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PECULIARITIES OF POPULATION STRUCTURE AND HYBRIDIZATION OF THE GENUS *CARASSIUS* (CYPRINIFORMES, CYPRINIDAE) IN POLYSSIA (NORTHERN UKRAINE)

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Peculiarities of Population Structure and Hybridization of the Genus *Carassius* (Cypriniformes, Cyprinidae) in Polyssia (Northern Ukraine). Mezhzherin, S. V., Kokodiy, S. V., Pukhtaevitch, P. P., Kulish, A. V. — Study of population structure of crucian carps in the mixed forests zone of Northern Ukraine (characterized by ample diversity of unregulated aquatic systems) showed the presence of diploid *C. carassius* and *C. auratus*, triploid *C. gibelio* (represented by a series of clones), *C. auratus* × *C. carassius* diploid hybrids, and tetraploid hybrids between *C. carassius* and *C. gibelio*. The crucian carps of the region compared with those of more southern zones of Ukraine are characterized by numerical prevalence of unisexual form of *C. gibelio*, and relatively restricted hybridization of *C. carassius* and *C. auratus*.

Key words: *Carassius*, hybridization, populations, cloning.

Introduction

Studies of population structure of the representatives of the genus *Carassius* Jarocki, 1822 in the European region have shown that it does not reflect the traditional views on population structures of amphimictic organisms. The populations can contain one or more clone forms of the triploid species *C. gibelio* (Bloch, 1782) which reproduces by gynogenesis and is actually a hybrid of *C. auratus* Linnaeus, 1758 with cogeners from the Far East (Shimuzu et al., 1993; Mezhzherin, Kokodiy, 2006, 2008). There can also be hybrids of *C. auratus* × *C. carassius* with unclear mechanisms of gametogenesis; diploid specimens of *C. auratus* (Linnaeus, 1758) which are unusually abundant in Ukrainian water bodies; and an aboriginal *C. carassius* (Linnaeus, 1758) which is declining in Europe (Mezhzherin, Lisetsky, 2004 a; Kokodiy, 2010, Kulish, 2013). At the same time, the numbers of *C. auratus* × *C. carassius* hybrids in several reservoirs was higher than that of *C. carassius*, and in general in many regions of Ukraine it was no less than the latter (Mezhzherin, Kokodiy, 2010). This supports the hypothesis that hybridization with *C. auratus* is one of the factors of elimination of *C. carassius* (Mezhzherin, Lisetsky, 2004 b). The relationship of *C. auratus* with *C. gibelio* is also of interest. It is known (Mezhzherin et al., 2015) that the diploid species supersedes the triploid one, and populations of the latter persist only in isolated water bodies.

Previously the studies of crucian carp were conducted on populations from river basins with advanced hydraulic development (Mezhzherin, Lisetsky, 2004 a; Kokodiy, 2010, Mezhzherin, Kokodiy, 2009; Kulish, 2013) and thus in severely affected ecosystems (Middle and Lower Dnipro River, and Siverskyi Donets River). It is known (Simberloff, 1996; Riley et al., 2003; Metcal et al., 2008; Sean et al., 2012; Muhlfeld et al., 2014) that hybridization events are happening most actively in the cases of species invasion, climate change, and deformation of natural landscapes. Hence it is interesting to study population in the regions with less affected aquatic systems. In Ukraine this would be Polyssia. Here, according to the official classification of water quality (Yatsyk, 2007), the chemical pollution of surface waters is sometimes less than significant, even reaching the level of “satisfactorily clean”. In contrast, the waters of other Ukrainian regions are at best “dirty” and usually “very dirty”. It can be assumed, that in Polyssia the hybridization processes between diploid crucian carps would be less intense, and the numbers of *C. carassius* would be substantially higher. There are also grounds to assume that in Polyssia the unisexual populations of *C. gibelio* would be much more common, since the ratio of its specimens in crucian carp populations increases to the North (Kulish, 2013). In order to test these assumptions, the genetic study of population structure of crucian carps of Polyssia was conducted.

Material and methods

Altogether 45 samples of carp from Sumy, Chernigov, Zhytomyr, Rivne and Volyn regions were studied (fig. 1). In total, 81 specimens were analyzed. Emphasize in material collection was put on small water bodies (forest lakes, peat bogs, ponds).

Electrophoretic analysis of allozymes was performed according to previously published methods (Mezhzherin, Lisetsky, 2004 a). The species and biotypes of crucian carps were determined using the following genetic markers: *Aat-1*, *Aat-2*, *Ldh-B*,

Pt-1B, *Pt-2*, *Es-3*, *Tf*, which are diagnostic for this species group (Mezhzherin, Kokodiy, 2008, 2010; Mezhzherin et al., 2012).

Cytometric analysis was additionally used to separate various clones of *C. gibelio*, and specimens of *C. auratus*. This method has been described in detail previously (Mezhzherin, Lisetsky, 2004 a; Mezhzherin, Kokodiy, 2009).

Results

Just as it was supposed, the structure of the crucian carp populations in the water bodies of Polissya was mosaic and highly diverse. The crucian carps diversity included two diploid species (*C. auratus* and *C. carassius*), two types of hybrids of *C. carassius*, and specimens of *C. gibelio* of various biotypes (table 1).

C. auratus. 281 specimens of the species were identified, comprising 32 % of all studied crucian carps. It was recorded in 20 water bodies, and in three cases (in Zhytomyr Region) the samples contained only this species (table 1).

C. carassius. The presence of this species in the region was insignificant (table 1). 71 individuals (8 % of all) were found. In nine cases, *C. carassius* was sampled together with other species, and only twice it was the only sampled species. It was mostly found in Zhytomyr Region, though there were some findings in Sumy Region.

C. gibelio. This species prevailed in water bodies of the studied area. Its triploidy was confirmed by cytometry. Altogether 515 specimens (58.5 % of all) were found (table 1). The species was represented by two basic biotypes. The *C. gibelio*-1 specimens can be classed as clone and the most common genetic form in the region, it accounted for about

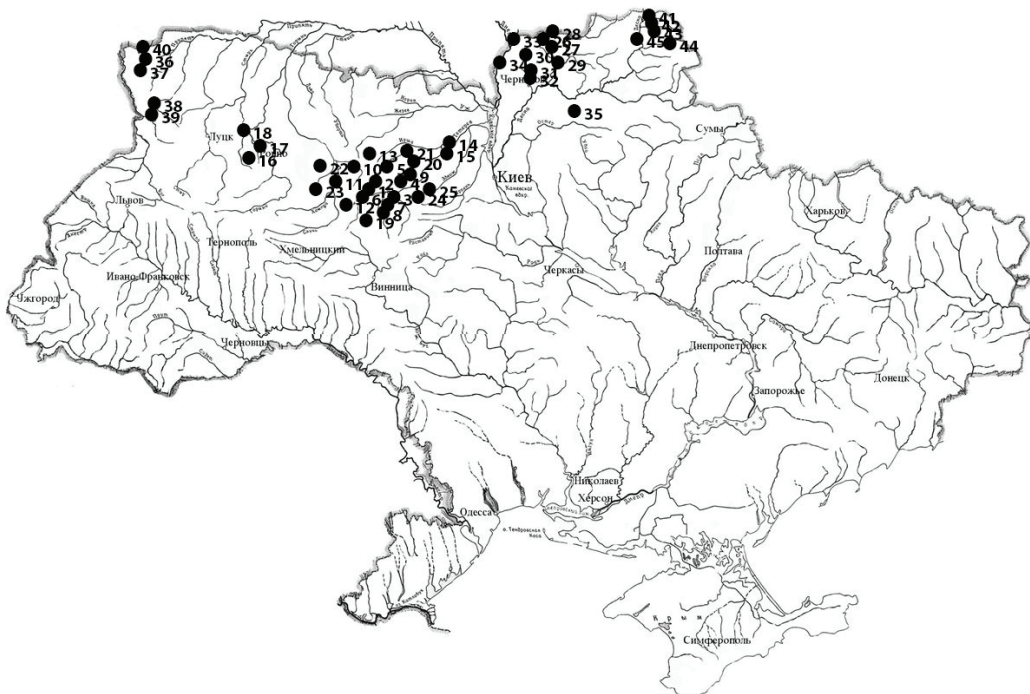


Fig. 1. Localities of crucian carp collection. The legend is given in table 1.

Table 1. Crucians carps populatons structure of Polyssia region (Northern Ukraine) by species and biotypes

N	Locality	Coordinates	<i>C. auratus</i>	<i>C. gibelio-1</i>	<i>C. gibelio-2</i>	<i>C. auratus</i> × <i>C. carassius</i>	<i>C. carassius</i> × <i>C. gibelio</i>	<i>C. carassius</i>
1	Pokostivka	50° 15 ' 24.9" N 28 ° 13 ' 34.4" E	7	1	2			
2	Staroshiyka	50° 12 ' 37.1" N 28° 16 ' 29.5" E	8		3			
3	Vysoka Pitch	50° 11 ' 59.9" N 28° 17 ' 15.8" E	5		7	1		2
4	Vysoka Pitch	50° 11 ' 58.8" N 28° 14 ' 45.1" E	10					5
5	Zamozhne	50° 14 ' 21.5" N 28° 17 ' 26.4" E		6	20			2
6	Krasnogirka	50° 00 ' 28.2" N 27° 59 ' 53.8" E	11					
7	Yasnogirka	49° 57 ' 45.5" N 27° 59 ' 24.4" E	9	2	1			
8	Gremyache	50° 09 ' 08.3" N 28° 14 ' 36.4" E	2		11			
9	Buky	50° 12 ' 08.0" N 28° 20 ' 11.8" E	7			1		9
10	Vila	50° 14 ' 41.7" N 28° 10 ' 35.9" E						19
11	Sobolivka	50° 15 ' 38.3" N 28° 04 ' 02.7" E	5			1		16
12	Godyha	50° 12 ' 09.6" N 28° 13 ' 34.9" E	6			2		5
13	Trudove	50° 16 ' 24.0" N 28° 13 ' 08.0" E	27					
14	Vepryn	50° 39 ' 00.4" N 29° 27 ' 31.1" E	13	3				1
15	Mygalki	50° 41 ' 01.1" N 29° 32 ' 27.0" E	16	5				
16	Kolodenka	50° 34 ' 47.0" N 26° 25 ' 45.6" E	4	6				
17	Hotyn	50° 42 ' 54.0" N 26° 14 ' 39.4" E		24				
18	Rubche	50° 44 ' 16.8" N 26° 09 ' 47.2" E	18					
19	Budychna	50° 04 ' 01.4" N 28° 01 ' 36.8" E	14					
20	Strybezh	50° 22 ' 19.5" N 28° 07 ' 45.3" E	1	9				
21	Sheremetev	50° 21 ' 01.0" N 28° 03 ' 46.5" E		3	21			
22	Golubin	50° 13 ' 55.4" N 27° 55 ' 28.7" E		4	26			
23	Vil'ha	50° 12 ' 27.2" N 27 ° 43 ' 53.5" E		25				
24	Dubyshche	50° 05 ' 12.4" N 28° 10 ' 31.4" E	4	4	19			
25	с. Дрыглов	50° 07 ' 03.4" N 28° 12 ' 20.1" E		5	15			
26	Buhlivka	52° 01.492' N 31° 18.621' E	12		8			
27	Gusyatne	52° 00.360' N 31° 19.314' E	2		18			
28	Verbochky	52° 00.267' N 31° 20.073' E		14	6			
29	Chaykino	52° 02.013' N 31° 19.647' E		1	19			
30	Smalevo	52° 00.032' N 31° 18.047' E			20			
31	Vyntivka	51° 47 ' 18" N 30° 59.643' E	1	19				
32	Il'yichivka	51° 47.441" N 30° 59.543' E	9	10	11			
33	Olexadrivka lake	51° 47.456" N 30° 59.864' E	7		13			
34	Prud lake	51° 47 ' 29.004" N 30° 59 ' 26.016" E	34		2			
35	Cholmy	51° 22 ' 13.26" N 32° 12 ' 18.31" E	16		2	6		
36	Shatsk-1	51° 30 ' 13.4" N 23° 57 ' 03.1" E	5	15				
37	Shatsk-2	51° 29 ' 58.3" N 23° 57 ' 01.5" E		20				
38	Luboml_1	51° 13 ' 42.8" N 24° 02 ' 03.6" E	6		4			
39	Luboml_2	51° 13 ' 44.2" N 24° 02 ' 50.1" E	18		2			
40	Mel'niki	51° 32 ' 50.26" N 23° 56 ' 08.93" E	4		12			
41	Otchkino-1	52° 13 ' 13.40" N 33° 21 ' 57.56" E		38		1	1	
42	Otchkino-2	52° 13 ' 14.80" N 33° 21 ' 39.65" E				2	11	
43	Krendinovka	52° 14 ' 6" N 33° 27 ' 59.004" E		30				
44	Mefedivka-1	52° 15 ' 6.984" N 33° 30 ' 51.012" E		7	12			
45	Mefedivka-2	52° 15 ' 6.984" N 33° 30 ' 51.012" E		20				
Total			281	291	224	11	3	71

