V.A. Kostitsin Eco-Genetic Model in Studying the Race Dynamics of the Multirakered Muksun of the Yenisei River

N D Haydenok¹, V F Chumakov¹, I V Chumakov¹
¹Reshetnev Siberian State University of Science and Technology

Abstract. The paper considers the results of studying the ordinary multirakered muksun race dynamics in the Yenisei River based on the eco-genetic model and resolves the issue of determining the fish farm locality, which is equivalent to defining which subpopulation should be strengthened through the artificial reproduction.

1. Introduction
In the time of the New Economic Formation in Siberia, a series of bans on fishing the semi-anadromous ichthyofauna were placed:
1. 1998 – Siberian sturgeon of the Yenisei River,
2. 2014 – muksun of the Ob River,
3. 2019 - inconnu, muksun, and omul of the Yenisei River.

The period of the ban placed on the sturgeon of the Yenisei River due to excessive consumer-oriented fishing since 1998, has not brought the expected increase in its population but determined the need for artificial reproduction of the above target species. In this regard, the below specific question arises: - where the artificial reproducers should be selected and the fish farms arranged?

2. Relevance
As for the Yenisei River, the fish farm arrangement area for virtually the entire semi-anadromous ichthyofauna should be a segment of the upper stretch of the Lower Reaches of the Yenisei from the Nizhnyaya Tunguska River to the Khantayka River – Fig. 1.
This conclusion is determined by both the current economic reasons, i.e. the presence of the Khantayskaya and Kureyskaya HPPs and ecological ones:

1. the availability of various forms (stocks, subpopulations) of each species – ‘from two’ [1, 4, 9],
2. the specifics of their spawning migrations - spawning on various grounds [4, 9],
3. the fishery nature since 1900 [5, 8].

3. Research objective
According to the above, the issue of determining the fish farm locality is equivalent to solving the problem ‘Which stock (subpopulation) should be strengthened through artificial reproduction?’

The analysis of the above factors is the research objective.

Then, the issue of determining the fish farm locality is equivalent to studying the race formation problem (deeper differentiation of subspecies or ranks that are determined by the formal principles of taxonomy) in the semi-anadromous ichthyofauna of the Yenisei River.

The situation in studying the race formation issue is hampered by the presence of outwardly different but phenomenologically equivalent terms for the concept of race, i.e. stock, subpopulation, form, morph, variety, migration type, reproductively isolated seasonal group, specific reproductive strategy bearer, etc.

The term variety considered is not certainly a result of an idle undertaking but reflects the relevant race formation aspects.

The work [3] studying the dynamics of the reproductive strategy bearers (in that case, mammals) that are the practical equivalence of the races typical for ichthyology and the race dynamics of the intraspecific continuum of the Yenisei muksun has become a progressive approach to solving the issue of forming races in ichthyology, which has shifted the situation with explaining its essence from the stage of ‘moving in a circle of purely eco-ichthyological aspects’ and confirmed the experience of using genetics in studying MMC (multirakered muksun continuum).

However, it is now required to give the below information concerning the specifics of using genetics in studying race formation. In terms of historical development, the entire genetics can be divided into three areas - experimental (primarily, the selection issues), formal, and instrumental or physicochemical ones.

It is true that instrumental genetics still does not work in general “deeper than not only a subspecies but also a species in some cases”, and approaches to ‘increasing depth’ are outlined only in the world's leading laboratories.

Also, the issue of guaranteeing that the signature obtained is responsible for certain environmental indicator remains open.

Therefore, to investigate the dynamics of races as intraspecific relations, we have the results of studies of the first two areas at our disposal. More precisely, mostly the formal one.

However, despite the rather non-optimistic prospects, instrumental genetics has determined the below ‘working’ rule for the duration of forming a race as an intraspecific phenomenon: in the first approximation, the regularity is valid that the ratio of decimal logarithms of the species (S) and race (R) forming duration is equal to the intraspecific race order, i.e. \( \log [S] / \log [R] = 3 \)

4. Theoretical
Thus, having determined the methodology frame, let us pass to investigating the race formation aspects for muksun of the Siberian rivers from the Ob River to the Lena River with the main emphasis on muksun of the Yenisei River.

