Natural Resources and Sustainable Development
Volume 11, Issue 1, 2021
DOI: 10.31924/nrsd.v11i1.066

A SHORT REVIEW OF MOLECULAR GENETIC STUDIES ON COMMON CARP (*Cyprinus carpio* L.) HIGHLIGHTED THE mtDNA MARKERS

Tóth Bianka*, Bagi Zoltán*, Balog Katalin, Bársony Péter***, Jávor Bence****, Kusza Szilvia ***#**

* Centre for Agrar Genomics and Biotechnology, University of Debrecen, 4032 Debrecen Böszörményi út 138., Hungary;
** Faculty of Science and Technology, University of Debrecen, 4032 Debrecen Egyetem tér 1., Hungary;
*** Fish Biology Laboratory, Faculty of Agricultural and Food Sciences and Environmental Management, University of Debrecen, 4032 Debrecen, Böszörményi út 138., Hungary;
**** Hódmezőgazda Closed Corporation, Hódmezővásárhely, 4014 Debrecen, Arany Sándor u. 17., Hungary;
e-mail: kuszasz@hotmail.com

Abstract

As a result of climate change, many fish species have now become endangered, including common carp too. Common carp (Cyprinius carpio L.) are widespread in Europe. It has a long cultural history and is the most economically valuable fish species in Hungary. Fish farms consider their common carp stocks as a separate strains. As a result, in contrast to its neighbouring countries, there are many strains in Hungarian fisheries but detailed genetic information can be found to a small extent in connection of these. In the present study, we aimed to summarize genetic methods on common carp, with a special focus on mitochondrial DNA (mtDNA) studies.

Key words: common carp (*Cyprinus carpio* L.), climate change, mtDNA, Hungary, history

INTRODUCTION

Nowaday, many fish species are endangered due to, among other things, habitat loss, over-exploitation, pollution and climate change. Temperature is a determining factor for all species, influencing physiology, phenotypic appearance, and genetic diversity (Power et al., 2005). Due to global climate change, changes in water temperature within aquatic life (Magnuson et al., 1990; Sharma et al., 2007; Carmona-Catot et al., 2011), for which wildlife temperature is a determining factor (Magnuson et al., 1990; Brown et al., 2004; Heibo et al., 2005) also pose a significant threat to fish stocks. Climate change can increase water temperature in the freshwater ecosystem, reduce dissolved oxygen levels (Mooij et al., 2007), and lead to eutrophication (Schindler, 1997). These habitat changes may affect the distribution of fish species (Heino et al., 2009; Jeppesen et al., 2012).

In European lakes, which show increased eutrophication through warming, common carp (*Cyprinus carpio* L.) are widespread (FAO, 2018), which can be explained by the species tolerance to environmental factors

Corresponding author

(Flajs'hans, Hulata, 2006). In addition, it is an important and one of the oldest domesticated species for aquaculture (Balon, 1995; Flajs'hans, Hulata, 2006; Teletchea, Fontaine, 2014), which is considered endangered in Europe (Freyhof, Kottelat, 2008). Common carp is a native fish of Eurasia, and it has been introduced to various regions of the world as a valuable commercial species and food source (Kohlmann et al., 2003). It also has a long cultural history in Hungary. There are many studies around the world about the genetic diversity of common carp species and strains which are use different methods (Lehoczky et al., 2005a; Lehoczky et al., 2005b, Xu et al., 2014; Napora-Rutkowsky et al., 2017).

Analyzes of genetic diversity of common carp species and strains have already been studied in Hungary, but the number of these studies is small, and these were not exhaustive for the population. Recently, we have read mostly about studies with microsellite markers (Bártfai et al., 2003; Lehoczky et al., 2005a, Lehoczky et al., 2005b, Lehoczky et al., 2010). The Hungarian researches using primarily mitochondrial DNA on Hungarian common carp strains can be read in one study (Lehoczky et al., 2005a), despite the fact that mitochondrial DNA polymorphisms have proven to be an useful tool in phylogenetic studies of freshwater and marine fish (Avise, 2000).

The aim of our present study were the mapping of the mitochondrial DNA (mtDNA) investigations in order to the foundation of future research based on mtDNA method in the Hungarian common carp.

DISTRIBUTION AND ORIGIN OF THE COMMON CARP (*CYPRINUS CARPIO* L.)

