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by A.K. Koz'min

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Systematically, Siberian whitefish are a subspecies of Coregonus lavaretus, which have an extensive habitat. Already A.N.Svetovidov in 1934, noting the systematic heterogeneity of the western Arctic whitefishes, suggested that each large water body generates its own peculiar forms [19]. N.A. Ostroumov [13], on the basis of a biometric analysis, growth rate and ecological characteristics, identified the whitefish from the Pechora river as an independent systematic unit of the "natio" order.

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The whitefish in the Pechora river basin are distributed everywhere. L.N. Solovkina [20] and E.S. Kuchina [8] believe that such large tributaries of the Pechora as the Usa and Kos'yu generate local whitefish populations which do not differ morphologically from those of the Pechora.

* Numbers in the right-hand margin indicate the page numbers of the original (Tr.).

However, these investigators, in their analyses of whitefish from the Usa and Pechora, confined themselves to comparing indexes, without calculating the standard deviations, and hence they were in no position to make reliable pronouncements regarding the morphological identity or distinction of the whitefishes from various ecological areas. The purpose of our study is to investigate the morphological distinctions of whitefishes from various areas of the Pechora basin--from Korovin Bay, Lake Golodnaya Guba, from the Pechora itself and from the Sula river, a left tributary of the lower Pechora (see fig. next page).

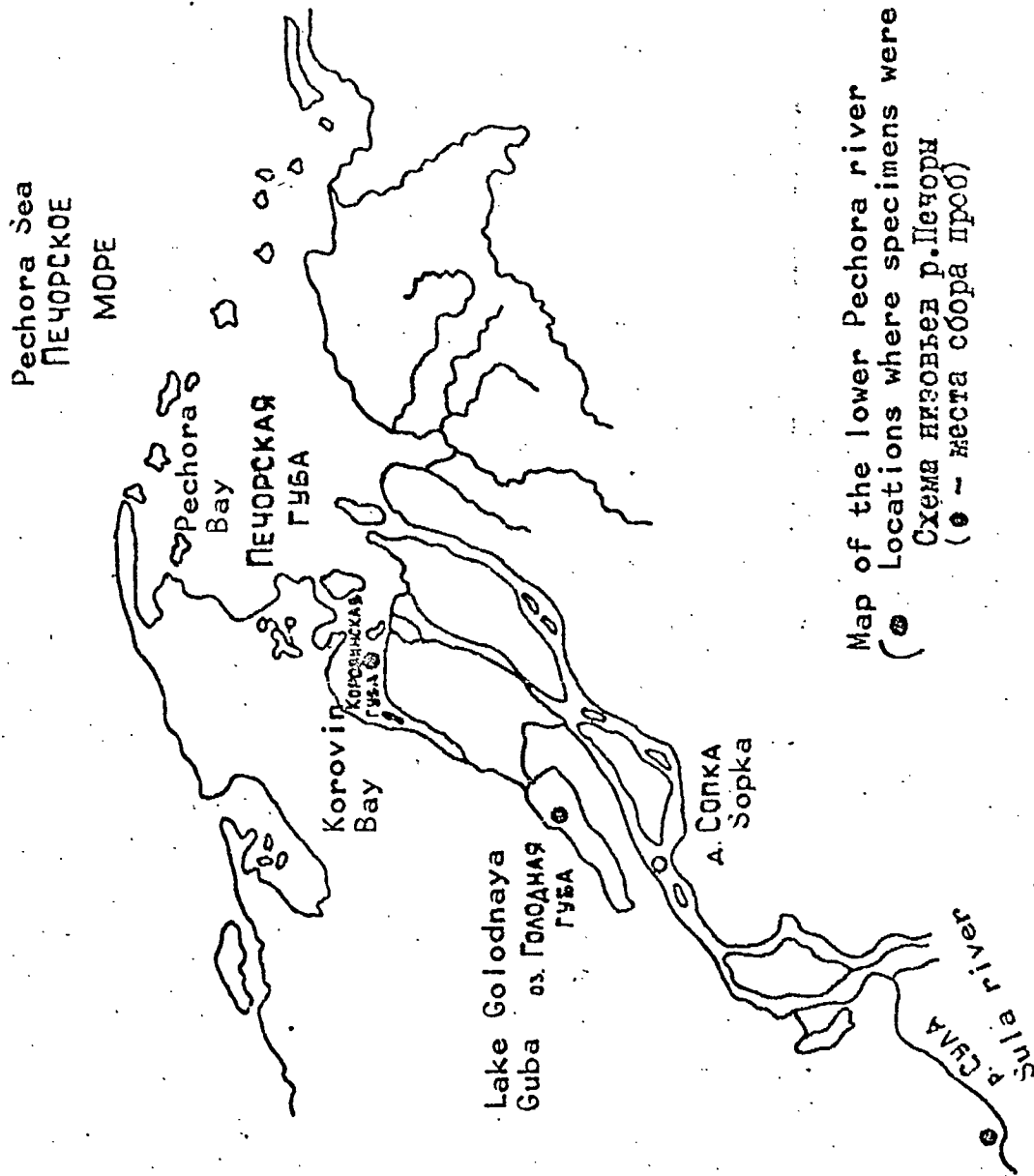
The morphological measurements were based on the scheme suggested by I.F. Pravdin [15] for measuring salmon. We measured 250 specimens of whitefish. The resulting data were grouped and processed biometrically.

