) Dniepr; 41) Don; 42) Kuban; 43) Mezyb; 44) Rivers of the west Trans-Caucasus; 45) Caspian; 46) Terek; 47) Kura; 48) Aral; 49) Syr-Darya; 50) Amu-Darya; 51) Zeravshan; 52) Rivers of Turkmen; *53) Numbers of species in groups is shown in % of the total number of species in the river; (Volga River is shown in paranthesis for comparison).

In northern rivers the psammophilous group is represented uniformly by two species only: one from the subfamily of gudgeons and one from the family of stone loaches (which disappear completely only in the extreme northeastern region). Therefore, the importance of this group there is not very great, but in the south it becomes the most important group, like the lithophilous group of Barbini. In rivers of the Black Sea and Azov Sea basins, this group is still as impoverished as it is in the north, with the difference that now the gudgeons dominate the group (2 species) over the

stone loaches (only one species; Table 85). In contrast, the number of gudgeons in the rivers of the Caspian and Aral Sea basins is most often limited to one species only, while the number of stone-loach species gradually increases from one to four in southern and southeastern directions. This increases their relative significance from 1.3% (in the Volga River) to 25% in the Zeravshan River. In the ichthyofauna of Middle-Asian rivers they acquire the same outstanding position as the lithophilous Barbini.

Unlike the northern rivers, the lithophilous Gobiidae and not the Cottidae are the most prevalent fish among the egg protecting species of the Black Sea and Caspian Sea basin. In the northern rivers, the relative importance of the Gobiidae is only slightly higher than that of the under-rock gobies. In rivers of the Lake Aral basin, except for the Syr-Dar River, the egg protecting lithophilous fish are completely absent. The tributaries of the Syr-Dar River are inhabited by only two species of underrock gobies, which distinguishes these rivers from the other rivers of the southern basin.

The northern rivers of the Black Sea-Azov Sea basin, from the point of view of the ratio of ecological groups, are similar to the rivers of the Baltic Sea basin. They differ negatively from the latter in their lack of lithophilous coregonids and semi-pelagophilous smelts and also by the lesser abundance of underrock gobies. Their positive differences are that they are inhabited by the Gobiidae and

pelagophilous Clupeidae, the barbels are distributed wider and there are more Percidae, Acipenseridae and psammophilous Cyprinidae. In the southeastern (mountain) rivers of the Black Sea basin (Shapsukho and other rivers) the significance of the lithophilous group increases, particularly that of the lithophilous Barbini (in rivers of the West-Trans-Caucasus); the egg-protecting Gobiidae are also on the increase while the underrock gobies and pelagophilous chekhon are disappearing.

From an ecological point of view, of all rivers of the Caspian Sea basin, the Volga River is closer to the Black Sea and Baltic Sea rivers than to the Terek and Kura rivers. The similarity with Baltic Sea rivers consists mainly in the presence of lithophilous coregonids and smelts while the abundance of gobies (Gobiidae), perches, lithophilous cyprinids (Leuciscini), phytophilous cyprinids and pelagophilous clupeids makes the Volga River similar to the rivers of the Black Sea basin.

The Terek and Kura rivers differ considerably from (313) the Volga River as well as from the rivers of the Black Sea basin. The number of egg-protecting and egg hiding fish species in these two rivers is lower (16% against 22% in the Volga River), the number of fish species which do not protect their eggs increases accordingly. The lithophilous group increases to its maximum (from 31% in the Volga River to 50% in the Kura River); the importance of the lithophilous barbels in the Kura River increases four fold (up to 20%); the significance of psammophilous stone loaches also increases

sharply. In contrast, the lithophilous coregonids, underrock gobies, pelagophilous clupeids and all semi-pelagophilous species are totally absent. All these differences between the Volga River and the rivers of the Black Sea basin, make the Terek and Kura rivers similar to the rivers of the related Aral Sea basin. The proportion of fish species which do not protect their eggs increases to a maximum here (i.e. up to 100%). Among them the importance of the lithophilous Barbini increases as well as that of the psammophilous stone loaches. The peculiarities of the ecological groups of the southeastern Black Sea basin rivers, the Terek and Kura, and also of those of the rivers of the Lake Aral basin, can be partially explained by the fact that all these rivers, throughout most or all of their courses, flow in the mountains; a circumstance which then predetermines the nature of adaptations of fish inhabiting these rivers.

The flatland rivers of various widths and lengths all are characterized by common features by which they differ from the mountain rivers. They are the richest in ecological groups. Only the flatland rivers are inhabited by pelagophilous, semi-pelagophilous and ostracophilous groups and groups of non-lithophilous fish which protect their eggs by various methods (builders of nests in the ground, within grass, etc.). The phytophilous group occupies a prominent position among the other groups; in a majority of the rivers this group follows the lithophilous group, immediately equaling it in number of species (in the Kuban River), or even surpassing

it (in the Daugava River). Acipenserids and Leuciscini are always present in the lithophilous group, while the Barbini are usually absent or are present in very small numbers. The psammophilous group is insignificant, ranking third.

In typical mountain rivers the lithophilous group prevails. In mountain rivers of Middle Asia the lithophilous Barbini predominate. They may be accompanied by the egg burying salmonids and the egg guarding species as well as the lithophilous Gobiidae or Cottidae. The psammophilous stone loaches acquire primary significance, i.e. numerically they do not yield to the Barbini or they follow them immediately. The lithophilous acipenserids and phytophilous, pelagophilous, semi-pelagophilous, ostracophilous and various egg protecting species (except the lithophilous Gobiidae or Cottidae) are totally absent.

Between the zones over the course of the river, the ecological groups are distributed unevenly and randomly, but in a certain order which reflects the nature of the adaptations of the fish, as pointed out by G. V. Nikol'skii in 1947.

In mountain rivers of Middle Asia, the sources of which are in the glaciers (the Naryn and Zeravshan rivers, Table 87), one species of lithophilous Barbini and one species of psammophilous stone loach are higher in the mountains than all other species. In the lower reaches they are joined by the lithophilous Leuciscini, psammophilous gudgeon and stone loaches, and further downstream--already in the flatland zone--by the phytophilous and other fish species. In addition

to this, in the lower reaches the numbers of Barbini and other fish groups also increase.

In the upper reaches of Trans-Caucasian rivers, along with the lithophilous Barbini, the salmonids also reside, while in the upper reaches of rivers of the northern Caucasus and in those of the Black Sea only the salmonids are present (1 species); there is no information concerning the stone loaches. Further downstream in all these rivers, other ecological groups appear approximately in the same order as in the mountain rivers of Middle Asia, i.e. the lithophilous Leuciscini and psammophilous gudgeons appear first, then, in the flatland zone, the phytophils and other fish species appear.

In the upper reaches of small mountain rivers in the Black Sea region, which collect their water from rainfall and springs (Mezyb River and others, Table 87), only the psammophilous stone loach is present. In the lower reaches the lithophilous Leuciscini and egg protecting gobies appear with a continuous numerical increase in number of species of both of them. There are no phytophilous nor any other flatland zone fish. This peculiarity of the Black Sea basin rivers is explained by the fact that beginning their course in the mountains these rivers empty directly into the sea without having a flatland zone. (315)

The high mountain zone of rivers, in contrast to the others, is characterized by its ecological uniformity and by the scarcity of species in the fish population. The

1) Distribution of ecological groups in various zones of mountain rivers and in the Volga River.