Presumably, the wild ancestor of common carp developed in the Caspian Sea region at the end of the Pleistocene. The post-glacial temperature optimum allowed some common carp strains to reach the water system of the Aral Sea, East Asia and the Black Sea. It appeared in the water system of the Danube 8-10 thousand years ago. Start of commencement mass production in the fishponds built for this purpose is described between 12^{th}-16^{th} centuries. Albertus Magnus in the 13^{th} century suggested that the species was also propagated in the lakes of the monasteries, because common carp farming was a secret of the monasteries for a long time. The common carp farming of the monasteries reached such a standard that the conscious selection of common carp began in the 14^{th}-16^{th} century. As a result of long-term inbreeding as well as fixed mutations, incomplete scaly common carp have emerged as a basis for breeding mirror strains. It was during this period that the first descriptions of common carp farming appeared. Medieval common carp farming developed mainly in the Czech and Poland. Large farms have developed in Silesia, around Krakow and Lublin, but the first farms are emerging in Germany. The domesticed common was introduced by the Romans in Hungary (Lehoczky et al., 2018).

Its natural range is considered to be Eurasia, but within this the origin of the species is disputed. It was initially assumed that it originated in Central Asia, from where it naturally spread eastward (all the way to China) and westward to the Danube water system (Froufe et al., 2002; Lehoczky et al., 2018). There have also been some reports that Lake Biwa in Japan has been designated as the site of the species's development. However, recent reports of genetic research suggest that this species originated in North Asia and that the subspecies known today have developed during its spread (Mabuchi et al., 2006; Lehoczky et al., 2018). Early studies distinguish two subspecies based on morphological stamps: Asian and European. Later, the separation of four or five subspecies was proposed (Kirpichnikov, 1972; Pintér, 1989). Subsequent genetic studies classify the currently existing common carp forms into three subspecies: European-Transcaucasian common carp (*C. c. carpio*), Far Eastern (Amur) common carp (*C. c. haematopterus*), Southeast Asian (North Vietnamese) common carp (*C. c. viridiviolaceus/C. c. rubrofuscus*) (Lehoczky et al., 2018) (Fig. 1).

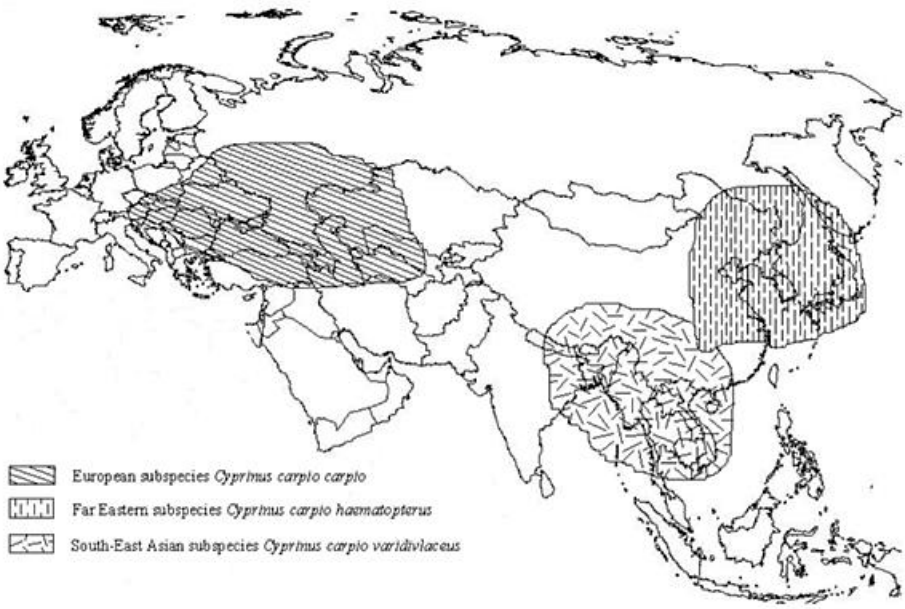

Fig. 1. Origin of the common carp (*Cyprinus carpio* L.) (Chistiakov-Voronova, 2009)

The first common carp farm in Hungary was built in Simontornya in 1894, which is named after Ottó Hermann and Béla Corchus. At the end of the 19th century, common carp farming began in Hungary, in connection with Ottó Hermann, who recognized that artificial common carp farming could be successful (Lehoczky et al., 2018). Imports of farmed common carp with different production characteristics, different body shapes, colors and scales,

such as Aischgründ scaly from Germany, Galician mirror from Czech Republic, Nasici and Poljana mirror from Croatia, and linear from Poland (Pintér, 1989). Fish farming started to develop rapidly in the 19th century, shortening the keeping time by 2-3 years with a developed new technology. The farms have been constantly expanding. Between the two World Wars, Hungary already had internationally recognized common carp strains. After World War II, a development process began, which contributed to the worldwide growth of common carp production, in which the Hungarians played a prominent role.