We calculated the arithmetic mean M and its error m , the average standard deviation σ and the coefficient of variation. On comparing these indexes of the two intervals or groups that interested us we calculated the reliability coefficient td for a given difference. The conjunction of the various indexes was determined with the help of the coefficient of variation cV . The degree of reliability of the difference between the two arithmetic means was judged on the basis of the size of the reliability coefficient td .

The confidence coefficient was assumed to be equal to 95%. When the confidence coefficient was less than 95%, the difference was considered unimportant and the index did not change, that is to say, the "null hypothesis" was not refuted.

Specific morphological description

The length of the lower jaw, as in all forms of this species, is usually somewhat shorter than the shortest height of the body. The back,



Map of the lower Pechora river
 (Locations where specimens were selected)
 Схема низовьев р. Печора
 (● - места сбора проб)

from the back of the head to the dorsal fin, is arched or humped. The width of the snout always exceeds its height. The lateral line is $76 \frac{9-11}{8-10}$ 98, D III-IV 9-13; A III-IV 11-14. The color of the whitefish varies from silvery-white to dark-gray. The usual length of a commercial whitefish is 32--38 cm, more frequently 34--35 cm. The average weight is 550--700 g, sometimes 1.5--2 kg. Occasionally one also meets larger specimens. For example, in Nov. 1969, at the Zakhrebetnoe section of Korovin Bay a whitefish was caught which had a length of 66 cm and weighed 5 kg.

When analyzing the morphological characteristics of intraspecific categories of whitefish, one should take into account individual variability with regard to age and sex so that the effect of these distinctions may be excluded from the morphological distinctions of the forms in question. This requirement [2, 3] is far from being fully observed even at present, even though many years have passed since it was first suggested.

Specimens of various linear dimensions, and caught in different seasons, were subjected to such morphological analysis. Before investigating the morphological characteristics of the intraspecific categories of whitefishes from different areas, the sex, age, seasonal and ecological variability of a given subspecies should be examined.

Sexual variability. Most of the attributes indicate no marked distinctions between male and female whitefish. Nevertheless, some distinctions do exist [7, 11--13].

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Since the specimens for the morphometric analysis were taken during different seasons of 1970, it became possible to determine sexual dimorphism with regard to seasonal variability. In order to reduce the

undetermined factors to a minimum, we selected 15 specimens of males and of females with identical linear dimensions separately from the February and from the October catches. In February the fish were caught in the feeding areas, and their sex products at that period were in the II--III stage of maturity. In October the fish were caught in the spawning areas (Sula river), at which time their gonads were in the prespawning state (Table 1).

Table 1 Таблица 1
Морфологические признаки сига-пыжьяна в различные периоды жизненного цикла (в % к длине тела)

Признаки Characteristics		feeding population / spawning population			
		Нагульное стадо		Нерестовое стадо	
		t	P	t	P
a	Длина тела (по Смитту)	+0,14	0,10	-0,9	0,100
b	Вес рыбы, г	-0,14	0,10	-2,0	0,050
c	Высота тела (наибольшая)	-1,00	0,10	-6,3	0,001
d	Расстояние				
	d1 антевентральное	-0,20	0,10	-3,7	0,001
	d2 антеанальное	-0,20	0,10	-2,3	0,050
e	Длина				
	P	+1,40	0,10	+2,7	0,050
	v	-0,40	0,10	+2,0	0,050
f	Заглазничный отдел головы	+1,60	0,10	-2,2	0,010
g	Расстояние P-v	-2,30	0,01	-4,3	0,001
h	Длина				
	h1 нижней челюсти	+2,80	0,01	+0,2	0,100
	h2 хвостового стебля	+3,16	0,01	+0,4	0,100

Table 1. Morphological characteristics of whitefish at various periods of their life cycle (percentages relative to body length).

a- body length (according to Schmidt; b- weight of the fish (g); c- body height (maximal); d- distance/ d1-pre-ventral; d2- pre-anal; e- length; f-postorbital part of the head; g-distance P--v; h- length/ h1-lower jaw; h2- caudal peduncle.

A comparison of the males and females from the feeding population revealed reliable distinctions ($t > 3$) with respect to only one characteristic--the length of the caudal peduncle, which turned out to be larger in the males than in the females.

Sexual dimorphism, based on several characteristics, is most distinct in the spawning period. Due to the intensive development of the sex products, there is a considerable increase in body height in females in the prespawning period, which entails several other deviations, particularly an increase in the depth of the head at the occiput. Reliable distinctions are revealed in the size of the pre-anal distance. There is also some distinction between males and females with regard to the length of the pectoral and pelvic fins (see Table 1).

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During the prespawning period male and female whitefishes also acquire breeding colors--pearl-like nodules on the scales along the entire body of the fish, but the epithelial nodules on the postorbital part of the head and on the gill covers are more vivid in males.

A comparison of the morphological characters of whitefishes from the spawning and feeding populations reveals that many distinctions are temporary in nature. Table 1 shows that the most permanent distinctions between males and females, regardless of the phenological conditions, are to be found in the pectoventral distance ["distance from pectoral to pelvic fins" Ricker].

Females were a little heavier than males even though their linear dimensions were identical. These distinctions are most clearly marked in the spawning period. This was already noted by N.A. Svetovidov [19] during his studies of the whitefish of the Kara Sea.

Since the distinctions between the males and females of the Pechora whitefish are most vivid in the spawning period, that is to say, in the fall, and find only insignificant expression during other periods, we can use these data without reference to the sex of the fish.

Age variability. In studying fish populations with these morphological methods it is important that their age variability be clearly identified, so as not to detract from the actual status of the forms under comparison [21].

Some investigators study age variability relative to body length, others relative to age. K.A. Savaitova [18] has suggested that changes in the ratios of individual parts of the body be studied not relative to the dimensions or age of the fish but to stages of development, each of which is characterized by specific relationships between the organism and its environment.

A.S. Novikov [11] is trying to identify the stages of development of the whitefish by analogy with the Kolyma whitefish. Analyzing the variability of the morphological characters throughout the entire life of the whitefish, Novikov identified four stages. Similar stages can apparently be identified in the life of the Pechora whitefish as well, but owing to the present lack of data on the ecology of the semidiadromous whitefish it is difficult to comment on its developmental stages. /123

In comparing the fish populations in question, we are primarily interested in the degree of character variability. To determine the nature of age variability, morphological measurements were made of specimens of various age groups. We established a series of lengths with an interval of 5 cm and selected 5--7 specimens from each size group. The average deviation was established according to N.A. Plokhinsky's

formula $\left[\sqrt{\frac{\sum D^2}{n-1}} / 14 \right]$. Data on the age variability of the whitefish from the lower Pechora are presented in Table 2.

Table 2 shows that the length of the head and the diameter of the eye correlate negatively with body length, that is to say, these indexes decline relative to the growth of the fish. The regression coefficient R, computed for the purpose of comparing the variability of the length of the head of the whitefish relative to its body length, indicated that a 5 cm increase in the length of the fish was paralleled by an average decline of the length of the head of 0.6 cm and by a corresponding 0.04 cm decline of the diameter of the eye.

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The length of the base of the anal fin ($r = +0.63$; $r = +0.76$) and the lowest height of the body correlate positively with body length. There is less correlation between the maximal height of the anal fin ($r = +0.25$) and maximal body height ($r = +0.25$) with body length.

Thus the whitefish has characters whose numerical value increases uniformly with age (the length of the base of the anal fin, maximal height of body, maximal height of anal fin and minimal height of body, in percentages relative to length of lower jaw), and also characters whose numerical value uniformly declines with age (length of head and diameter of eye).

Ecological variability. Continually interacting with an environment that is specific for each body of water and possessing considerable phenotypic flexibility, the whitefish in large rivers can generate forms that are diadromous, lacustrine and fluvio-lacustrine [17].

A certain portion of the Pechora whitefishes feed in lakes. They develop a natural system of adaptations according to phenotypes. The

Table 2 Таблица 2
Характер изменения морфологических признаков
 сига-пыжьяна в связи с его ростом (в % к длине
 тела)

	Признаки Characters	t					Г	R	
		15-20	15-25	15-30	15-35	15-40			15-45
a	Длина головы	-0,1	+1,5	+1,8	+5,8	+3,1	+6,2	-0,7	0,60
b	Диаметр глаза	+1,5	+4,1	+5,3	+8,1	-3,6	+9,2	-0,24	0,04
c	Длина основания А	-1,5	-2,4	-3,8	-2,0	-3,1	-4,5	+0,63	0,08
d	Наибольшая высота А	-1,4	-	-4,7	-5,1	-3,4	-3,8	+0,25	0,10
e	Высота тела								
e1	наибольшая	-3,7	-4,7	-3,8	-6,0	-3,0	-8,7	+0,11	0,25
e2	наименьшая ^{x/}	+3,5	+2,0	-2,3	-3,1	+0,3	-2,5	+0,76	0,90

^{x/} в % к длине нижней челюсти.

Table 2. Variability of morphological characters in whitefish in relation to growth (percentages relative to body length).

a- length of head; b- diameter of eye; c- length of the base A; d- maximal height of A; e- height of body/ e1-maximal; e2- minimal; x/--percentage relative to length of lower jaw.

height of the body increases; the length of the head and the pre-ventral distance correlate negatively with body height. The specimens inhabiting rivers usually have a streamlined body and a shortened caudal peduncle [10].

The length of the head in Pechora whitefish varies considerably. After taking the extreme values from an experimental distribution of points (the specimens selected were of identical linear dimensions) we found the average value for the meristic and morphological characters of 15 long- and 15 short-headed specimens which differed from the rest (Table 3).

Under conditions obtaining in the Pechora river, the longheaded whitefish apparently inhabit the rivers and the shortheads are found in the lakes.

Once the sexual, age, seasonal and ecological variabilities of the meristic and morphological characters of the lower Pechora whitefishes are established, a comparison can be made of the specimens from the various sections of the basin (see map, p.3). Morphological data on whitefish from different areas of the lower Pechora are shown in Table 4.

As was already noted, the whitefish spawn in the Sula river. /128
Our selections in this river were made during the spawning period. The morphological measurements in the three other sections were made during the winter, when the sex products were in their II and III stages of maturity. To eliminate the effect of seasonal variabilities on the actual morphological status of the different ecological forms, we shall consider the whitefish from the spawning and feeding populations separately. In comparing the whitefishes from Korovin Bay and from the Pechora delta, we obtained reliable distinctions ($t > 3$) only with regard to the length of the middle part of the head. A comparison of the whitefishes from Lake Golodnaya Guba--a typical lake-type body of water - with those from other reservoirs indicated that in this area the whitefish in their external form resemble the lake forms, that is to say, they have a long caudal peduncle, a relatively high body and, as a rule, a short lower jaw.