Таблица 87

1 Распределение экологических групп по зонам течения горных рек и Волги

2 Р е к и	3 Зоны течения	4 Н е о х р а н я ю щ и е										5 О х р а н я ю щ и е		23 Примечание
		6 литофильные			7 фитофильные			8 полу- пела- го- филь- ные	9 псаммофиль- ные		10 инди- фе- рент- ные	11 ли- то- филь- ные	12 фи- то- филь- ные	
		Leuciscini	Barbini	Aspenseridae	Cyprinidae	Esocidae	Cobitidae	Gadidae	Cyprinidae	Cobitidae	Percidae	Gobiidae	Siluridae	
11 Зеравшан	Горная . . . 16	—	1	—	—	—	—	—	—	1	—	—	—	24 По Ф. А. Тур- дакову
	Предгорная . . . 17	2	3	—	—	—	—	—	—	2	—	—	—	
	Средняя . . . 18	4	3	—	—	—	—	—	—	4	—	—	—	
	Нижняя . . . 19	3	2	—	4	—	—	—	1	—	—	—	—	
12 Нарын	Горная . . . 16	—	1	—	—	—	—	—	—	1	—	—	—	25 По Ф. А. Тур- дакову (не- опубликова- но)
	Предгорная . . . 17	—	1	—	—	—	—	—	1	1	—	—	1	
	Средняя . . . 18	2	1	1	2	—	—	—	1	1	—	—	—	
13 Меzybь (Западный Кавказ)	Верхняя . . . 20	—	—	—	—	—	—	—	—	1	—	—	—	
	Средняя . . . 18	2	—	—	—	—	—	—	—	—	—	1	—	
	Нижняя . . . 19	4	—	—	4	—	—	—	—	—	—	4	—	
14 Псекупа (горный приток Кубани)	Верхняя . . . 20	7	—	—	—	—	—	—	1	?	—	2	—	26 По С. К. Тро- ицкому
	Средняя . . . 18	8	1	—	4	1	1	—	1	—	3	2	1	
	Нижняя . . . 19	7	1	—	5	1	1	—	1	—	3	2	1	
15 Волга	1-й район . . . 21	1	—	—	—	—	—	—	1	1	—	—	—	27 По Д. А. Ла- сточкину
	2-й "	2	—	—	1	1	—	1	1	1	1	—	—	
	3-й "	3	—	—	1	1	—	1	1	1	2	—	—	
	Средняя Волга . . . 22	4	—	—	3	1	—	1	1	1	4	—	1	

2) rivers; 3) zones of the river's course; 4) not protecting; 5) protecting;
6) lithophilous; 7) phytophilous; 8) semi-pelagophilous; 9) psammophilous;
10) indifferent; 11) Zeraвшan; 12) Naryn; 13) Mezyb (western Caucasus);
14) Psekups (mountain tributary of the Kuban River); 15) Volga River;
16) mountain; 17) pre-mountain; 18) middle; 19) lower; 20) upper; 21) first
region; 22) middle course of the Volga River; 23) notes; 24) data of F. A.
Turdakov; 26) data of S. K. Troitskii; 27) data of Lastochkin; 25) data of F.A.
Turdakov, unpublished.

only species which inhabit this zone are one species of each of the lithophilous Barbini, the egg hiding lithophilous salmonids and the psammophilous stone loaches.

The next zone of mountain rivers is characterized by the appearance of lithophilous Leuciscini and psammophilous gudgeons. The other zones of mountain rivers, of various lengths and in various regions, are ecologically different.

The upper reaches of flatland rivers are also characterized by the scarcity of fish species inhabiting them. In the upper reaches of the Volga River (according to D. A. Lastochkin, Table 87) only the psammophilous gudgeon and stone loach, and the lithophilous minnow are encountered. They are joined in the lower reaches by phytophils and other fish. The number of species in the leading ecological groups also increases. Thus, from an ecological point of view, the upper reaches of flatland rivers have fewer similarities with the upper reaches of mountain rivers than with the next zone of these rivers, which is populated by lithophilous and psammophilous cyprinids. No other regular patterns of distribution of the ecological groups have been established within the various zones of the courses of rivers as yet, because the zonal distribution of the ichthyofauna in rivers is little explored.

3. Lakes.

Ecologically, lakes differ considerably from large rivers, being much more uniform than the latter. In lakes the ecological groups of fish which reproduce there are less numerous and their ranking order is different from that in rivers.

Large flatland lakes are the richest in ecological groups however among them only Lake Ladoga and Lake Onega are ecologically somewhat similar to the main rivers of their basins. In these lakes all corresponding ecological groups are represented. Among them, like in the rivers, the lithophilous fish predominate, with coregonids being the leaders. However, after subtracting from the numbers shown in Tables 88 and 89 those coregonid and salmonid fish which enter these lakes only for foraging, but reproduce in rivers, then the relative number of lake spawning, lithophilous fish and of those which bury their eggs will be considerably lower than in rivers. Correspondingly the relative number of phytophilous fish increases (these species are not excluded, because the author does not have data concerning their exact number).

Other flatland lakes (except Lake Khanka), unlike the rivers, are characterized by a relative and absolute predominance of phytophilous fish which do not protect their eggs and ecologically related indifferent species (cyprinids and perches); the relative number of the former is from 32 to 75% while in rivers it does not exceed 32%. The few lithophilous fish which do not protect their eggs inhabit

only the flow-through flatland lakes but in most of the other lakes they are absent.

In European flatland lakes there are no egg burying fish (salmonids), and in most of them the egg protecting lithophils and other fish are also absent. Psammophilous fish are found more often in these lakes than lithophils, and in greater numbers. The prevalence of phytophilous fish, which distinguishes the flatland lakes from the rivers, and the more or less complete absence of lithophilous and other fish which deposit their eggs on the bottom, is apparently due to the abundance of decaying organic sediment and to the lack of oxygen on the bottom of flatland lakes making them unsuitable for egg development. (319)

Although the flatland lakes have these common features, in other aspects they differ from each other considerably.

The large European flatland lakes, such as Chudskoe and Onega, as mentioned, are characterized by a relative abundance of ecological groups. In addition to the predominant phytophilous fish they are inhabited by lithophilous, pelagophilous, semi-pelagophilous, indifferent and psammophilous species as well as fish species which in one way or another protect their eggs; the latter represent not more than 13.5% (in Lake Onega, Tables 88 and 89). Ecologically, the Aral Sea closely resembles these lakes. It differs from these lakes mainly in the smaller number of lithophilous species which reproduce in it (only one species of the five which

live there) and by the complete absence of psammophilous and pelagophilous fish. Evidently, from an ecological point of view, the Aral Sea is a typical flatland lake--it does not resemble a sea at all.

In other Middle European through-flowing-lakes, pelagophilous and egg protecting fish are absent while the few lithophils living there reproduce mainly in the tributaries (lakes Yazno and Pereslavskoe). In closed or oxygen deficient lakes (Lake Glubokoe and others), the lithophilous and psammophilous fish are also absent, however in some of these lakes only the phytophilous or indifferent fish species live and reproduce.

The lakes of the Far East are very different from the lakes of Siberia and Europe. In Lake Hanka, as in a typically flatland lake, the lithophilous and egg burying fish are absent. However the number of phytophilous fish there is only 20%, i.e. relatively much fewer than in European lakes (in the latter, except for lakes Ladoga and Onega, the phytophils amount to 32-75%), while the indifferent fish (perches) are completely absent. In contrast, the number of egg protecting and egg hiding (ostracophilous fish) species in Lake Khanka amount to 25%, i.e. they are more abundant than the phytophilous fish; in most of the European lakes the egg protecting fish are either completely absent or their number is very small. Moreover Lake Khanka is characterized by an abundance of psammophilous cyprinids (4 species, while in other lakes they are represented by one species only).