In the late 1950s, common carp strains typical of farms emerged. In the 1960s, live common carp gene bank was established in Szarvas, which later formed the basis for the production of common carp hybrids (Bakos, 1968; Bakos et al., 1997). During this period, common carp hatchery breeding technology was developed, which revolutionized common carp breeding with technology to eliminate the stickiness of eggs. By the spread of the method and the development of the transport technology, the mixing of hitherto isolated species, stocks and populations also started. In 1965, crossing of strains with different genetic backgrounds began. In the 1980s, three Szarvas hybrid strains were established with Szarvasi 215 mirror, Szarvasi P31 heterozygous scaly, Szarvasi P34 scaly. In 1993, common carp were included in the farmed animal species (1993. CXIV. act on Animal Husbandry), and the maintenance of the breed begins. In 1996 the Common Carp Performance Testing Code was completed, which included a test protocol for the recognition procedure for each strains.

Currently, the common carp can be found in fish farms, fishing lakes, water reservoirs, backwaters and larger canals in Hungary. It appear in fallowing waters: Öreg-Duna, Mosoni-Duna, Duna, Rábca, Rába, Lapincs, Pinka, Strém, Marcal, Ipoly, Zala, Sió, Sárvíz, Kapos, Koppány, Dráva, Mura, Rinya, Karasica, Tisza, Öreg-Túr, Szamos, Kraszna, Bodrog, Keleti-főcsatorna, Nyugati-főcsatorna, Sajó, Rakaca, Hernád, Zagyva, Tarnóca, Hármas-Körös, Kettős-Körös, Fekete-Körös, Fehér-Körös, Hortobágy-Berettyó, Sebes-Körös, Berettyó, Ér, Maros, Balaton, Kis-Balaton, Fertő, Velencei-tó, Tisza-tó.

Common carp is one of the most important fish species in Hungarian fish production, we have the most breeding experience for its breeding, and our natural endowments are also important to get to know the species as widely as possible, including the assessment of genetic reserves (Kánainé, 2019).

Hungarian fish farms consider their common carp stocks as a separate strains (Lehoczky, 2006; Gorda, 2012), as a result of which we may have a significant gene pool, the exploration of which is essential for the preservation and development of the common carp. In Hungary, only strains

or hybrids that have been recognized or declared for strains recognition and that have strains recognition for their origin can be propagated (Lehoczky, 2006; Gorda, Borbély, 2014). Currently, 21 breeding organizations in Hungary officially maintain a total of 33 strains (Udvari, 2017), crossbreeds and hybrids.

Performance testing does not include genetic screening (Lehoczky et al., 2005a; Tóth et al., 2019). Genetic variation in a species determines its ability to survive in nature and also affects its ability to adapt to various environmental changes. Thus, genetic variation is required for the survival and resistance of a species (Bataillon et al., 1996). The management and conservation of genetic variations require the characterization of the genetic diversity of species, varieties, strains (Pujolar et al., 2009) as well as the constant monitoring of their genetic status (Ghelichpour, 2013).

APPLIED GENETIC METHODS FOR STUDY OF GENETIC DIVERSITY IN COMMON CARP

Protein transferrin polymorphism studies were the first applied methods for common carp diversity in Hungary (Márián et al., 1984; Szerencsés et al., 1990; Váradi et al., 1993; Csizmadia et al.; 1995). The method was very labor intensive and difficult to evaluate. Few proteins were suitable for the study and their variability was low.

Total mitochondrial DNA as well as ribosomal RNA were then examined by restriction fragment lenght polymorphism (RFLP) method, and genomic DNA analysis was started by random amplification of polymorphic DNA (RAPD) and RFLP methods (Gross et al., 2002). These methods are still frequently used for genetic diversity studies. Several studies supplement the investigation with microsatellite markers, for example, to provide even more information.

In subsequent studies, variable number tandem repeats (VNTR) were preferred. Initially, the multilocus minisatellite fingerprint was used in studies (Carter et al., 1991; Vos et al., 1995; Wang et al., 2002), which had the disadvantage of a complex pattern that was difficult to analyze and that the samples tested on different gels were not comparable. This method was followed by single-site minisatellite DNA probes. The disadvantage of this method was that it was difficult to accurately identify the size of the alleles (O'Connel, Wright, 1997).