Таблица 2. Distribution of crucian carps population by communities types

Community type	Middle Dnipro		Severskiy Donetz		Polyssia	
	N ₁	N ₂	N ₁	N ₂	N ₁	N ₂
<i>C. auratus</i>	2		10	1	4	
<i>C. auratus</i> , <i>C. gibelio</i>	10	4	11	1	19	1
<i>C. auratus</i> , <i>C. carassius</i>	1	1			4	3
<i>C. auratus</i> , <i>C. carassius</i> , <i>C. gibelio</i>	1	1	4	3	2	1
<i>C. carassius</i>					2	1*
<i>C. carassius</i> , <i>C. gibelio</i>	3	3			2	1*
<i>C. gibelio</i>	4	1	1		13	1

Notes. N₁ — general samples number, N₂ — samples number, where *C. auratus* × *C. carassius* hybrids were found.

* Occurred *C. carassius* × *C. gibelio* hybrids.

33 % of all specimens. Genetically the biotype was distinguished by the fact that all individuals clearly belonged to one clone identifiable by several constant heterozygous allozyme spectra (Mezhzherin, Kokodiy, 2006, 2009). Particularly, these were *Aat-1*^{100-110/110}, *Aat-2*^{100/110}, *Gpi-1*^{90/100}, *Gpi-2*^{100/110}, *Pt-2*^{100/105}, *Tf*^{acc}, and *Es-1*^{abc}. The spectra *Aat-2* and *Gpi-1* also contained the products of *Aat-2*¹¹⁰ and *Gpi-1*⁹⁰ loci. These alleles are uncharacteristic of *C. auratus* and are hence introduced to the triploid genome by hybridization of *C. auratus* specimens with an unidentified representative of the genus. As for the second biotype, *C. gibelio-2*, for now it remains unclear whether this is a multitude of closely related clones or a single hypervariable biotype of clonal nature. The latter is supported by the large number of singular specimens with unique genotypic combinations. The spectra corresponding to constant heterozygotes in this case were found at the following loci: *Aat-1*^{100/110} (in several cases), *Pt-2*^{ab}, *Gpi-1*^{100/110}, *Gpi-2*^{100/110}, and also loci *Es-1* and *Tf*, which added the most to the observed genotypic variability within this biotype. Another genetic peculiarity of *C. gibelio-2* is that all alleles of aforementioned loci are characteristic to *C. auratus*. It is no coincidence that earlier researchers have pointed to the surprising genetic proximity of these triploid and diploid species (Mezhzherin, Lisetsky, 2004 c; Mezhzherin, Kokodiy, 2010). This may indicate either that the gynogenetic unisexual form of *C. gibelio* has originated from different forms of *C. auratus*, or that it is an

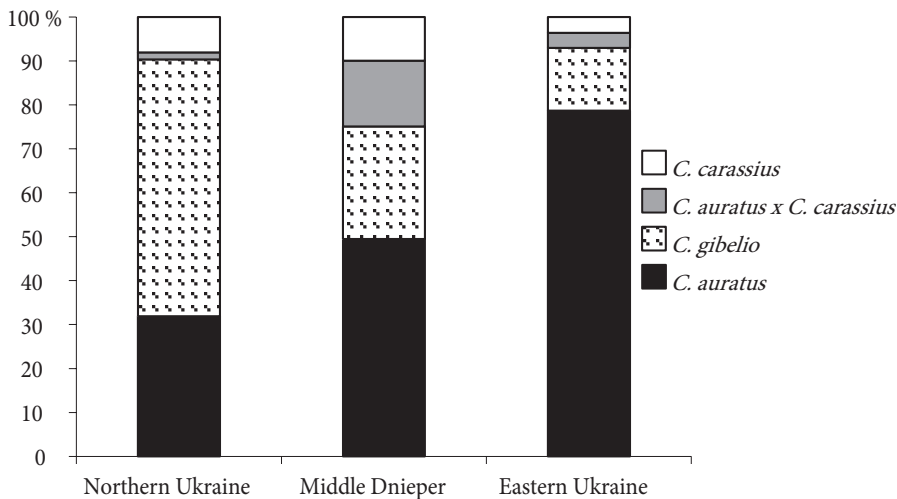


Fig. 2. The ratios of species and biotypes of crucian carps in water bodies of three areas of Ukraine.

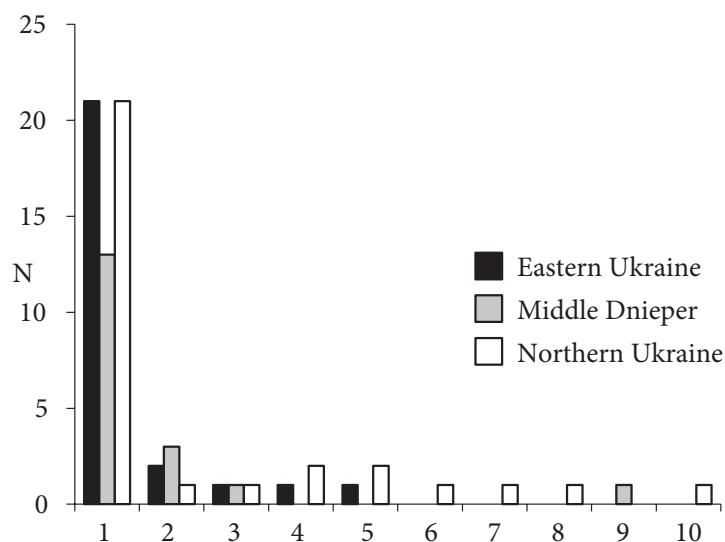


Fig. 3. The distribution of *C. gibelio-2* clones according to the number of specimens in water bodies of three areas of Ukraine.

autopolyploid, or there are genomic flows between the triploid and diploid forms. There are publications in favor of the first (Mezhzherin, Kokodiy, 2009), the second (Qin et al., 2016) and the third (Jakovlić, Gui, 2011) assumptions. Although in the case of polyclonal biotype *C. gibelio-2* the explanation may involve a poorly studied phenomenon of inheritance in triploid organisms combining cloning and Mendelian inheritance, as described in triploid amphibians (Stöck et al., 2012). The mechanism of the phenomenon is that individual loci, chromosomes or even whole oocyte genomes can be replaced in sperm-dependent parthenogenesis by genes, chromosomes or genomes of the spermatozoa. The offspring then will be peculiar hybrids that have a recombinant genotype. The quite possibly hybrid nature of singly sampled biotypes of *C. gibelio* has been considered previously (Mezhzherin, Kokodiy, 2010). *C. auratus* × *C. carassius* hybrids were found in five populations, but only in one case they were not single specimens (Kholmy, Chernihiv Region). There were 11 specimens altogether (table 1). The frequency of these hybrids in Polyssia was only 1.3 %, much lower than in other water basins of Ukraine (Kokodiy, 2010; Kulish, 2013) and six times lower than the abundance of *C. carassius* in the area. As for *C. carassius* × *C. gibelio* hybrids, there were single specimens and in one pond only (Ochkino, Sumy Region).

In the studied area, there were seven types of crucian carp communities (table 2). The most numerous communities were mixed populations of *C. auratus* and *C. gibelio*, with the latter being more abundant. Unisexual *C. gibelio* populations were almost as frequent, comprising one or several biotypes. *C. carassius* hybrids were found in all types of mixed crucian carp populations. This diversity of populations and the obvious prevalence of *C. gibelio* in them distinguishes the populations of Polyssia from those of Middle Dnipro (Kokodiy, 2010) and more so from those of Siverskyi Donets (Kulish, 2013). In the latter case the prevailing populations were those with either only *C. auratus* or mixed populations of *C. auratus* and *C. gibelio*, in which the latter was represented by single specimens.

Discussion of results

The peculiarities of crucian carp populations in Polyssia are made clear in comparative analysis with data from other earlier studied regions (Kokodiy, 2010; Kulish,

2013) (fig. 2). In Polyssia, *C. gibelio* is the most abundant form, it comprises more than half of all caught crucian carps (58.4 %), while at Middle Dnipro it comprises almost a quarter of all sampled congeners (25.6 %), and a seventh share (14.9 %) of all fish in the Siverskyi Donets River basin. The abundance of *C. auratus* which is an invasive species changes conversely. The frequency of sampling this species by the transect Polyssia → Middle Dnipro → South-East of Ukraine varies as follows: 32.4 → 49.5 → 82.1 %. The frequency of finding *C. carassius* in the samples in Polyssia (8.4 %) is similar to that in Middle Dnipro (10 %) and more than twice higher than in Siverskyi Donets (3.8 %). As for the hybrids, their frequency does not correspond to the occurrence of *C. carassius*. They are most frequently caught in Middle Dnipro (15 %), more so than specimens of *C. carassius*. In Eastern Ukraine the hybrids comprise 3.5 % of samples and are almost as frequent as *C. carassius*. In the water bodies of Polyssia the *C. carassius* hybrids are caught more rarely, their frequency (1.5 %) is four times less than that of *C. carassius* (table 1, fig. 2).

Thus, in many respects the described situation is expected. Ukrainian Polyssia with its natural aquatic landscape and quite a lot of shallow forest water bodies and peat bogs is mainly populated by *C. gibelio*, and the hybridization of *C. carassius* and *C. auratus* is nearly four times less frequent than in the Middle Dnipro and Eastern Ukraine. It is obvious that *C. auratus* has not yet permeated the Northern Ukraine. Here it mostly inhabits the large watercourses and large artificial reservoirs. Though there are single-species populations of *C. carassius* in the small forest water bodies and peat bogs of Polyssia, it would be wrong to assume that it is more numerous here than in the basin of the Middle Dnipro River. Still it occurs much more often in Polyssia than in the East of Ukraine.

It seems relevant to consider the factors which cause the prevalence of the triploid ginogenetic form in Polyssia. One of them could be the higher adaptability of this form to the conditions of small water bodies and peat bogs which are more suited for the dwelling and reproduction of *C. gibelio* than for *C. auratus*. But that's not entirely true since according to observations in other regions of Ukraine (Kulich, 2013) *C. auratus* easily populates water bodies of every type with stagnant fresh or brackish water. Thus the most probable reason of the prevalence of *C. gibelio* in Polyssia is its long-term history of dwelling and high abundance in the Northern Ukraine. There is every reason for this assumption since it is known that in the middle of the XXth century the ginogenetic triploid crucian carp has been distributed in European part of U.S.S.R. (Cherfas, 1966) while the diploid bisexual form (then imported from Amur river) has spread only in several fisheries of Belarus. Also possible is that triploid crucian carps have been imported to Ukraine together with the invasion of *C. auratus* which has happened in 1960s in Lower Dnipro (Demchenko, 1981). In the Amur River basin the triploids occur together with diploid crucian carps (Brykov et al., 2005). But then the question of numerical prevalence of *C. gibelio* in Polyssia remains unsolved. Another very interesting problem is the genetic structure of the *C. gibelio*-2 biotype. In Polyssia, 31 clones (genotype) of that form are identified by allozyme markers. The average number of individuals per clone is 8.16, and the number of unique singular genotypes is 21. The most common biotype was comprised of 224 specimens and was found all over the area of research (table 1, fig. 3). It is also interesting that the individuals with unique genotypes are characteristic of populations with numerical prevalence of *C. auratus*, while *C. gibelio*-2 is represented by literally single specimens. In the samples containing only *C. gibelio*-2 or also single specimens of *C. auratus*, the population structure is strictly clonal (all specimens of *C. gibelio*-2 share the same set of allozyme spectra). This proves that the individuals of that biotype reproduce by cloning, as also follows from cytogenetic studies of meiosis in triploid crucian carp (Cherfas, 1987), although there are obvious deviations in reproduction in presence of spermatozoa

of *C. auratus*. The trend holds for crucian carp populations in other regions. For example, in Siverskyi Donets River unisexual crucian carp populations are almost absent and all clonal specimens are found in insignificant quantities mixed with *C. auratus* population. There, clone diversity is maximum: 1.42 specimens per clone. In water systems of Middle Dnipro the studied *C. auratus* specimens comprise about half of all collected, the population structure is interim, and the number of specimens per clone is 4.76 (Kokodiy, 2010) (fig. 3).

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