(317)

Table 38

(316)

6

Озера

40

Примечание

Ладожское	16	5	—	(2)	(9)?	3	6	—	—	1	1	—	1	1	1	1	(6)?	—	—	1	1	—	—	—	—	—	По В. В. Петрову	41
Онежское	17	3	—	1	(5)?	3	7	1	—	1	1	—	1	1	1	1	(5)?	—	—	2	1	1	—	2	—	—	» Н. Пушкарёву	42
Чудское	18	5	—	—	2	3	6	1	—	1	—	—	2	1	1	1	—	—	—	—	—	—	2	—	—	То же	"	43
Арал	19	1(2)	(2)	(2)	—	3	4	1	—	1	1	—	—	—	—	—	(1)	—	—	—	1	—	1	—	—	По Г. В. Никольскому	44	
Язю (Белорус.)	20	2	—	—	—	3	7	2	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	» Ч. В. Хмелевскому	45	
Переславское	21	2	—	—	1	3	4	1	—	1	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	» П. Г. Борисову	46	
Глубокое	22	—	—	—	—	2	4	1	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	» А. В. Подлесному	47	
Тургояк	23	1?	—	—	—	2	1	2	—	1	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	То же	"	48
Мясоево	24	1?	—	—	—	2	3	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	По А. И. Букрину	49	
Чилинаовские (Омская область)	25	—	—	—	—	2	3	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Итакуль (Минусинск)	26	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Омская (Минусинск)	27	—	—	—	—	1	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Гусиное (Селенга)	28	—	—	—	(1)	1	2(?)	1	—	1	—	—	—	—	1	—	—	3?	—	—	1	—	—	—	—	По А. Л. Таранду	50	
Тимь (гуадраое озеро)	28a	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	—	То же	"	51
Везианное (на Амуре у Болона)	29	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Халка	30	(1)	—	(2)	(2)	—	3	2	1	1	12	1	—	1	4	1	—	3	1	—	1	1	1	1	1	—	По В. Е. Розову	52
Имандра	31	1	—	—	2	1	—	—	—	1	—	—	—	1	1	—	—	5(?)	—	—	—	—	—	1	—	» В. П. Петрову	53	
Марка-куль (Алтай)	32	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	» М. И. Меншикову	54	
Телецкое (Алтай)	33	2	—	—	2	1	—	—	—	1	—	—	—	1	1	1	3	—	—	1	—	—	—	—	—	» Н. А. Барлаховскому и Н. А. Гладкову	55	
Абрау	34	1	—	—	—	—	2	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Севан	35	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—
Иссык-куль	36	1	3	—	—	—	1	—	—	—	—	—	—	—	—	1	3	—	—	—	—	—	—	—	—	» Л. С. Бергу	56	
Балкаш	37	3	4	—	—	1	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	То же	"	57
Байкал	38	(9)	—	(1)	(3)	1	(1)	(1)	—	(1)	—	—	—	—	1	1	—	(3)	—	—	14	—	—	—	—	2	» " " (317)	168

54. В скобках указаны виды, не размножившиеся в озерах; знак вопроса указывает на то, что точное количество этих видов неизвестно.

Table 88

1) Distribution of ecological groups in lakes*. (316)

(317)

2) absolute number of species in groups; 3) not protecting; 4) hiding; 5) protecting; 6) lakes; 7) lithophilous; 8) indifferent; 9) phytophilous; 10) pelagophilous; 11) semi-pelagophilous; 12) psammophilous; 13) lithophilous; 14) ostracophilous; 15) viviparous; 16) Ladoga; 17) Onega; 18) Chudskoe; 19) Aral; 20) Yazno (Bielorussia); 21) Pereslavl'skoe; 22) Glubokoe; 23) Turgoyak; 24) Miasovo; 25) Chilikanovskie (District Omsk); 26) Itkul' (Minusinsk); 27) Fyrkal'skie (Minusinsk); 28) Gusinoe (Selenga); 28a) Tym' (tundra lake); 29) Bezmyannoe (in Amur and Boloni region); 30) Khanka; 31) Imandra; 32) Marka-Kul (Altai); 33) Teletskoe (Altai); 34) Abrau; 35) Sevan; 36) Issyk-Kul; 37) Balkhash; 38) Baikal; 40) notes; 41) according to V. V. Petrov; 42) N. Puchkarev; 43) G. V. Nikol'skii; 44) Ch. V. Khmelevskii; 45) P. G. Borisov; 46) A. V. Podlesnii; 47) A. I. Bukirev; 48) A. Ya. Tarants; 49) V. E. Rozov; 50) N. I. Menshikov; 51) N. A. Varpakhovskii and N. A. Gladkov; (52); 53) L. S. Berg.

*) 54) numbers in parentheses indicate species which do not reproduce in lakes; the question mark indicates that the exact number of these species is not known.

However the most distinguishing feature of Lake Khanka is the abundance of pelagophilous fish (37% or 12 species; in other lakes they are either represented by only one species or are completely absent). The ecological peculiarity of the Lake Khanka ichthyofauna reflects the ecological peculiarities of the whole Amur River basin. The abundance of pelagophilous, psammophilous, ostracophilous and other egg protecting fish and the deficiency in phytophilous fish

Table 89

1) Distribution of ecological groups in lakes.

Таблица 89

1 Распределение экологических групп в озерах

4 Озера	5 Абсолютное количество видов	2 Относительное количество видов в группах (в % от общего количества видов, размножающихся в озере)																16 Итого					
		6 не охраняющих	7 охраняющих и пресечуших	3 не охраняющие											3а охраняющие и т. п.								
				8 фитофильные		10 литофильные					11 псаммофильные		12 пелагофильные		13 полупелагофильные	14 индифферентные	15 протачивающие		Cobitidae	Cyprinidae и Cyprinodontidae	Gasterosteidae	Copephoridae	
				9 всего	Cyprinidae	9 всего	Copephoridae	Leuciscini	Barbini	Acipenseridae	9 всего	Nemachilini	9 всего	Cyprinidae									
17 Ладожское	40	77	22	17	15	40	22	12	—	5	5	2	2	2	2	7	15	—	—	—	—	—	—
18 Онежское	37	73	27	24	19	27	16	8	—	2	5	2	2	2	2	8	13	—	—	—	—	—	—
19 Чудское	25	92	8	32	24	28	8	20	—	—	8	4	—	—	8	12	—	—	—	—	—	—	—
20 Арал	13	84	15	46	30	7	—	7	—	—	—	—	7	7	—	15	—	—	—	—	—	—	—
21 Язено	16	100	—	62	43	12	—	12	—	—	6	6	—	—	—	18	—	—	—	—	—	—	—
22 Переславское	14	100	—	42	28	21	7	14	—	—	7	—	—	—	—	21	—	—	—	—	—	—	—
23 Глубокое	9	100	—	66	44	—	—	—	—	—	—	—	—	—	—	22	—	—	—	—	—	—	—
24 Тургояк	9	100	—	55	32	—	—	—	—	—	11	—	—	—	—	22	—	—	—	—	—	—	—
25 Мясоево	8	100	—	62	50	—	—	—	—	—	—	—	—	—	—	25	—	—	—	—	—	—	—
26 Чиликановские	7	100	—	56	42	—	—	—	—	—	14	—	—	—	—	28	—	—	—	—	—	—	—
27 Иткуль	1	100	—	—	—	—	—	—	—	—	—	—	—	—	—	100	—	—	—	—	—	—	—
28 Фыркальские	4	100	—	75	75	—	—	—	—	—	—	—	—	—	—	25	—	—	—	—	—	—	—
29 Гусиное	7	85	14	56	28	—	—	—	—	—	—	—	—	—	—	7	—	—	14	—	—	—	—
30 Тым	2	50	50	—	—	—	—	—	—	—	—	—	—	—	50	—	—	—	—	50	—	—	—
31 Безымянное	2	50	50	50	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	—
32 Ханка	35	75	25	20	8	—	—	—	—	—	14	2	37	34	—	—	—	—	—	—	—	20	—
33 Имандра	13	53	46	7	—	22	15	7	—	—	—	—	—	—	7	7	98	—	—	—	—	—	—
34 Марка-Куль	4	50	50	—	—	—	—	—	—	—	50	25	—	—	—	—	50	—	—	—	—	—	—
35 Теленкое	13	69	30	7	—	30	15	15	—	—	15	7	—	—	—	7	22	—	7	—	—	—	—
36 Абрау	5	80	20	40	40	20	—	20	—	—	—	—	20	—	—	—	—	—	—	—	—	20	—
37 Севан	4	50	50	—	—	50	—	—	50	—	—	—	—	—	—	—	50	—	—	—	—	—	—
38 Иссык-Куль	9	100	—	11	11	44	—	14	22	—	44	33	—	—	—	—	—	—	—	—	—	—	—
39 Балхаш	12	100	—	—	—	58	—	24	33	—	33	33	—	—	—	8	—	—	—	—	—	—	—
40 Байкал	20	20	80	—	—	5	?	5	—	—	10	—	—	—	—	—	—	—	—	—	—	—	—

2) relative number of species in groups (in % of the total number of species reproducing in the lake); 3) non protecting; 3a) protecting; 4) lakes; 5) total (absolute) number of species; 6) non-protecting; 8) phytophilous; 9) total; 10) lithophilous; 11) psammophilous; 12) pelagophilous; 13) semi-pelagophilous; 14) indifferent; 15) hiding; 16) other; 17) Ladoga; 18) Onega; 19) Chudskoe; 20) Aral; 21) Yazno; 22) Pereslavskoe; 23) Glubokoe; 24) Turgoyak; 25) Miasovo; 26) Chilikanovskie; 27) Itkul'; 28) Fyrkal'skie; 29) Gusinoe; 30) Tym'; 31) Bezymyannoe; 32) Khanka; 33) Imandra; 34) Marka-kul'; 35) Telenkoe; 36) Abrau; 37) Sevan; 38) Issyk-Kul'; 39) Balkhash; 40) Baikal.

are the features which make Lake Khanka similar to the Amur River. Lake Khanka differs from the Amur River in the absence of lithophilous and semi-pelagophilous species of fish which hide their eggs in the ground, as well as in the relatively high number of phytophilous fish in the lake: 20% in Lake Khanka and 9% in the Amur River.

The small far eastern lakes, like Lake Khanka, differ from European and Siberian lakes in their relative abundance in egg protecting fish and in the absence of the indifferent perches. In other respects they are very individualistic. Thus, an un-named small lake in the floodplain of the Amur River (near Boloni) is populated by non-protecting and egg-protecting phytophilous fish (lake minnow and rotan). A tundra lake, isolated from the Tym River (on Sakhalin Peninsula), according to data of Tarants, is populated by semi-pelagophilous and egg-protecting fish (smelt and stickleback).

The mountain lakes, unlike the flatland lakes, are inhabited mainly by lithophilous species and fish which hide their eggs in the ground. Moreover, some of them are abundant in psammophilous stone loaches. In contrast, phytophilous fish are completely absent in most of the mountain lakes while in others they are very scarce (not more than one species).

The fact that lithophilous fish and fish which bury their eggs in the ground predominate in mountain lakes, is evidently due to the low water temperature, to the clarity of (320) the water and to other reasons. The excellent bottom aeration permits eggs deposited or buried there to develop normally,

without suffering from oxygen deficiency. The lack of phytophilous fish can be partially explained by the absence of shoreline grass pads which are necessary for these fish to deposit their eggs.

The mountain lakes are not uniform. The lakes of Altai (Lake Teletskoe) are characterized by the predominance of fish species which bury their eggs in the ground (salmonids) and lithophilous fish. The latter is represented by coregonid and cyprinid species. In addition, the egg protecting underrock gobies and phytophilous (the pike), indifferent and psammophilous fish can be encountered in these lakes. In ecological terms, the ichthyofauna of the large lakes of Kola Peninsula (Lake Imandra) resemble the mountain lakes of the Altai mountains. The Trans-Caucasian lakes (Lake Sevan) are inhabited by only the lithophilous Barbini (which are lacking in northern European mountain lakes) and by salmonids. The lithophilous Leuciscini, phytophils and other fish, encountered in Altaic lakes are absent. The high mountain lakes of the northern Caucasus are inhabited by salmonid species only. Lake Abrau, situated between mountains near the Black Sea, resembles flatland lakes from an ecological point of view, but at the same time is quite peculiar. Phytophilous cyprinids predominate in this lake (40%). In addition, there is the lithophilous minnow (one species), the pelagophilous sprat, which is found in only one other lake (Lake Paliostom), and the egg protecting, artificially acclimatized American perch (Micropterus salmonides). The mountain lakes of Middle Asia (Issyk-Kul, Balkhash) differ

from mountain lakes of other regions mainly in their lack of egg burying salmonids and fish that protect their eggs; the prevalent fish are the lithophilous Barbini (22 to 33%) and the psammophilous Nemachilini (33%). In other lakes they are absent or are represented by only one species. In addition, these lakes are inhabited by the lithophilous Leuciscini, the phytophilous common carp (in Lake Issyk-Kul) and the perch (in Lake Balkhash). The high mountain lakes of Middle Asia are inhabited by only the lithophilous osman.

Ecologically, Lake Baikal occupies an exclusive position, not only among our lakes, but also probably among the lakes of the whole world. In contrast to the mountain and flatland lakes, except for the indifferent perch and the semi-pelagophilous burbot, no other species which do not protect their eggs reproduce in this lake. The phytophilous, lithophilous and psammophilous fish which inhabit this lake spawn in rivers or in flood-plain lakes; the bulk of the main fish reproducing in Lake Baikal (i.e. 80 to 90%) care for their eggs: species of the Cottidae and Cottocomephoridae families (70 to 80%) deposit their eggs in clusters under stones and guard them; the species of Comephoridae (10%) are viviparous. The latter, as mentioned, differ from the viviparous fish of other bodies of water in that their fecundity is higher than related fish which deposit demersal eggs. Thus, Lake Baikal, in spite of its huge dimensions, is ecologically very uniform. It differs from other freshwater reservoirs in its unusually small number of fish species

which do not protect their eggs and in the prevalence of egg protecting species, such as the lithophilous Cottidae, and related fish which deposit their eggs in clusters, as well as by the peculiar viviparous golomankas. The absence of fish species which do not protect their eggs but deposit them on the bottom and the abundance of lithophilous fish which do protect their eggs make Lake Baikal similar to the seas, particularly to the Kara Sea (Tables 91 and 92 in the chapter "Seas").

4. Seas.

In the seas, in contrast to the freshwater reservoirs, there are very few, not more than five, fish species that disperse their eggs on the bottom and do not protect them (Table 90). This numerically exceptionally small group is represented by only a few species with peculiar adaptations-- (321) by the herring, garfish and atherinid (Table 91). All other fish which disperse their eggs on the bottom and do not protect them--the lithophils, phytophils, psammophils etc.--do not reproduce in the sea. The absence of lithophils and other fish, which produce demersal eggs and do not protect them, is explained by the fact that predators of demersal eggs in the sea are much more abundant than in freshwater reservoirs. In the sea, the eggs are eaten by numerous goby species, blennies and other fish, as well as by crabs. Moreover, the fish species which bury their eggs in the ground

are completely lacking in the seas. The absence of these fish is explained by the fact that there is no place in the sea where the eggs could be buried: in the surf zone, where the conditions of aeration are favorable, this is not possible because the surf, moving the ground continuously, would destroy the eggs; below the surf zone where the ground is immobile, the burying of eggs is impossible because they would perish because of the lack of oxygen in the ground. For these reasons the evolution of fishes in the sea proceeded mainly in two ways, in opposite directions to the evolutionary paths of freshwater fishes: some of the fish, in line with their biology, became pelagophilous, i.e. began to release pelagic eggs, thus saving them from destruction by benthonic enemies; the others, mainly benthonic fish, developed various adaptations for protection of the eggs. The fish which do not protect their eggs, the pelagophils, and the egg protecting fish are those which predominate in the seas, thus distinguishing the latter from freshwater reservoirs (Table 90).

The numerical ratio between species of these two groups, in various seas, is not the same. They vary inversely: if there are more pelagophilous fish, there are fewer egg protecting fish, and vice versa. In southern seas, the smallest number of pelagophilous fish is in the Caspian Sea (17%, Table 92). In the range from the Azov and Black seas to the Baltic Sea, the number of pelagophilous fish gradually increases up to 69.3%. In the northern seas their number again decreases gradually from the Barents Sea to the Kara

Sea. In the White Sea there are as few pelagophilous fish as in the Azov Sea (about 38%), but in the Kara Sea they are at their minimum--only 15% (only three species). In contrast to these changes in the abundance of pelagophilous fish, the relative abundance of egg protecting fish gradually decreases in a direction from the Caspian Sea to the Baltic Sea and then increases again from the Barents Sea to the Kara Sea. The number of egg protecting fish in the Caspian Sea represents 83% whereas they reach a minimum in the Baltic Sea with 30.7% and increase to a maximum (85%?) in the Kara Sea.