The most significant distinctions are found between the whitefishes from the Pechora and those from the Sula rivers. Excluding the seasonal

Table 3 Таблица 3

Морфологическая дифференциация длинно- и короткоголовых печорских сигов

Примечание Characters	short-headed Короткоголовые (n = 15)				long-headed Длинноголовые (n = 15)			
	M ± m	σ	CV	lim.	M ± m	σ	CV	lim.
a Длина (по Смитту), см	34,2				35,0			
b Вес рыбы, г	510				546			
c Число el чешуй в боковой линии	83,70±1,48	3,9	4,7	78-88	85,40±2,54	6,7	7,9	78-98
c2 тычинок на первом жаберной дугке	21,30±0,49	1,3	6,1	19-24	23,00±0,53	1,4	6,1	21-24
d Длина d1 рыла	4,60±0,11	0,28	6,1	4,1-4,9	5,00±0,084	0,23	4,5	4,6-5,3
d2 средней части голо- вы	12,9±0,30	0,80	6,2	11,7-14,3	14,26±0,16	0,43	3,0	13,7-14,9
d3 головы	17,4±0,29	0,78	4,5	16,6-17,9	18,80±0,20	0,53	2,8	17,7-20,0
d4 нижней челюсти	5,65±0,10	0,26	4,6	5,1-5,9	7,07±0,09	0,25	3,5	6,8-7,3
e Расстояние e1 антевентральное	45,30±0,36	0,95	2,0	43,3-46,1	47,57±0,40	1,05	2,2	46-48,5
e2 антеанальное	70,40±0,25	0,67	0,9	66,0-72,0	72,40±0,70	1,86	2,6	70,5-75,0
f Глазничный отдел головы	53,47±0,68	1,80	3,4	51,5-56,0	51,50±0,57	1,50	2,9	48,5-53,60
g Ширина лба	31,74±0,60	1,60	5,0	29,4-41,4	30,30±0,41	1,10	3,6	23,0-32,1
h Длина нижней челюсти	32,40±1,04	2,70	8,3	26,5-34,5	37,00±0,57	1,50	4,0	35,2-39,0
z Высота де в % к длине нижней челюсти	28,40±4,30	11,35	9,0	116,0-150,0	104,00±2,38	5,80	5,5	96,0-113,0

Table 3. Morphological differentiation of short- and long-headed Pechora whitefish.

a- length in cm, according to Schmidt; b-weight of fish (g); c-number/ cl-of scales along the lateral line; c2-rakers on the first gill arch; d-length/d1-of snout; d2-of the middle part of head; d3-of head; d4-of lower jaw; e-distance/el- pre-ventral; e2-pre-anal; f-postorbital distance; g-width of forehead; h-length of lower jaw; i-minimum body height in % relative to length of lower jaw.

МЕРИСТИЧЕСКИЕ И ПЛАСТИЧЕСКИЕ ПРИЗНАКИ СИГА-ПЛЯМНА ИЗ РАЗНЫХ УЧАСТКОВ НИЖНЕГО ТЕЧЕНИЯ ПЕЧОРЫ

Признаки characters	1		2		3		4		5						
	М ± m	CV	М ± m	CV	М ± m	CV	М ± m	CV	М ± m	CV					
а Длина тела (по смуту), см	35,80±0,334	9,2	35,49±0,445	8,2	33,79±0,202	2,2	37,60±0,505	6,9	50,6±0,652	3,5	2,7	3,2	7,0		
б Число															
б1 Чесуи по боковой линии	86,65±0,395	4,5	86,53±0,350	2,3	86,80±1,300	5,4	87,73±0,650	3,9	0,1	0,1	0,1	0,2	1,4	1,6	0,6
б2 Забарных тычинок	23,12±0,149	6,4	23,05±0,249	7,1	23,72±0,333	5,1	22,49±0,021	4,0	0,2	1,6	1,5	4,2	2,2	3,0	
в % к длине тела															
с Длина рыла	4,82±0,030	6,2	5,07±0,124	1,5	4,79±0,066	5,0	5,26±0,048	4,7	1,4	1,5	2,0	7,4	0,4	6,7	
д Диаметр глаза	3,74±0,027	7,2	3,70±0,102	1,7	3,66±0,064	6,3	3,70±0,050	7,0	0,4	1,2	0,3	0,6	-	0,5	
е Задглоточный отдел головы	9,39±0,039	4,1	9,60±0,042	3,5	9,52±0,078	3,0	9,61±0,054	3,0	3,7	1,5	0,9	3,3	0,1	1,1	
ф Длина															
ф1 Средняя часть головы	13,47±0,049	3,6	13,31±0,091	4,5	13,21±0,158	4,3	13,85±0,077	2,9	1,6	1,6	0,5	4,2	4,6	3,8	
ф2 Головы	18,03±0,060	3,3	18,11±0,107	3,8	18,04±0,169	3,4	18,35±0,091	2,7	0,7	0,1	0,4	2,8	1,6	1,6	
г Высота головы у затылка	13,68±0,072	5,2	14,07±0,090	4,2	13,59±0,153	4,0	14,52±0,108	3,7	0,8	0,5	2,5	6,5	3,2	5,1	
г1 Ширина лба	5,52±0,074	13	5,63±0,050	5,9	5,54±0,063	4,1	5,57±0,046	4,3	1,4	0,2	1,3	1,0	1,0	0,4	
г2 Длина															
и1 Верхнечелюстной кости	4,57±0,031	6,8	4,49±0,134	19	4,50±0,033	2,7	4,71±0,042	4,7	0,6	1,6	0,1	2,8	1,6	4,2	
и2 Нижней челюсти	6,46±0,098	15	6,34±0,118	12	6,19±0,089	5,2	6,40±0,060	4,8	0,8	2,1	1,1	0,5	0,4	2,0	
ж Высота тела															
ж1 Наибольшая	24,02±0,176	7,3	23,86±0,194	5,3	24,46±0,252	3,8	25,14±0,400	8,1	0,8	1,5	2,0	2,4	3,0	1,5	
ж2 Меньшая	7,43±0,034	4,6	7,29±0,057	5,2	7,42±0,081	4,0	7,39±0,067	4,7	2,3	0,1	1,3	0,6	0,3	0,3	

Table 4. Meristic and morphological characters of whitefish from different sections of the lower Pechora river.

1-Pechora; 2-Korovin Bay; 3-Lake Golodnaya Guba; 4-Sula river; 5-differentiation of the series of whitefish from different sections;
 a-body length (cm), according to Schmidt; b-number/bl-of scales along the lateral line;
 b2-of gill rakers; c-length of snout; d-eye diameter; e-postorbital distance; f-length/fl-of middle part of head; f2-of head; g-depth of the head at the occiput; h-width of forehead;
 i-length/il-of maxillary bone; i2-of lower jaw; j-body depth/j1-greatest; j2-smallest.

Table 4 (cont'd)

k	Расстояние	42, 31±0, 115 2,7 42, 51±0, 222 3,4 42, 59±0, 272 2,3 42, 21±0, 169 2,0 0,8 1,0 0,2 0,6 1,1 1,2
k1	антедорсальное	43, 52±0, 154 3,5 43, 28±0, 130 2,7 43, 59±0, 245 2,4 42, 83±0, 203 2,5 1,0 0,3 1,0 2,9 1,7 2,4
k2	постдорсальное	46, 65±0, 049 1,1 46, 56±0, 195 2,7 45, 57±0, 427 3,4 47, 26±0, 267 2,9 0,5 2,5 2,1 2,3 7,0 3,4
k3	антевентральное	71, 92±0, 127 1,8 71, 99±0, 230 2,1 70, 70±0, 341 1,7 71, 53±0, 286 2,0 0,3 3,4 3,0 1,3 1,2 1,9
k4	антеанальное	
L	длина	
L1	хвостового стебля	13, 30±0, 098 7,3 12, 98±0, 114 5,8 13, 09±0, 264 7,3 11, 99±0, 135 5,7 2,7 0,7 0,4 8,1 5,7 3,8
L2	основания D	11, 91±0, 076 6,4 11, 88±0, 104 5,7 11, 73±0, 202 6,2 11, 74±0, 124 5,3 0,3 0,8 0,7 1,2 0,9 0,5
m	наибольшая высота D	16, 53±0, 138 7,8 16, 21±0, 134 6,8 14, 60±0, 390 7,0 15, 63±0, 191 6,2 1,6 4,6 3,8 3,8 2,2 2,5
n	длина основания A	11, 71±0, 087 7,4 11, 46±0, 100 5,7 12, 40±0, 095 2,7 11, 79±0, 134 5,7 1,9 5,6 8,0 7,2 0,3 3,8
o	наибольшая высота A	12, 36±0, 123 10 12, 16±0, 208 7,7 11, 55±0, 131 4,1 10, 97±0, 124 5,7 0,9 4,5 2,5 8,2 4,9 8,4
p	длина	
p	P	15, 08±0, 084 5,5 15, 01±0, 194 7,2 14, 60±0, 325 6,2 15, 18±0, 104 3,4 0,3 1,4 1,1 0,8 0,8 1,7
p	V	16, 06±0, 122 8,1 14, 96±0, 184 7,2 13, 99±0, 364 7,3 13, 74±0, 112 4,1 0,4 2,9 2,5 8,2 5,9 0,7
r	Расстояние	
r	P M V	29, 44±0, 122 8,1 29, 19±0, 184 4,2 28, 56±0, 352 4,4 29, 70±0, 316 5,3 1,1 2,4 1,6 0,8 1,4 2,4
r	and	27, 24±0, 125 4,6 26, 96±0, 194 4,8 26, 02±0, 188 2,6 26, 12±0, 242 4,7 1,2 2,8 1,3 4,4 2,7 0,3
r	V M P	27, 04±0, 152 5,8 27, 84±0, 212 5,0 25, 93±0, 372 5,2 28, 10±0, 230 4,1 3,0 2,8 4,5 3,6 0,8 2,4
s	длина рыла	30, 61±0, 154 5,0 39, 65±0, 206 4,3 30, 57±0, 211 2,8 30, 76±0, 288 4,8 0,2 0,1 0,3 0,1 0,3 0,5
t	длина носа	
u	длина	
u1	верхнечелюстная кость	25, 31±0, 140 5,5 24, 75±0, 233 6,1 24, 97±0, 187 2,5 24, 84±0, 185 3,8 2,1 1,5 1,1 2,1 0,5 0,5
u2	нижней челюсти	35, 54±0, 171 4,8 34, 86±0, 210 4,0 33, 86±0, 475 4,8 34, 45±0, 338 5,0 2,5 3,3 2,0 3,0 1,0 1,0
v	наименьшая высота тела X/	113, 11±0, 765 6,7 116, 96±1, 24 7,0 123, 90±2, 36 6,6 132, 20±0, 63 2,4 2,6 7,3 2,6 3,2 8,0 3,4

X/ в % к длине нижней челюсти. x/ --percentage relative to length of lower jaw.

k-distance/ k1-predorsal; k2-post-dorsal; k3-pre-ventral; k4-pre-anal; L-length/L1- of caudal peduncle; L2- of base D; m-greatest depth of D; n-length of base A; o-greatest depth of A; p-length (P, V); r-distance; s-length of snout; t-width of forehead; u-length/ u1-of maxillary bone; u2-of lower jaw; v-smallest body depth

variability of certain characters of the two ecological forms, reliable distinctions between these forms were revealed with regard to the length of the caudal peduncle, the ventral distance and the greatest depth of the dorsal and anal fins. It should also be noted that the whitefish from the Sula river have the least number of gill rakers and a somewhat greater number of scales along the lateral line.

Long-headed specimens predominated in the spawning beds in the headwaters of the Sula river (see Table 4). Hence one can assume that the fish spawning in the Sula river, where they have to overcome fast currents, especially in the shallows, are morphologically adapted to river-type biotopes.

Thus the morphological characters of the Pechora whitefish vary with regard to season, sex, age and ecology. Moreover, the morphological characters of the various ecological groups of Pechora whitefishes reveal clear traces of a parallel variability, that is to say, there exist among them more or less individuated lake (high bodies) and river (stream-lined) forms. The establishment of the degree of individuation of these forms has important practical significance with regard to forecasting commercial catches.

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On the phenotypic variability in whitefish from
the Pechora River

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S u m m a r y

The morphometric measurements of whitefish taken from various localities in the downstream area of the Pechora River have revealed that the plastic features of the species vary with seasons, sexes, ages and ecology. Besides, there are more or less isolated lake (high body) and river (streamlined body) forms in the species.