Following these methods, assays using microsatellite markers were developed by researchers (Crooijmans et al., 1997; Bártfai et al., 2003; Kohlmann et al., 2003; Lehoczky et al., 2005a). Microsatellite markers have proven to be particularly suitable for detecting genetic differences between closely related populations, due to their high mutation rate (Avise, 2000) and codominant inheritance (Fésüs et al., 2000). It is a popular marker to date.

The potential of next-generation sequencing (NGS) may have a significant impact on the study of common carp genetic resources in the near future. Nowadays, such studies are being conducted, witch of QTLs related to feed sales, standard body length, body weight, growth rate and body shape (Zhang et al., 2008, Li et al., 2009; Wang et al., 2012; Zhang et al., 2013). These assays can be used in Marker Assisted Selection (MAS) to increase the efficiency of common carp farming programs in the future.

CHARACTERISTICS OF THE MITOCHONDRIAL GENOME AND mtDNA STUDIES IN COMMON CARP

The evolution of mtDNA dates back 2 billion years, which is a highly variable genome relative to the nuclear genome (Lang et al., 1999; Lane, Martin, 2010), the self-inherited material of mitochondria located in the cytoplasm of the cell (Brown et al., 1979). It has been considered an extremely popular marker in evolutionary studies, species identification, biodiversity monitoring, and phylogenetic analyzes (Allio et al., 2017).

In most animals, it is a short, circular molecule involved in aerobic respiration (Ladoukakis, Zouros, 2017). In the common carp, the mtDNA molecule has about 16 kilobase pairs and a total of 37 genes. In contrast to nuclear genome, the haploid mtDNA is maternally inherited, does not recombine, and has an elevated mutation rate (Ladoukakis, Zouros, 2017; Allio et al., 2017). About 93 % of the mtDNA is a coding sequence with very short introns. It is not bound to proteins and is therefore less protected against mutagenic effects (Li, 1997). Furthermore, because the mitochondria lack an excisional system to repair established mutations, there is no improvement in established mutations (Li, 1997).

The D-loop region, which is the non-coding region of mtDNA, is often studied and, as a result, no protein synthesis occurs in the region and is therefore suitable for diversity analysis (Bernatchez et al., 1992). Furthermore, the cytochrome b (cyt-b) region of mtDNA is suitable for the study of phylogenetic analyzes due to its universal and conservative nature (Johns, Avise, 1998). A major disadvantage of the mtDNA is that it does not reflect changes in the nuclear genome, so it can not be used for diversity estimation alone (Liu, Cordes, 2004) (Figure 2).

Genetic studies are ongoing in the world due to the economic and ecological importance of the common carp (Zhou et al., 2004; Zhang et al., 2008; Kongchum et al., 2010) wich are essential for the management of fish according to researchers. Furthermore, it is also important to counteract the possible genetic effects caused by fish hatcheries in order to genetically improve for species and varieties (Vandeputte, 2003; Mabuchi et al., 2006; Mondol et al., 2006; Chistiakov, Voronova, 2009). Various region (the most often D-loop and cyt-b) of mitochondrial DNA is used as genetic marker in

several fisheries and aquaculture research (Xiao et al., 2001; Kohlmann et al., 2003; Thai et al., 2004; Tang et al., 2016).