The systematic and quantitative composition of the main ecological groups is not uniform but it is specific for each individual sea. In the Caspian Sea, the pelagophilous fish are represented by clupeids of Ponto-Caspian origin (6 species; Table 91). In other seas they are gradually joined and finally displaced completely by pelagophils of other origins and of other families. In the Azov Sea the flounders (four species), wrasses and others appear. The eight species of herrings in the Black Sea are joined by numerous species of Percidae, flounders, mullets and other fish, mainly of Mediterranean origin. In the Baltic Sea only three species of pelagophilous clupeids remain; here, the gadoids and flounders predominate. In other northern seas, from the Barents Sea to the Kara Sea, the pelagophilous clupeids and many other fish of southern origin are completely absent. In these seas, pelagophilous arctic flounders and

gadoids reproduce. In the Kara Sea only three species of these fish remain.

There are various ways by which the marine non-pelagophilous fish care for their eggs. The overwhelming majority of them (about 75 species) release the eggs on the bottom and stand guard over them for the whole period of embryonic development. Some of these fish spread their eggs (322) on the surface of stones in a single layer (Gobiidae, Blenniidae, Gobiesocidae, some of the Labridae, the pike-perch, Fig. 100), the others deposit them in more or less compact clusters, usually under the stones (Cottidae, Anarrichadidae, and others). Some of the fish are able to deposit their eggs within vegetation by affixing them to plants (in Tables 91 and 92 these fish are not shown separately from the lithophilous fish which deposit their eggs in clusters). The other, less numerous fish, representing not more than 11 species, build nests for the protection of their eggs (3 species of sticklebacks), give birth to developed fry (viviparous blenny) or carry their eggs in brood pouches or on the surface of their bodies (7 species of Syngnathidae).

In the southern seas--in the Caspian, Azov, and Black seas--the lithophilous fish which deposit their eggs in clusters are completely absent. Thus, in these seas, not counting the pelagophils, only the fish which

deposit their eggs in a single layer predominate. The proportion of these fish decreases from 75.6% in the Caspian Sea to 32.3% in the Black Sea. This is accompanied by an increase in the number of pelagophilous fish. In the Caspian and Azov seas, the fish that deposit their eggs in one layer are represented exclusively by species of the family Gobiidae most of which are restricted to a Ponto-Caspian origin. In the Black Sea the same gobies predominate (20%), but in addition to them, there are also the fish that deposit their eggs in a layer: Blennidae, Gobiessocidae and Labridae of Mediterranean origin. In the Baltic Sea, the abundance of fish which deposit their eggs in a layer decreases to 8% and they are already replaced by the Cottidae and other fish of northern origin that deposit their eggs in clusters (11%). In other northern seas, unlike the southern seas, the fish which deposit their eggs in a layer are missing completely. Only the Cottidae and other fish which deposit their eggs in clusters reproduce there. The relative abundance of the latter increases from 48% in the Barents Sea to 80% in the Kara Sea and is accompanied by a corresponding decrease in the abundance of pelagophilous fish in these seas.

The relative and absolute number of fish that care for their eggs, as mentioned, is not high: it varies from one sea to another, without a regular pattern, within the limits from 5 to 16%. Of these fish only the nest building sticklebacks are present in all seas; they are most abundant in the Baltic Sea and the Barents Sea (3 species

in each). The egg carrying Syngnathidae inhabit mainly the southern seas. They are most abundant in the Black Sea (7 species). The viviparous fish (1 species) live only in the northern seas--in the Baltic, Barents and White seas.

The reasons for the absence in the southern seas, of fish that deposit their eggs in clusters, and for the abundance of those which deposit their eggs in a layer, in the northern seas, as well as the reasons for the scarcity of pelagophilous fish in the Caspian Sea and in the Kara Sea, along with other patterns of distribution of the ecological groups, are not well understood at the present time.

Besides the marine fish, the seas are inhabited by diadromous and semidiadromous fish which reproduce in fresh water and are often of freshwater origin. The relative abundance of these fish in the various seas varies between the limits of 13 and 45% (Table 92). The diadromous (and semidiadromous) species are at a minimum in the Barents Sea (13%) and the Black Sea (19%). In increasing order of abundance of species, these seas are followed by the White Sea (23%), Baltic Sea (34%), Kara Sea (37%), Caspian Sea (43%) and Azov Sea (45%). The biological reasons for such a distribution of these fish, are not established as yet.

The diadromous and semidiadromous fish, unlike the marine fish, belong to ecological groups of fish which do not protect their eggs but usually release demersal eggs, i.e. among them are lithophilous, phytophilous, indifferent, semi-pelagophilous, egg burying and a small number of

pelagophilous fish (Table 91). There are no egg-protecting (323) fish among them (not counting the stickleback). The lithophilous group prevails over the others. It is present in all seas and comprises more species than the other groups (from 37 to 83 %). The proportion of diadromous lithophils is particularly high in the Kara Sea (83%), then in the Barents Sea (53%). They are least important in the Baltic Sea (37%); in other seas their relative abundance varies from 40 to 44%. Egg-burying fish are present in all seas, excepting the Azov Sea. They are most abundant in the Baltic, Barents and White seas (3 species in each).

The other ecological groups of diadromous fish are distributed in the seas in a more differentiated manner. The southern seas--the Caspian, Azov and Black seas--are characterized by the fact that besides the predominant lithophilous fish, the phytophilous (16 to 33%), pelagophilous (12 to 20%) and indifferent fish (perches: 9 to 12%), and the egg-protecting catfish are also present there. The egg-burying salmonids are present only in the Caspian and Black seas, while the semi-pelagophilous fish are absent in both. The lithophilous fish in these seas are represented by a larger and almost equal number of species of cyprinids and acipenserids (5 to 7 species in each; Table 91); only one species of coregonid is present in the Caspian Sea. The pelagophilous diadromous fish are represented by species of Ponto-Caspian clupeids (3 to 4 species) and by the chekhon. The phytophilous fish are represented by species of the family Cyprinidae (up to 8 species) and by loaches (2 species).

Table 90

1) General ecological description of the fish of the main freshwater bodies and seas.

Таблица 90

1 Общая экологическая характеристика рыб главных пресноводных водоемов и морей

2 Водоемы	3 Количество видов в группах (в % от общего количества видов)						
	4 разбрасывающие икру				7а	8	9
	5 фито- фильные и др.	6 пелаго- фильные	7 неиз- вестные	7а причужде	8 охраняющие	9 разбрасыва- ющие всех групп	10 причужде и охраняю- щие вместе
Пресные воды СССР 11	62.68	8.3	3.16	9.9	15.4	74.44	25.3
Они же, кроме Байка- ла и Амура . . . 12	73.1	8.1	—	11.1	12.5	76.3	23.8
Амур 13	37	27	10	12.3	13.6	64	26
Волга 14	72	6	—	6	15	78	22
Онежское озеро 15	70.3	2.7	—	13.5	13.5	73	27
Аральское море 16	77.2	7.6	—	—	15.2	84.8	15.2
Ханка 17	37	37	—	8	16	75	25
Байкал 18	20	—	—	—	80	20	80
Каспийское море 19	2.4	14.6	—	—	83	17	83
Черное » 20	2.8	56.1	—	—	41.1	58.9	41.1
Балтийское » 21	3.2	66.1	—	—	30.7	69.3	30.7
Карское » 22	—	15	—	—	85	15	85

2) bodies of water; 3) number of species in groups (in % of the total number of species); 4) dispersing eggs; 5) phytophilous and others; 6) pelagophilous; 7) unknown; 8) protecting; 9) dispersing, of all groups; 10) hiding and protecting together; 11) freshwaters of the U.S.S.R.; 12) same, without Lake Baikal and the Amur River; 13) Amur River; 14) Volga River; 15) Lake Onega; 16) Lake Aral; 17) Lake Khanka; 18) Lake Baikal; 19) Caspian Sea; 20) Black Sea; 21) Baltic Sea; 22) Kara Sea.
7a) hiding.

With respect to the nature of the diadromous fish and the marine fish as well, the Baltic Sea occupies an intermediate position between the southern and northern seas. All ecological groups of the southern seas are present as well as the semi-pelagophilous smelt, which does not exist in the southern seas but is typical of the northern seas. The pelagophilous fish in the Baltic Sea are represented by only the chekhon; the southern Ponto-Caspian herrings are absent.

Table 91

1). Distribution of the ecological groups of fish in the seas and in Lake Baikal.

Таблица 91

1 Распределение экологических групп рыб в морях и в Байкале

(324)

(325)

		2 Абсолютное количество видов в группах																													
		3 размножаются в море														4 Мигрируют в реки															
8 Моря	10 Общее количество видов	5 Не охраняющие				6 Охраняющие и прочие										5 Не охраняющие				24						25		26 неизвестные			
		9		12 Фито- фильные	11 и прочие	13 Литофильные					16 Кучно отклады- вающие икру	17 Живородящие	17a Плавающие	18 Строители	19 гнездобу- дители	21		22 Псаммо- фильные	23 Индиффе- рентные	24		25 охраняющие фитофиль- ные	26 неизвестные								
		14 Икру				15																									
		Clupeidae	и прочие	Salonidae и Atherinidae	и прочие	некро	Gobiidae	Blennidae	и прочие	некро	Colitidae и Callotomus phoridae	и прочие	Zoarcidae и проч.	Synbranchi- dae	Gasterostei- dae	Clupeidae	Cyprinidae	Osmorhizidae	некро	Cyprinidae	Gobiidae	некро	Cyprinidae	Coregonidae	Acipenseridae	Cyprinidae и Colitidae	Percidae	Salmonidae	Siluridae		
Каспийское	27	41	6	—	1	—	32	31	—	1	—	—	—	1	1	32	3	1	—	10	3	2	13	6	1	6	—	3	1	1	—
Азовское	28	36	4	8	2	—	16	16	—	—	—	—	—	4	2	30	3	1	—	10	3	2	12	7	—	5	—	3	—	3	—
Черное	29	105	8	51	3	—	34	24	8	5	—	—	—	7	2	25	4	1	—	4	2	2	11	5	—	6	—	3	1	1	—
Балтийское	30	62	3	33	1	1	5	2	3	—	4	3	1	3	3	32	—	1	—	9	3	1	12	7	—	4	1	2	3	1	—
Баренцово	31	81	—	35	1	1	—	—	—	39	10	29	1	1	3	13	—	—	3	—	—	—	7	—	6	1	—	3	—	—	—
Белое	32	23	—	10	—	1	—	—	—	15	4	11	1	—	2	9	—	—	2	—	—	—	4	—	4	—	—	3	—	—	—
Карское	33	20	—	3	—	—	—	—	—	16	6	10	—	—	1	22	—	—	1	—	—	—	10	—	8	2	—	1	—	—	—
Байкал	34	20	—	—	4	—	—	—	—	14	14	—	2	—	—	13	—	—	—	3	1	1	7	3	3	1	2	—	3	—	—

- 2) total (absolute) number of species in the groups; 3) reproduce in the sea;
 4) migrate into rivers; 5) non-protecting; 6) protecting and others; 8) seas;
 9) pelagophilous; 10) total number of species; 11) other; 12) phytophilous;
 13) lithophilous; 14) deposit eggs in a layer; 16) deposit eggs in clusters;
 17) viviparous; 17a) Zoarcidae and others; 18) carrying; 19) nest builders;
 20) total number of species; 21) pelagophilous and semi-pelagophilous;
 22) psammophilous; 23) indifferent; 24) hide their eggs in the ground;
 25) egg protecting phytophils; 26) unknown; 27) Caspian; 28) Azov; 29) Black;
 30) Baltic; 31) Barents; 32) White; 33) Kara; 34) Baikal.

Table 92

1) Distribution of leading ecological groups of fish in the seas and Lake Baikal*).

Таблица 92

(324)

I Распределение руководящих экологических

групп рыб в морях и в Байкале*

Table 92

(325)

2 Моря	I. Размножаются в море										II. Мигрируют в реки								III. Мигрируют в реки							
	A не охраняющие				B охраняющие и прочие						A не охраняющие								A не охраняющие							
	3 общее количество морских видов	4 мелагофильные	5 фитофильные	6 прочие	7 общее количество видов	8 литофильные				11 индифферентные	12 прятающие икру	13 охраняющие	4 мелагофильные	10 покулиагофильные	5 фитофильные	11 индифферентные	8 литофильные	12 прятающие икру	13 охраняющие							
						9 расклевывающие икру		10 кутно откладывающие																		
						7 общее количество видов	Collidae	7 общее количество видов	Collidae																	
						8 находящиеся и прочие																				
Каспийское	14	17.0	14.6	2.4	—	83.0	75.6	75.6	—	—	4.8	43	5.4	—	13	4	17	1	1	12	—	31	9	40	3	3
Азовское	15	33.8	33.3	5.5	—	61.2	41.4	44.4	—	—	13.8	45	6.0	—	15	4	18	—	1	13	—	33	10	40	—	3
Черное	16	58.9	55.1	2.8	—	41.1	32.3	20.0	—	—	8.3	19	3.7	—	3	2	9	0.8	0.8	20	—	16	12	44	4	4
Балтийское	17	69.3	63.1	1.6	1.6	30.7	8.0	3.2	11.1	6.4	11.1	34	1.0	1	9	3	12	3	1	3	3	27	9	37	9	3
Баренцево	18	45.6	43.2	1.2	1.2	51.4	—	—	33.1	12.3	6.1	13	—	3	—	—	7	3	—	—	23	—	—	53	23	—
Белое	19	37.8	34.4	—	3.4	62.2	—	—	51.7	13.7	10.3	23	—	3	—	—	10	7	—	—	22	—	—	44	33	—
Карское	20	15.0	15.0	—	—	85.0	—	—	30.0	30.0	5.0	37	—	3	—	—	31	3	—	—	8	—	—	83	8	—
Байкал	21	29.0	—	—	20	89.0	—	—	70.0	70.0	10.0	39	—	—	3	—	21	9	—	—	—	23	—	53	23	—

22* Цифры указывают: в разделе I — количество видов в экологических группах размножающихся в море; в разделе II — количество видов в экологических группах проходных рыб в процентах от общего количества видов рыб, встречающихся в море; в разделе III — количество видов рыб тех же групп в процентах от общего количества видов проходных рыб.

I--reproduce in the sea; II--migrate into rivers; III--migrate into rivers;
 A) not protecting; B) protecting and others; 2) seas; 3) total number of marine species; 4) pelagophilous; 5) phytophilous; 6) other; 7) total number of species; 8) lithophilous; 9) deposit eggs in a layer; 10) deposit eggs in clusters; 11) indifferent; 12) hide their eggs in the ground; 13) protecting; 14) Caspian; 15) Azov; 16) Black; 17) Baltic; 18) Barents; 19) White; 20) Kara; 21) Baikal; 22) *) numbers indicate: in section I--number of species in the ecological groups of fish, reproducing at sea, expressed in % of the total number of species which reproduce in the sea; in section II--the number of species of migratory fish in the ecological groups, in % of the total number of fish species encountered in the sea; in section III--the number of fish species of the same groups, in % of the total number of species of diadromous fish.

Among the lithophilous fish, in addition to the cyprinids which are typical of southern seas, the northern coregonids occupy a prominent place (four species), while the number of acipenserids is reduced to one species (in the southern seas they are represented by 5 to 6 species). The number of salmonids is three times as high as in the south.

In the northern Barents, White and Kara seas, unlike (326) southern seas, there is a complete absence of diadromous pelagophilous fish. They are replaced by the semi-pelagophilous smelts. Moreover, there are neither phytophilous nor indifferent fish and the catfish is also absent. In the lithophilous group of northern seas, the cyprinids, which are typical of the southern seas, are lacking. In northern seas, they are replaced by coregonids, which predominate over all other diadromous fish. Acipenserids are scarce (one or two species), or totally absent. The salmonids are as numerous as in the Baltic Sea (one to three species).

As is typical of all northern seas, the Kara Sea is characterized by the prevalence of diadromous lithophilous fish (83%), and correspondingly, by the scarcity of the two other ecological groups--the semi-pelagophilous and egg burying groups. These ratios between the diadromous fish of the Kara Sea are very similar to the ratios between its groups of marine fish: in the Kara Sea, as mentioned, there are 80% lithophilous, egg protecting fish, and correspondingly, very few pelagophilous (15%) and other fish. The reasons for this coincidence are not understood as yet.

The peculiarities in the distribution of ecological groups of migratory and semimigratory fish, partly reflect the ecological peculiarities of the tributary rivers. As mentioned, the southern rivers are characterized by the prevalence of lithophilous and phytophilous cyprinids and by the presence of pelagophilous herrings, while the northern rivers are characterized by the predominance of lithophilous coregonids over the phytophilous and lithophilous cyprinids and by the lack of pelagophilous fish.

5. Spawning migrations of fish.

The adaptations of fish to precisely defined conditions of reproduction and development, create the necessity for spawning migrations and predetermine the fundamental features of these migrations. Therefore, the spawning migrations reflect the specifics of the ecological group of fish as well as the peculiarities of the bodies of water inhabited by them.

Only the viviparous and many of the fish which protect their eggs, do not move far away from their usual habitat. All fish which deposit demersal eggs and do not protect them, many pelagophils and other fish migrate, during their reproductive period, for more or less long distances in search of places suitable for development of their eggs. The fate of the eggs after deposition is determined mainly by the level of protection from predators and how well they are provided with oxygen. Since the potential for protecting

the eggs from predators and securing an adequate oxygen supply for their development are different for fish of various ecological groups, their migrations are also different.

Within lakes and other bodies of freshwater, the phytophilous, indifferent and psammophilous species along with many other fish, have the least extensive migrations (Table 93). During the reproductive period they do not migrate beyond the limits of those lakes in which they normally reside. They only approach the shores where they find the necessary surroundings for their eggs--pads of aquatic plants (phytophilous fish), sand (psammophils), etc. For instance, in Issyk-Kul, the Aral Sea and Lake Khanka, all the phytophilous fish which live there reproduce locally; not a single species migrates into the rivers. In contrast, the lithophilous fish in most flatland lakes do not find the conditions which are necessary for their reproduction: in such lakes there are either only a few sandy or stony places or there are none that are suitable for the deposition of eggs. Moreover, there are many predators which are able to destroy the eggs deposited in open areas (gudgeons, sticklebacks and others). For these reasons, the lithophilous fish of various families (cyprinids, coregonids, acipenserids), in contrast to the phytophilous fish, migrate from most of the flatland lakes, to spawn in rivers on sandy-rocky shoals, where the developmental conditions for them are more favorable in all respects. Thus, all (327) lithophilous fish of Lake Khanka--the cyprinids, acipenserids and coregonids (5 species)--leave the lake to spawn in rivers

(Table 93); all acipenserids, barbels, and lithophilous Leuciscini, except the shemaia, leave the Aral Sea for spawning.

In mountain lakes with impoverished ichthyofaunas, which consist mainly (in Lake Issyk-Kul) or completely (in Lake Sevan) of lithophilous fish, they find the same conditions for reproduction as in the rivers: egg predators in both places are scarce and the conditions of aeration at the bottom are equally favorable. For these reasons the lithophilous fish reproduce in these lakes as well as in the rivers. During the spawning period they approach the shores and disperse their eggs on the sandy-rocky shoals. Some of them, like the Issyk-Kul's chebachok, are completely tied to the lake. The others--the lake Barbini--segregate into schools according to age groups. Some of these reproduce in the lake while the others migrate into mountain tributaries. Thus the barbel and khramulya, which inhabit Lake Sevan, spawn not only in the lake but also in its tributary rivers. When young, the marinkas and the osman of Lake Issyk-Kul reproduce in the cold rivers during the second half of summer, leaving the lake when its water temperature rises above 17 C; at a more advanced age the same fish reproduce in Lake Issyk-Kul itself during the spring and first half of summer, while the water temperature is still below 17 C (V. V. Vasnetsov's data). The migration of Lake Sevan lithophilous fish into rivers is explained by the necessity for expanding the spawning areas to alleviate the egg losses due to the overloading of the lake's spawning beds; the migration of the Lake Issyk-Kul

Barbini into rivers is due to the same reasons, compounded by unfavorable conditions of some kind, linked to the summer warmup of the lake.

The salmonids, which bury their eggs in the ground, like the lithophilous fish, do not reproduce in the flatland lakes. This is explained by the inadequate aeration of the ground in the flatland lakes and the resulting losses of eggs due to their death from suffocation. The salmonids leave the flatland lakes, enter the rivers and migrate either up or downstream, and bury their eggs in well irrigated sand-gravel bars, where the conditions of aeration for the buried eggs are the most favorable. The salmonids which live in clear mountain lakes reproduce, like their neighbors--the lithophilous cyprinids--in these lakes and in their tributaries as well. For instance some of the Lake Sevan trout spawn in the lake, near the sandy and rocky shores, where wave action, along with other factors, creates favorable respiratory conditions for the eggs; some of them migrate and spawn in rivers. Evidently, such diversity in the spawning localities of salmonids is also explained by the necessity for expanding the area of their spawning grounds in order to avoid harmful overloading of the spawning beds.

From the point of view of water clarity, temperature conditions and other hydrological conditions, Lake Baikal resembles high level mountain lakes. The conditions of aeration at the bottom are favorable throughout its coastal zone. But this lake, unlike all other lakes, is rich in

predators of demersal eggs such as the underrock gobies and other related fish. Therefore, the spawning migrations of Lake Baikal fish, in the first place, reflect the requirements for protection of the eggs from their predators. As mentioned, the egg-protecting fish reproduce almost exclusively in Lake Baikal: the underrock gobies and others (Tables 92 and 93). Most of the fish which do not protect their eggs (except the perch, burbot, minnow and maybe the gudgeon and stone loach) do not spawn in Lake Baikal. The phytophilous fish (cyprinids and the pike) reproduce in the flood plain lakes, which are overgrown estuaries, half isolated from Lake Baikal and resembling typical flatland lakes. There they deposit their eggs on plants. The lithophils --the cyprinids, acipenserids, coregonids and salmonids--migrate into rivers where they (328) deposit their eggs on sand-gravel bars. The migrations of fish of both groups save their eggs from destruction by the Lake Baikal underrock gobies.

As indicated, pelagophilous fish and species which protect their eggs in various ways reproduce in the seas. Almost all marine species that deposit demersal eggs and do not protect them, a few of the pelagophilous fish and all the egg-burying species migrate into rivers to reproduce (Tables 91 and 92). These migrations, like in Lake Baikal, are caused by the necessity of saving the eggs from destruction by benthonic predators which are very abundant in the seas (V. V. Vasnetsov).

The phytophilous cyprinids, the egg protecting catfishes and the indifferent perches find suitable sites for reproduction--places with abundant growth of aquatic plants, etc.--in river deltas and estuaries; their migrations are therefore limited to these regions; none of the phytophilous fish ascend the river beyond this zone. In contrast, the conditions in the river deltas and in the lower course of the rivers are not suitable for reproduction of lithophilous fish which bury their eggs (there are no stony banks, the bottom is silted, the current is retarded, etc.) For these reasons, they ascend the rivers much higher than the lithophilous fish do in their search for spawning grounds. The length of their migration depends upon the nature of the river. In small mountain rivers they find suitable spawning beds not far from the mouth of the river; in large flatland rivers they have to migrate upstream for several hundred kilometers or more. Thus, the lithophilous vimba and shemaya migrate from the Azov Sea into the tributaries of the Kuban River (Psekups and Pshish) for spawning while in the Black Sea mountain rivers these fish spawn within a few (5 to 10) kilometers from the delta. The lithophilous acipenserids ascend the Volga River up to Stalingrad or higher, but in the Kura River up to Mingechaura, etc. Particularly long migrations have to be performed by the lithophilous coregonids and the egg burying salmonids. These fish ascend the large rivers up to their upper reaches, covering more than a thousand kilometers.

As mentioned, most of the pelagophilous fish reproduce in the seas. Their spawning migrations are determined by the necessity of releasing their eggs in areas with suitable currents which would provide the necessary conditions for development. Only the pelagophils of the Ponto-Caspian area--the chekhon and seven species of *Caspialosa*--enter the rivers to spawn. The chekhon's spawning migration is short. For instance, the chekhon that enter the Don River from the Azov Sea spawn, somewhere near Azov. The spawning migration of this fish of freshwater origin (which resides permanently in many freshwater reservoirs) allows it to extend its foraging areas beyond fresh waters. At the same time, these migrations reflect the lack of adaptation of the chekhon to reproduction in the sea (its heavy eggs are able to float only in river currents; in still water they sink).

The Ponto-Caspian herrings enter the rivers, but for different distances. Some of them spawn within the delta or slightly above it, however, the herrings of the Volga River migrate up to Kuibishev and even up to Vyatka, i.e. exceptionally far. The reasons for the migration of Ponto-Caspian herrings into rivers and for the various lengths of these migrations are not yet fully understood. Since many of the related pelagophilous species of the genus Caspialosa reproduce in the sea, then it is possible that the purpose of these migrations into the rivers is to provide the opportunity for the young diadromous herring to get familiar with the freshwater foraging grounds, inaccessible to the progeny of

herrings which reproduce in the sea. The explanation for the origin of pelagophilous herrings and for their migrations into rivers must be sought in those conditions which determined the division of ^{the} Ponto-Caspian ichthyofauna into two ecological groups: the one which comprises the pelagophilous herring which does not protect its eggs, and the other comprising the egg protecting lithophils.

Table 93

1) Ecological groups of fish of some large lakes*.

(329)

Таблица 93

1 Экологические группы рыб некоторых больших озер *

15 Озера	2 Абсолютные количества видов в группах												
	3 размножаются в озере							4 мигрируют в реки					
	5 не охраняющие						12	13	14	5 не охраняющие			прятущие икру в грунт
	6	7	8	9	10	11	прятущие икру в грунт	остранофильные	охраняющие и пр.	литофильные	фитофильные	псаммофильные	
Севан 16	2	—	—	—	—	—	2	—	—	(2)	—	—	(2)
Иссык-Куль 17	2	—	—	47	—	—	—	—	—	(2)	—	(2)?	—
Аральское 18	1	5	3	—	1	—	—	—	2	6	—	—	1
Ханка 19	—	7	—	5	4	—	—	2	6	5	—	—	—
Байкал 20	17	—	1	22	—	1	—	—	16	7	3	7	3

21 * В скобках указаны виды, не только мигрирующие в реки, но размножающиеся также и в озерах.

2) total number of species in each group; 3) reproduces in the lake; 4) migrate into rivers; 5) not protecting; 6) lithophilous; 7) phytophilous; 8) indifferent; 9) psammophilous; 10) pelagophilous; 11) semi-pelagophilous; 12) hide their eggs in the ground; 13) ostracophilous; 14) protecting and others; 15) lakes; 16) Sevan; 17) Issyk-Kul; 18) Aral; 19) Khanka; 20) Baikal;

21) * the figures in brackets denote species which not only migrate into rivers but also reproduce in lakes.

6. Resettlement of fish.

The process of resettlement of freshwater fish into seas and of marine fish into freshwater reservoirs is continuing at present and, as in the past, it requires certain changes in the inherited adaptations associated with reproduction and development, and therefore, on the whole, this process depends on these changes.

Coming from rivers, many species of freshwater fish families: the acipenserids, salmonids, coregonids and fish of the perch family, have settled in our seas. However, all these species, except for the marine pike-perch, only forage in the sea. For reproduction they return to their native environment--fresh water--thus preserving a vital link with fresh water. As mentioned, they all do not care for their eggs: some of them bury their eggs in the ground, the others (lithophilous, phytophilous and pelagophilous) disperse their eggs. Only the marine pike-perch, which protects its eggs, and some of the viviparous tropical catfishes reproduce in the seas, i.e. they have completely severed their ties with fresh water becoming marine fish in all respects.

Species of many marine fish families: Anguillidae, Clupeidae, Serranidae, Cottidae, Gobiidae, Syngnathidae, Gasterosteidae, Mugilidae, Gadidae and others have penetrated from the sea into fresh water. Some of these fish release pelagic eggs (Anguillidae, Clupeidae, Serranidae), others

protect their eggs (Cottidae, Gobiidae, Gasterosteidae) while a third group carry their eggs (Syngnathidae). All these species, excepting the eel, have adapted to fresh water completely; they not only forage but also reproduce there, i.e. they do not return to the sea to spawn. Only the pelagophilous eel returns to its native environment--the ocean--during the spawning period.

Thus, most of the fish that came from freshwater differ from the marine fish by the fact that during the spawning period they preserve their ties with the native environment from which they came, whereas most of the marine fish do not preserve these ties. The impression may be created that the freshwater fish are more strongly attached to their initial origin than the marine species, and that they are more conservative in their adaptations associated with reproduction and development; however these impressions are deceptive. Actually, the described diversity between the marine and freshwater fish, reflects the differences (330) in environmental demands which both of these fish groups have to face during resettlement. As mentioned, the marine conditions are fully adequate only for reproduction of pelagophilous fish and those which in one way or another protect their eggs. Fish of other ecological groups--the lithophils, phytophils and others, cannot reproduce in the sea because of the abundance of egg predators there. All these fish are of freshwater origin and only there is the environment fully adequate for reproduction. For permanent

resettlement in the sea, they had to adapt themselves not only to the salinity of the water, but also to the new kinds of predators endangering their eggs, embryos and larvae; i.e. they had to cease to be lithophilous, phytophilous or other types of fish, and had to evolve as pelagophilous fish, or fish that protect their eggs in some manner. However, this requires changes not only in the life habits of adult fish, but also in the structure of eggs, embryos and larvae as well, i.e. it requires a fundamental reconstruction of the whole process of development. Avoiding such very difficult rearrangements, the majority of freshwater fish adopted marine conditions by developing the adaptations of returning to rivers for spawning thus preserving their previous, freshwater manner of reproduction and development. However, the few fish of freshwater origin which developed adaptations associated with development adequate for marine conditions, i.e. began to guard their eggs like the marine pike-perch or became viviparous, thereby acquired the potential for reproduction in the sea without the necessity of returning to the rivers.

The marine fish, which entered and settled in fresh water, except for the eel, did not have such difficulties as the freshwater fish which settled in the sea had. Adapted to release pelagic eggs or to guard them in some manner, they found favorable conditions for reproduction in fresh water because their adaptations associated with development almost completely satisfied living conditions in fresh water.

and considerable reconstruction of the organism was not required. The pelagophilous fish which immigrated into fresh water, except for the eel, had only to reinforce somewhat the buoyancy of the eggs and embryos, i.e. the perivitelline space (herrings), or the fat drop (perch of China, mullet and others) had to be slightly enlarged, changes that decreased the specific gravity of the eggs. The other fish, which guard their demersal eggs (Gobiidae, Cottidae, Gasterosteidae) or those which carry them in brood pouches (Syngnathidae), did not even have to perform these insignificant changes in order to reproduce in fresh water. Like the pelagophilous fish, they had to adapt themselves to the lowered osmotic pressure of the environment. Thus, all the fish of marine origin which have settled in fresh water have preserved their original marine manner of development, as the freshwater fish which settled in the seas preserved their freshwater form of development. However, unlike the latter, they do not have to return into their original (marine) environment to reproduce because their marine adaptations allow them to reproduce in fresh water without any considerable reconstruction of the organism.

Only the eel, adapted to development in very specific oceanic conditions, does not find the necessary conditions for development in fresh water and, in contrast to the other marine emigrants, is unable to reproduce in the new environment without a fundamental reconstruction of the whole process of development. For this reason the eel, like

most of the freshwater fish that immigrated to the sea, preserves its ties with the original environment and during the reproductive period returns there to spawn.

It is evident, that both the marine and the fresh- (331)
water fish, when emigrating into the new element, do preserve the basic adaptations associated with development which were evolved in the initial environment, or change them only insignificantly; therefore both groups are equally progressive and equally conservative. The ability to reproduce in the new environment, as well as the necessity of returning to the old environment for reproduction are determined not by the progressiveness or conservatism of the fish, but by the degree in which their basic adaptations are suited to the conditions of the new environment, and by the quality of the reconstruction of the organism, which would be required.