Let us consider this issue on the example of the intraspecific muksun continuum of the Yenisei River using the genetics laws to explain the intraspecific structure.

Indeed, “the seasonal MMC races, which are virtually indivisible morphometrically, are an example of the Mendelian MMC segregation in monohybrid crossing, where instead of the yellow and green peas, the early and later races are considered as a discriminant feature; they are differentiated by the length of spawning anadromy associated by classical Yenisei ichthyologists from V.L. Isachenko
to A.A. Kuklin [5] with the gonadal maturity degree (Fig. 2) corresponding to the spawning ground types and genetically fixed in innate instincts reflecting such an aspect of the biological phenomenon of “the life pressure in the form of an expansion of the areal” as endorestriction by population density in relation to food supply [1]”.

Naturally, the presence of individuals with different gonadal maturity migrating to different spawning grounds in the spawning stock is extremely far from a genetic indicator such as the ‘reaction norm’ – at a certain average size, the population includes both slowly and rapidly growing individuals, which form the corresponding races according to the Lamarckism principles. Here, the situation represents the classic phenomenon of the r and K strategy. I.e., speaking in an agricultural language, "there are not large and small individuals of a single breed but two different slowly and rapidly growing breeds, each of which, in turn, includes large and small individuals."

Let us study the MMC race dynamics using mathematical simulation based on the modified V.A. Kostitsin eco-genetic model [7] (cited, p. 99).

Before proceeding to the analysis, note that according to a classic concept, tropho-demographic characteristics such as height, weight, and living matter production rate are determined by not a single gene (DNA section) but a complex of genes - a cluster, which can be in several states called alleles in respect of the gene.

Therefore, it would be more correct to use the term ‘gene complex’ or ‘gene cluster’ or ‘gene cluster type’ instead of ‘gene’. However, in tribute to tradition, the terms ‘gene’ and ‘genotype’ are still used here.

Let according to [7, p. 101], $N_1$, $N_2$, and $N_3$ are the numbers of individuals with genotypes AA, Aa, and aa; $N = N_1 + N_2 + N_3$ is the total population.

Then, the dynamics of $N_1$, $N_2$, and $N_3$ is described by the below differential equation system (1) [7]:

\[
\begin{align*}
\frac{dN_1}{dt} &= \alpha_1 N_1 - \beta_1 N_1 N_2 - \gamma_1 N_1 N_3 \\
\frac{dN_2}{dt} &= \alpha_2 N_1 - \beta_2 N_1 N_2 - \gamma_2 N_2 N_3 \\
\frac{dN_3}{dt} &= \alpha_3 N_1 - \beta_3 N_1 N_2 - \gamma_3 N_3 N_2
\end{align*}
\]

where $\alpha_i$, $\beta_i$, and $\gamma_i$ are the parameters of the model.
where \( \varphi \), \( m_i \), \( \mu \) are the fertility rate or fitness function, the mortality of the \( i \)-th genotype, and endorestriction coefficient.

Building the system (1) is based on Mendel's first law and methodology for describing a) the Verhulst - Pearl equations of the general laws of genotype dynamics and b) the Lotka - Voltaire system of endorestriction and competition of genotypes.

Indeed, in the equations, the first terms are formed based on the allele balance - Table 1.

**Table 1. Allele Balance.**

|   | \( N_1 \) = AA | \( N_2 \) = Aa | \( N_3 \) = aa |
|---|----------------|----------------|----------------|
| A | 1              | 1/2            | 0              |
| a | 0              | 1/2            | 1              |
| \( \Sigma \) | 1              | 1              | 1              |

Based on the allele balance matrix, we obtain equations for the corresponding gametes (2):

\[
A = N_1 + \frac{1}{2} N_2 + N_3, \tag{2}
\]

\[
a = 0 N_1 + \frac{1}{2} N_2 + N_3,
\]

\[
AA = (N_1 + \frac{1}{2} N_2)^2,
\]

\[
Aa + aA = (N_1 + \frac{1}{2} N_2) (\frac{1}{2} N_2 + N_3) + (\frac{1}{2} N_2 + N_3) (N_1 + \frac{1}{2} N_2) = 2(N_1 + \frac{1}{2} N_2) (\frac{1}{2} N_2 + N_3),
\]

\[
aa = (\frac{1}{2} N_2 + N_3)^2,
\]

Despite their extreme uncertainty in genetics [7, p. 96], from the demographic point of view, the fertility rate or fitness function values represent the net population growth rate \( r \) [6] determined based on the age distributions of sex maturity of females, the proportion of females in the age class, fertility, and mortality.

In this regard, in the system (1) in the first ‘working’ approximation, \( m_i \) should represent only fishing mortality since natural one has already been included in \( r \).

The aggregate genotype competition and endorestriction coefficient determined as the product of the total population and a certain genotype number will be considered by the effect of the feed level on \( r \) through the dependence of fertility (proportional to the individual diet \( C \)) on the feed level \( B \) (3),
which is the Holling’s functional response type III - Fig. 3.

\[ C(B) = C_b \frac{X^n}{X^n + a^n}, \quad X = \frac{B}{(N_1 + N_2 + N_3)} = \frac{B}{N}, \]  

\[ C(B) = C_b \frac{B^n}{(B^n + (aN)^n)}, \]

\[ \text{Figure 3. Holling’s Functional Response Types (1969).} \]

Based on (3), let us represent the dependence of the i-th genotype fertility \( P_i \) in the form (4) on the total population \( N \) (feed areas and food spectra of both phenotypes and genotypes are similar):

\[ P_i(B/N) = P^m \frac{B^n}{(B^n + (aN)^n)} = P^m/(1 + (a_iN/B)^n), \quad n \geq 2 \]

(4)

The food supply level undoubtedly changes the proportion of sexually mature individuals: the age distribution will shift towards greater ages by at least a year.

Before proceeding to further analysis of the modification principles, let us link the above genotypes to the elements of the intra-subspecies MMC structure: the AA and Aa genotypes will correspond to the dominant later MMC race and the aa genotype - to the subdominant early one (Fig. 4) since it appears on the Upper Spawning grounds only at a sufficiently high total population. This correspondence is fully determined by both the former fishing volumes in the relevant spawning ground areas and the specifics of the spawning runs.

The fishing mortality is determined based on the nature of linking the races to genotypes; since the majority of the early race runs from autumn to autumn either under ice or during a spring flood, when it is hardly accessible to fishing gear, its fishing mortality is lower than that of the later race running in summer. I.e., \( m_1 \) and \( m_2 > m_3 \).

But the most radical change in the net population growth rate \( r \) occurs with the change in the mortality rate ‘fish eggs – 0+’ due to the high (5/2) ratio of catadromy lengths - Fig. 4, a.
Figure 4. Relation of Genotypes to Spawning Grounds and Anadromy Length, km.

Even at the simplest linear decrement, the mortality rate ‘fish eggs – 0+’ will increase by 2.5 times. But since 0+ from the Upper Spawning Grounds will approach the Lower ones in very shabby conditions and further will also be exposed to a violent stream, a cumulative effect expressed in an exponential decrement, the value of which, according to the most conservative estimates, will increase the catadromy length ratio from 2.5 to 3–4, is already observed here.

Then, the net population growth rate $r$ equal to 0.17 for the MM [2] will decrease towards the middle of the interval 3–4, i.e. 3.5 times according to Laplace’s principle of insufficient reason.

However, considering the Middle Spawning Grounds, the decrement $r$ should be taken equal to the lower variation limit of 3.

The above 0+ mortality increase specifics and a decrease in the net population growth rate allow determining the general spawning ground structure. It has two elements, i.e. a base core and a peripheral explosion or diffusion region, depending on the penetration rate - Fig. 4, b.

Moreover, in reality, the explosion – diffusion region may hardly be simply connected or continuous one; as a rule, it has a hierarchical structure (Fig. 4, a, c), where contact with other morphs or subspecies is even possible.

Thus, having determined the most ‘problematic’ of the basic genetic indicators, i.e. $r$, let us analyze the general frame (1).

In (1), let us adopt $m_i = \text{const}$ and sum the right- and left-hand sides of the equations. As a result, we obtain the classic Verhulst - Pearl equation for the total population $N$ (5):

$$\frac{dN}{dt} = (\varphi - m)N - \mu N^2 = (b - \mu N)N, \quad b = \varphi - m,$$

(5)

the right-hand side of which is qualitatively similar to the classic Ricker's relationship ‘offspring – parent’.

5. Practical significance
The main V.A. Kostitsin system value is that it not only reflects the main ecological patterns but also, most importantly, allows reproducing the dynamics of transitions between genotypes while considering specific ecological and fishing conditions.

Here, already the classic patterns of Mendel’s first law ‘¼ - ½ - ¼’ may radically change. E.g., in some specific agrotechnical conditions such as soil moisture, planting density, etc., the subdominant green pea variety took over the dominant yellow one.

Let us return to the V.A. Kostitsin system modification specifics adopted herein. On the right-hand side of the system (1), only two terms remain, the first of which is responsible for describing the dynamics of transitions between genotypes, considering the food endorestriction, and the second one...
reflects the effect of fishing mortality on each genotype. The food endorestriction nature for each genotype expressed through a drop \( r_i \) proportional to the \( i \)-th genotype fertility \( P_i \) (4) is shown in Fig. 5, a, where the difference in the \( N \) values, at which decrements \( r \) of genotypes \( N_1, N_2 \) (taken equal according to Mendel’s first law), and \( N_3 \) take place, is determined by a slowdown in both the total growth of gonads and their maturity rate at low food supply. In \( N_3 \), according to this study, at the start of spawning migration, it is less than in \( N_1 \) and \( N_2 \), i.e. II-III and III versus III-IV, IV, and IV-V – Fig. 4.

\[
r_i(N) = \frac{r_i m_i}{1 + \left( \frac{a_i}{BN} \right)^n}, \quad a_1 \approx a_2 > a_3 \approx 0.5a_2.
\]

is shown in Fig. 5, b. As is easily seen, it is identical to the qualitative form of the classic Ricker’s relationship ‘offspring – parent’ [6].

Then, based on the above, considering (6), the system (1) will take the form (7):

\[
\begin{align*}
\frac{dN_1}{dt} &= \frac{r_1(N)}{N(N_1 + 0.5N_2)^2} - m_1 N_1 \\
\frac{dN_2}{dt} &= \frac{2r_2(N)}{N(N_1 + 0.5N_2)(0.5N_2 + N_3)} - m_2 N_2 \\
\frac{dN_3}{dt} &= \frac{r_3(N)}{N(0.5N_2 + N_3)^2} - m_3 N_3
\end{align*}
\]

Having obtained an equation system describing the dynamics of transitions between genotypes depending on the ecological and fishery conditions, let us represent the results of simulating the genotype dynamics (Fig. 6) at actual fishing volumes based on tropho-demographic parameters and fishing statistics [2]. Here, the simulation results speak for themselves:

1. “In the 1950s, the population situation was the most ominous” [8],
2. “By the end of the 1980s - beginning of the 1990s, after a long pause, the MMC producers began to emerge on the Upper Spawning Grounds” [4].
Fig. 6. Dynamics of Genotypes and Fivefold (Scale) Catch (C<sub>nf</sub>), t, 1943 – the actual catch is 860 t.

Fig. 6. clearly shows that at population biomass corresponding to the MMC MSY (optimal fishing level) equal to ~ 1,200 t of N<sub>3</sub> individuals 14+ - 16+ emerge on the Upper Spawning Grounds. As is easily seen, this occurs only at the total biomass N ≥ 1.2 MSY, point N<sub>3</sub> in Fig. 6, b.

6. Conclusion
The dissipative structure of the N<sub>3</sub> genotype emergence on the Upper Spawning Grounds is an indicator of achieving the MMC MSY level, which should be significantly exceeded given the high consumer-related catch, as the imposed ban shows.

In conclusion, let us consider the eco-genetic role of the MMC races.

The dominant later race gets its status in view of energy savings for spawning anadromy and clearly dominates during the period of low total MMC population.

From an ecological point of view, the early race is an ‘explosive bearer’ and reaches significant levels only in years of the high population [2]; an increase in its population leads to negative impacts, i.e. high energy expenditure on anadromy and elevated mortality in the 0+ age class. Its life niche is determined by the phenomena of a higher half-saturation constant (Fig. 5, a) and lower fishing mortality as compared to the later race.

The positive contribution of the early race should be attributed to only a significant increase in the spawning ground areas, which provides additional population stability when environmental conditions change [1].

7. References
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