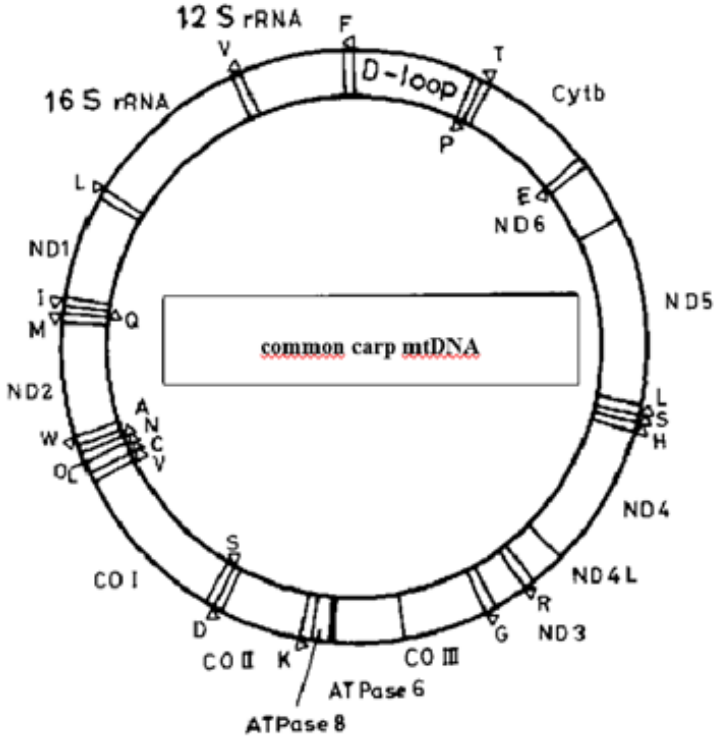

Fig. 2. The mitochondrial DNA (mtDNA) genome of common carp (*Cyprinus carpio* L.) (Chang et al., 1994)

Mirror common carp, which appear in the Songhua River and have been even more common since 2014. Tang et al., 2016, where the cyt-b region of mtDNA has been analyzed. They sought to answer the question of the extent to which mirror common carp are genetically present in bred stocks and their effects on bred stocks and wild strains. It was noted that gene flow as a consequence of cultured populations can also have negative consequences in wild populations. Mirror common carp farmed in the Amur River Basin have adapted to cold weather and have other advantages such as disease resistance and a high growth rate compared to their wild counterparts.

Because they are the same species, they can easily hybridize (Tang et al., 2016). Xiao et al., 2001, analyzed the mtDNA sequence of individuals belonging to the *C. c. xenocyprinae* subfamily from China. The results were used to establish and evaluate intraspecific, interspecific, and intergeneric phylogenicity in a biogeographic context. *C. c. xenocyprinae* individuals (n=30) were analyzed by cyt-b (1140 bp) sequence analysis. High levels of

nucleotide variation were observed between populations of species and genera.

The D-loop region of the common carp mtDNA has been studied Thai et al., 2004, to explore genetic variations and to provide further results in the global genealogy of the common carp. Levels of haplotype diversity varied across countries. The greatest diversity was shown by Chinese, Vietnamese, and Indonesian common carp, while Japanese koi and European common carp contained undetectable nucleotide variations. Genealogical analyzes confirmed a close relationship between Vietnamese koi and Chinese Color Carp strains. Based on their results, Chinese and Indonesian common carp strains were the most diverse and did not support their affiliation with Asian and European lines and their current taxonomic classification (Thai et al., 2004). Thai et al., 2006, examined 20 strains of 968 Vietnamese common carp individuals by analysis of mitochondrial D-loop region and Single Strand Confirmation Polymorphism (SSCP). For comparison, common carp individuals from China, Japan, Indonesia and Hungary were involved. The result was that Vietnamese common carp have a high haplotype and low nucleotide diversity, which is a mixture of indigenous and introduced strains. The Hungarian strains differed greatly from all the other strains studied. It was found that the Hungarian strain did not significantly contribute to the formation of cultured Vietnamese strains based on the D-loop of the mitochondrial sequence.

The largest freshwater fish family, *Cyprinidae*, was analyzed in Vietnam by Thai et al., 2007. In Vietnam, the *Cyprinidae* fish family includes more than 220 recognized species, for which the relationships between the main *Cyprinidae* strains are poorly understood and the taxonomic validity of many strains is under discussion, similar to the question of the existence of Hungarian strains (Tóth et al., 2020). Thai et al., 2007, included 25 Vietnamese common carp strains in their study. The 16S rRNA, D-loop, and cyt-b regions of the mtDNA sequence were examined. Their molecular studies supported the division of the *Cyprinidae* family into two parts: *Cyprinines* and *Leuciscines*. However, he did not substantiate his affiliation with the *Danioninae* line. Many of the subfamily boundaries were questioned and doubt was raised on some of the generic level classifications (Thai et al., 2007).

Kohlmann et al., 2003, examined the genetic variability and population structure distribution of domesticated and captive common carp stocks from Europe, Central Asia, and East and Southeast Asia in addition to allozyme, mtDNS (21 populations) and microsatellite markers. The results of the 21 populations with the mtDNA marker showed that all but one of the European populations clustered into a haplotype that dominated Central Asia, but was completely absent in East and Southeast Asia, so the result obtained with the

mtDNA marker also confirmed that the European common carp are native to Central Asia. Kohlmann and Kersten, 2013, in their study examined the disputed origin of the common carp using with mtDNA marker. The D-loop region of mtDNA was analyzed in 24 populations of 248 individuals from Western Europe (Spain) and Central Asia (Uzbekistan). A total of nine haplotypes were detected, of which 7 haplotypes were first described by them. All nine European/Central Asian haplotypes were closely related and grouped into a single group with 94 % bootstrap support. They found that the center of origin of modern European common carp may have been located in or near Central Asia (Ponto-Caspian Sea basin), given that the number of all regions and endemic haplotypes was highest in this region. Based on their results, the European and Central Asian populations are grouped into two haplotypes (H2 and H5) for the D-loop region of mtDNA. Furthermore, it was found that in the wild and wild/feral populations, haplotypes from H2 to H5 are present with the same frequency in the domesticated populations.

The genetic structure of *Carassius gibelio* and *Cyprinus carpio carpio* populations in Western Greece was studied by RFLP and mitochondrial DNA sequence analysis (D-loop, cyt-b)(Tsipas et al., 2009). In their analysis, two haplotypes were detected in *C. c. carpio* populations and two haplotypes in *C. gibelio* populations. High nucleotide divergence was found for the two species and two genetically distinct populations of *C. gibelio* were found in two different habitats (Tsipas et al., 2009).

Zhou et al., 2003, in their study examined the following common carp: German common carp, Russian scattered scaled mirror carp, Volga River wild common carp (*Cyprinus carpio carpio subspecies*), Yangtze River wild common carp (*Cyprinus carpio haematopterus*) and Xingguo red carp (*Cyprinus carpio haematopterus*). Their aim was to clarify the existence of European domesticated common carp. In their phylogenetic analysis, they obtained the result that German mirror common carp and Russian mirror common carp are two separate subspecies. Based on their results, *C. c. carpio, C. carpio haematopterus* and European common carp had different ancestors: German mirror common carp were dominated from European subspecies of *C. c. carpio*. Russian mirror common carp and *C. c. haematopterus* are native to the Asian subspecies.

The total mtDNA sequence of the wild common carp population of Lake Biwa (LBW) was determined by a PCR-based method Mabuchi et al., 2006. The phylogenetic status of the LBW strain within common carp was re-examined using the already published mtDNA sequences of several genes. It was concluded that the low level of nucleotide divergence in the mitochondrial genome revealed by a comparison of the total mtDNA of LBW and a Taiwanese strain showed that no coding/non-coding region could

provide sufficient information to resolve phylogenicity. LBW strains are closely related to strains of the "Eurasian" species (Mabuchi et al., 2006).

Polish strains were analyzed by Napora-Rutkowski et al., 2017. They used three different types of genetic markers: AFLP, microsatellite and mtDNA sequence (D-loop region). Examining the D-loop region of mtDNA, only two haplotypes (H2 and H5) were detected in all Polish common carp strains analyzed (54 randomly selected individuals out of 20 strains analyzed) where H2 was the most prevalent. A difference was found between the two haplotypes in the AT repeat motif variable number (10 or 14) at the 811 nucleotide position. The total D-loop lengths were 930 bp (H2) and 938 bp (H5). The two identified haplotype sequences were identical to the haplotype sequences in the NCBI gene bank (JQ390594 and JQ390597).

Unfortunately, despite the commercial importance of Hungarian common carp strains and the huge market demand, few molecular genetic studies can be found. We found a study supported by mtDNA analysis dealing with Hungarian common carp strains (Lehoczky et al., 2005a), where wild common carp individuals from the Tisza and Danube were analyzed in order to determine whether there are individuals of Asian origin in the stocks maintained in the gene bank (NARIC, Hungary) of common carp. According to their results, the wild common carp stocks in the gene bank do not contain individuals of Asian origin (Lehoczky et al., 2005a).

In line with the above, we believe that it is important to get to know the genetic structure of Hungarian common carp strains as widely as possible, both in terms of their production traits, to improve the heterosis effect, to avoid inbreeding and to increase their survival traits in ponds.

Acknowledgment

The work was supported by the European Regional and Development Fund and the Government of Hungary within the project GINOP-2.3.2-15-2016-00025.

The work/publication is supported by the EFOP-3.6.1-16-2016-00022 project. The project is co-financed by the European Union and the European Social Fund.

REFERENCES

1. Allio R., Donega S., Galtier N., Nabholz B., 2017, Large Variation in the Ratio of Mitochondrial to Nuclear Mutation Rate across Animals: Implications for Genetic Diversity and the Use of Mitochondrial DNA as a Molecular Marker, