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Causes of the variability of the fecundity and age of sexual maturation in monocyclic fish, based on the example of *Oncorhynchus* salmons

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Causes of the variability of the fecundity and age of sexual maturation in monocyclic fish, based on the example of *Oncorhynchus* salmons

by V.N. Ivankov

It has been shown that the level of potential fecundity (PF) in monocyclic fish (members of the genus *Oncorhynchus*) is determined by the conditions of embryonic and larval development and by the amount of food available to the immature fish at the early stages of life. The variability of potential fecundity is directly associated with the rate of gonadal development in the young fish. Ultimate fecundity is determined by the level of potential fecundity. The age of sexual maturation depends to a great extent on the condition of the gonads at the earliest stages of life.

Up to the present time, a fairly large number of papers has been published on the variability of fecundity in fish under the effect of various factors (Swardson, 1949; Nikolsky, 1953, 1974; Anokhina, 1969, etc.). As we know, fish of the same species but of different populations may have different levels of fecundity due to dissimilar feeding and breeding conditions, pressure from predators, etc. Within the same population, fecundity varies in fish of different age, size and condition. The annual fluctuations of fecundity also depend on population density and the fluctuations in the numbers of food organisms. All of these

*The numbers in the right-hand margin are the pages of the Russian text - translator factors have a similar effect on the changes in the fecundity of both polycyclic and monocyclic fish. However, there is one circumstance which adds a certain specificity to the functioning in monocyclic fish of the relationships between fecundity and the factors on which it depends. The fact is that, in contrast to polycyclic fish, there is no reserve of sexual cells in maturing monocyclic fish, as all the oocytes found in their ovaries develop almost synchronously and there are no longer any oogonia left by that time. Unlike that in polycyclic fish, the maximum number of sexual cells in the ovaries of monocyclic fish is established very early.

In Far Eastern salmons, i.e. Oncorhynchus masu (Brev.) and some populations of O. nerka (Walb.), it is noted in immature fish prior to downstream migration, when the oocytes are at the 3rd and 3rd-4th stages of protoplasmic growth (Iyevlev, 1974; Ivankov, Chikina, 1977). In O. gorbuscha (Walb.), the highest level of potential fecundity (PF) is noted in the fry long before downstream migration (Persov, 1963), and in O. keta (Walb.) soon after downstream migration (Grachev, 1971). In cyclostomes such as O. gorbuscha, the maximum number of sexual cells is observed at the fry stage (Hardisty, 1964).

While determining the number of sexual cells in monocyclic fish and ichthyoids, we found that it increased up to a certain point, and then gradually diminished, right up to the maturation of the gonads and spawning time. This is quite clearly traced in such species as O. gorbuscha and O. masu (fig. 1). Maximum potential fecundity is observed at a length of about 3 cm in O.

gorbuscha, and at 8-10 m in O. masu. Since monocyclic fish have no reserve of sexual cells, the level of ultimate fecundity cannot be greater than the level of maximum potential fecundity which is established in these fish at the early stages of life.

The resorptive processes, which result in the destruction of the sexual cells and a decrease in their number, are noted throughout life right up to the time of spawning in monocyclic fish (806) (Ivankov, 1976). It follows from this that the number of oocytes decreases in these fish with growth, i.e. the older and larger the fish, the lower the level of fecundity. If we analyze the change in fecundity in an individual fish, we find that this is what really occurs. However, in any population, older and, therefore, larger fish are characterized by a higher fecundity. We have also noted that different fish of the same size have a fecundity which sometimes differs several-fold.

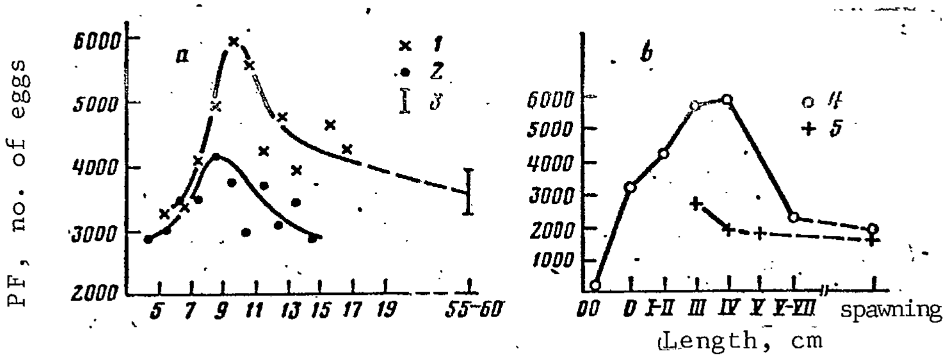

Fig. 1. Changes in the number of oocytes in O. masu (a) and O. gorbuscha (b) in the course of biological development: 1 – Kiyevka R.; 2 – aquarium specimen; 3 – variation range of mean absolute fecundity of O. masu during different years; 4 – the Arctic; 5 – southern Sakhalin. On the X-axis of b: 00 – beginning of incubation, 0 – hatching stage, I-VII – months after hatching. Data on O. gorbuscha from G.M. Persov (1963)

What is the cause of this significant variability in the value of the absolute fecundity of these fish?

We have attempted to clarify this question. As an example, we used O. masu, a monocyclic species which matures at different times. Our model was the masu which breeds in the rivers of the Maritime Territory (Kiyevka, Uspeniye, El'duga). We also analyzed material on a number of other species (O. keta, O. nerka, O. gorbuscha).

Table 1. Absolute fecundity of Maritime masu (Kiyevka R.), 1976

Length of body, cm	Absolute fecundity, no. of eggs		No. of fish
	variation	M±m	
46.1-48	1130-2820	2345±106	5
48.1-50	1910-3580	2412±83	10
50.1-52	1690-4550	2904±68	24
52.1-54	1820-3910	2858±73	25
54.1-56	1950-4940	3079±65	33
56.1-58	1850-4890	3423±81	22
58.1-60	2440-5320	3671±78	22
60.1-62	1758-5440	3966±101	13
62.1-64	2850-4130	3567±123	6
64.1-66	-	4520	1
Average	1130-5440	3142	163

A study of the absolute fecundity of masu which migrates to the Kiyevka R. to spawn enabled us to establish that the number of oocytes varied 2—3-fold in equal-sized salmons of this basin (table 1). For example, in 50.1 -52.0 cm fish that migrated upstream to spawn in 1976, the minimum fecundity was equal to 1690 eggs, and the maximum fecundity 4550 eggs; in 60.1-62 cm fish, these figures were equal to 1758 and 5440 eggs respectively (table 1). Similar variations in fecundity were also noted during other years. One can assume that the level of absolute fecundity of fish entering the river to spawn is determined to some extent by the level of their potential fecundity during the early period of life. In order to verify this assumption, we analyzed the potential fecundity of immature masu from the Kieyevka R. The young salmons were caught both in the main river channel, and in its tributaries (Shalomai and El'dagou springs), as well as in Kiyevka Bay after the downstream migration of the young fish. (807)

Variability of potential fecundity and its relationship with ultimate fecundity

Our study of the potential fecundity of immature fish revealed a high variability of this index in fish of the same age and similar size. It has already been shown (Ivankov, Chikina, 1977) that the highest level of potential fecundity in masu is established in the fingerlings (autumn). It decreases significantly by the age of two. As we can see from table 2, the maximum potential fecundities in the immature fish caught in the Shalomai and El'dagou springs and in the main river channel differ significantly. The maximum PF of fingerlings from the Shalomai Spring averaged 6385 eggs, and that of fingerlings from the El'-dagou Spring only 3780 oocytes. In fish of age 1+, which were to migrate downstream in spring—beginning of summer the following year, the number of oocytes was 3998 and 2582 respectively. In autumn, the fish caught in the main river channel had 5908 (4824-6200) oocytes at age 0+ and approximately 4500 (2984-5986) oocytes at age 1+.

As we can see, different masu, even at a young age, have a different number of sexual cells in the ovaries. As in the mature fish, the maximum PF is usually 2-3 times greater than the minimum PF.

Table 2. Potential fecundity of O. masu from the Kiyevka R. basin (1976)

Sampling site	Date	Age	No. of oocytes	Body length, cm	No. of fish
Shalomai Spring	9 Aug	0+	6385 (4462-9278)	9.9(8-10.9)	4
		1+	3998 (2364-5876)	11.9(11.2-12.5)	5
El'dagou Spring	1 Sept	0+	3780 (3176-4384)	10.0(9.7-10.4)	3
		1+	2582 (1446-5420)	12.2(10.7-13.4)	6
Kiyevka R. (main channel)	16 Sept	0+	5908 (4824-6200)	8.9(6.5-9.2)	10
		1+	4528 (3266-5561)	13.8(12.5-15.2)	5
Ditto	2 Oct	1+	4473 (2984-5986)	12.0(10.5-14.0)	10
Kiyevka R. (mouth of old channel)	22 May	2+	5143 (3652-5880)	14.8(13.5-15.6)	5
Kiyevka Bay	Beginning of June	2+	5903 (2588-10420)	17.4(15.9-19.3)	9

Since the potential fecundity is higher than the ultimate fecundity both in polycyclic and monocyclic fish (Ivankov, 1976), the fish that migrate downstream with a low PF will naturally have a low fecundity at the time of maturation, and vice versa, the fish with a high PF will most likely have a high ultimate fecundity. This can also be illustrated on the masu that reproduce in the Kiyevka R. basin. Several years of observations have shown that late, highly fertile masu come to spawn in the Shalomai Spring which is located near the mouth of the Kiyevka R., whereas the smaller and less fertile masu of earlier runs spawn in the El'dagou Spring which is much farther from the mouth. As indicated earlier, the immature fish from the El'dagou Spring also has a lower PF in comparison with those from the Shalomai Spring.

During our study of the PF of O. masu from various rivers (table 3), we found that the PF of the fish in smaller rivers is lower than in large ones. For example, in the small Uspeniye R. where comparatively small masu come to spawn (according to observations in 1974-1978), the PF of the fish is much lower than in the fish of the Kiyevka R. where large, highly fertile masu reproduce in the majority of tributaries.

Consequently, there is a distinct positive correlation between the potential and ultimate fecundity in O. masu and, apparently, all monocyclic fish.

(808)

Table 3. Potential fecundity (PF) of masu from different rivers of the Maritime Territory

River	Date	Age	No. of oocytes	Body length, cm	No. of fish
El'duga	28 March 1974	0+	3252 (2332-5272)	6.7 (5.6-7.7)	10
		1+	4862 (4159-5903)	10.0 (8.2-12.5)	10
Uspeniye	16 Aug 1974	1+	3696 (2717-4447)	11.7 (14.5-16.0)	10
	9 Sept 1975	1+	2724 (1128-4138)	12.0 (10.8-13.5)	20
	22 May 1976	2+	3622 (2418-5412)	15.3 (10.7-12.8)	10
Kiyevka	16 Sept 1976	0+	5908 (4824-6200)	8.9 (6.5-9.2)	10
		1+	4528 (3262-5561)	13.8 (12.5-15.7)	5
	22 May 1976	2+	5143 (3652-5880)	14.8 (13.5-15.6)	5

Causes of fluctuations in potential fecundity (PF)

It is natural to assume that the PF level is primarily affected by the conditions in which the young fish develop. It has been shown that the potential fecundity is at a lower level in the El'duga R. where the conditions are worse than in the Kiyevka R. and the condition of the fish is much lower (Ivankov, Chikina, 1977). For instance, in 7.0-8.5 cm fish, the potential fecundity was equal to 3950-4940 oocytes in the first case, and 4660-5650 oocytes in the second case.

Experimental data also point to a close relationship between the conditions of the habitat and the potential fecundity. A comparative analysis of the change in the potential fecundity of immature fish caught in the Kiyevka R. and fish reared under aquarium conditions[1] enabled us to establish that the PF level in fish from a natural population was much higher. If in the first case the maximum PF level averaged 6000 oocytes, it was only slightly higher than 4000 oocytes in the second case (see fig. 1).

We should note that, according to the data of V.V. Gorban' for 1975-1976, the stomachs of the immature masu from the Kiyevka R. contained 53 food ingredients, the basic food being the larvae of flying insects (Chironomidae, caddis-flies, stoneflies, May-flies, etc.), as well as crustaceans. Under aquarium conditions, the young fish obtained less diverse, though high-energy foods, most of which consisted of minced fish. The temperature of the water in the aquariums was kept at a constant 14-16°C, whereas it fluctuated in the Kiyevka R. from fractions of a degree to 17-18°C, depending on the season. It should be said that, because of the high temperature of the aquarium water throughout the rearing period, beginning with the embryonic stage, the salmons developed and grew rapidly. The eggs were taken for incubation in September, and by spring the young fish in the aquariums were already 13.0-14.5 cm long, i.e. their length was equal to that of the downstream-migrating masu from the Kiyevka R. (downstream-migrants average 12.3 at age 1+ and 14.1 cm at age 2+).

At the present time, it is difficult to say exactly why the accelerated development and extremely rapid growth of the young

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[1]Rearing of young fish was carried out by staff members of the Pacific Scientific Research Institute of Fisheries and Oceanography (TINRO) in the aquariums of the Far Eastern State University and TINRO.

fish in the aquariums resulted in a decrease of PF, but the fact remains that the maximum PF level in the young fish from the Kiyevka R. was 1.5 times higher. We believe that the physiologic development of the organism in the first case lagged behind the extremely rapid increase in body length and mass. Apparently, a certain (greater) period of time is required for a large number of oocytes for form in the ovaries. Thus, excessive forcing of growth caused the PF level to drop. In the given case, the change in the PF value was effected by at least two factors, the temperature of the water and the qualitative composition of the feed.

Table 4. Potential fecundity of young O. keta raised in sea ponds under various feeding conditions

Pond No.	Type of feed	No. of oocytes			Student criterion			
		range	M±m		1	2	3	4
1	Pasty feed	3152-4737	3922±253	565	-	3.27	1.20	2.57
2	Krill with chitosan	3355-5744	4749±350	927	-	-	2.51	0.51
3	Fish feed	3377-5059	4226±208	623	-	-	-	1.06
4	Krill	3879-4960	4573±252	501	-	-	-	-

Let us examine a case where the formation of PF is affected by only one factor, the food consumed by the fish. Table 4 contains data on the potential fecundity of young O. keta raised in (809) sea ponds in Alekseyev Bay (Popov Is., Peter the Great Gulf) under various feeding conditions[2].

As we can see from table 4, the potential fecundity of salmons raised on a pasty feed differs significantly (confidence level 99.9%) from the PF of salmons raised on krill with chitosan.

[2] Rearing of young fish was carried out by staff members of TINRO during the summer of 1980. PF was determined at the Department of Hydrobiology and Ichthyology of the Far Eastern State University.

A 95% confidence level is observed in the difference between the PF of the first and fourth ponds, and the second and third ponds. The pasty feed (pond 1) had the lowest calorie value and contained the smallest number of ingredients (only six). The highest number of ingredients (13) was found in the feed given to the salmons in pond 2. As we can see, the lowest PF was observed in pond 1, and the highest in pond 2.

We should add that all the salmons with which the ponds were stocked came from the same batch, and were of the same size prior to stocking. Consequently, we observed that the potential fecundity in this case changed only under the effect of the qualitative composition of the feed. Thus, we have established that the PF level is affected by the feeding conditions of the young fish at the earliest stages of life.

Turning back to the analysis of tables 2 and 3, we should note that the potential fecundity of salmons varies not only in different rivers and tributaries of the same river. A high variability of PF is also noted within each sample. For instance, the potential fecundity of fingerlings from the Shalomai Spring varies from 4467 to 9288 oocytes, that of second-year fish from the main channel of the Kiyevka R. from 2984 to 5986 oocytes, etc. (see table 2). The same is also noted for other rivers (table 3).

It is quite possible that such significant fluctuations in the individual PF level are determined by the degree of oocyte development. For example, in young masu of age 2+ caught on 22 May 1976 in the Uspeniye R., the average diameter of the oocytes varied from 144 to 210 μ in different individuals. This is due to the fact that the number of sexual cells at different stages of protoplasmic growth varied in different specimens. For example, the number of oocytes at the 3rd stage of growth varied from 11.3 to 90.3%, and those at the 4th stage of growth from 0 to 79.3%. Similar data were also obtained when we analyzed the size and condition of the sexual cells in the salmons of other samples.

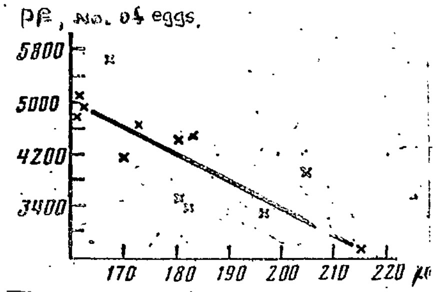

Fig. 2. Relationship between oocyte diameter (μ) and the value of potential fecundity (PF) in young O. keta

Fig. 2 depicts the relationship between the PF value and the diameters of older-generation oocytes in young keta salmon. As we can see, the potential fecundity is much higher in the salmons with ovaries containing large oocytes. Naturally, this relationship is not a strict one, as the variability of the PF level is also affected by hereditary factors. On the other hand, it is obvious that the size variability of the sexual cells cannot but affect the variability of the individual PF value even at the early stages of development of young fish.

(810)

Interrelationship of the condition of the ovaries in young downstream-migrants, the rate of maturation and the fecundity of salmons

The data available at present permit us to say that the rate of maturation in fish of different species and populations is correlated to a certain extent with the condition of the gonads in immature fish during their downstream migration from fresh waters to the sea. In the fast-maturing salmon O. gorbuscha which spawns at age 1+, the third stage of oocyte growth sets in 1-2 months after hatching; in O. keta and O. nerka which mature mainly during the 4-5th year, it sets in after 6-7 months, and in Salmo salar L. after 12-24 months (Persov, 1975). Whereas the downstream-migrants in O. gorbuscha of some populations often have oocytes at the 4th and even 5th stage, those of O. keta are are only at the 1st and 2nd stages (Persov, 1966).

Within a species in populations where the immature fish migrate to the sea with less developed gonads, we note later maturation and arrival at the spawning grounds at an older age. In O. nerka of Lake Kurile, we have noted that most of the fish mature at an older age in comparison with specimens of the same species from other bodies of water (Yegorova et al., 1961). Consequently, the downstream-migrants of this population have the most weakly developed oocytes - mainly at the 2nd stage, less commonly at the 3rd stage of growth. O. nerka of Lake Dal'neye, which spawns at a young age, migrates downstream to the sea with gonads containing oocytes of mainly the 4th and even 5th stage of growth (Iyevleva, 1970). In O. gorbuscha of the southern Kurile Islands, which spawns quite late (especially the autumn race), the immature fish which had migrated downstream to forage near the shores in July-August, had oocytes at the 2nd and 3rd stages of growth (Ivankov, Chikina, 1977). In O. gorbuscha of other populations, which entered the rivers to spawn earlier, the oocytes in the ovaries were at more advanced stages of growth during downstream migration (Persov, 1966). Obviously, such correlations between the condition of the gonads of individuals at the stage of downstream migration and the age of maturation also exist within a population.

We have noted that the condition of the ovaries in downstream-migrating young fish of the same age varies even in specimens caught on the same day (from the same concentration). For example, in downstream-migrating masu of the Uspeniye R. caught on 22 May 1976, we encountered specimens with oocytes at the 4th stage of growth and individual fish with oocytes not in this condition; the ovary of a 16 cm specimen contained 79.3% oocytes at the 4th stage of growth, while a 15.4 cm specimen had 63% oocytes at the 3rd stage and 37% oocytes at the 2nd stage of growth. In some fish which had migrated downstream and were caught in Kiyevka Bay in June 1977, 64-77.5% of the cells in the ovaries were at the 5th stage of growth, while in other fish this stage was not observed at all and oocytes of an earlier stage of growth predominated. In a specimen with 10,420 oocytes in its ovary, 29.6% first-stage oocytes was observed together with cells of the 3rd and 4th stages of growth. Such individual differences in the condition of the ovaries were also noted in downstream-migrating young keta (Persov, 1965) and nerka (Iyevleva, 1970).

As we have already mentioned, there is an inverse relationship between the size of the oocytes and the PF level. This has been noted for the young of O. keta raised in ponds. The relationship between the condition of the ovaries in young fish and their potential fecundity is also observed in natural populations. In downstream-migrating masu of the Uspeniye R., the potential fecundity averaged 3997 oocytes in fish with oocytes mainly at the 3rd and partly at the 2nd stages of growth, and 3340 cells in those which also had oocytes of the 4th stage. In young fish foraging after downstream migration in the pro-estuarine parts of Kiyevka Bay, the ovaries contained only fourth- and fifth-stage oocytes, and their PF was equal to 3911 oocytes; in young fish which also had second- and even first-stage oocytes, but no fifth-stage ones, the PF was equal to 5698 oocytes (10,420 cells in one specimen, 444-4508 cells in the others).

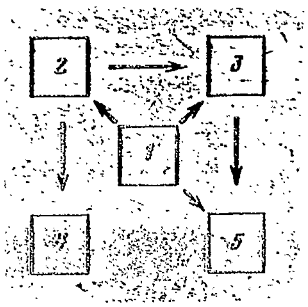

Fig. 3. Diagram of relationships between the rate of growth, gonadal development, fecundity and the age of sexual maturation in monocyclic fish.

1 - rate of growth of the organism; 2 - rate of gonadal development in young fish at the early stages of life; 3 - potential fecundity; 4 - age of sexual maturation; 5 - ultimate fecundity

Thus, a relationship has been established between the condition of the oocytes in young downstream-migrants and the age of maturation, as well as between the first characteristic and the PF level of the downstream-migrants. Since the young fish migrating downstream with a low fecundity have more developed gonads and this results in earlier maturation, the salmons with a low PF at the downstream-migrating stage should mature at a younger age. On the basis of this, it can be said that the PF level in young downstream-migrants not only determines the fecundity of the spawners, but is also in positive relationship with the age of the sexual maturation of the fish.

This explains why the older specimens in monocyclic fish have a higher fecundity on the average. Their late maturation is determined by the slowed development of the gonads in the young fish, and delayed gonadal development results in the formation of a higher potential fecundity.

Thus, in the given case, we are dealing with a system of relationships, i.e. the rate of gonadal development of the young fish—potential fecundity—growth—the age of sexual maturation——ultimate fecundity (fig. 3).

Naturally, a factor such as growth rate, beginning with a certain stage in the development of the organism in monocyclic fish, cannot produce an increase in the number of sexual cells in the ovary, but a deterioration of habitat conditions or other factors can bring about a considerable decrease in the number of sexual cells. For instance, during maturation in fresh waters (without migrating to the sea to forage), the number of sexual cells in salmons can decrease several-fold. For example, in neotenic masu females which mature in the river, the number of sexual cells decreases at least 6-fold (from 1656 to 250-280) the year before spawning (Ivankov et al., 1981).

Conclusions

1. The ultimate fecundity of monocyclic fish depends primarily on the PF level of the individual fish.

2. The PF value is determined by the conditions of development and the amount of food available to the young fish at the early stages of life.

3. The individual and interpopulational variability of potential fecundity is correlated with the rate of gonadal development of the young fish prior to their migration from fresh waters to the sea.

4. The age of sexual maturity is determined to a great extent by the condition of the gonads at the early stages of life. In fish of the same population which mature earlier, the potential fecundity is lower than in those which mature later.

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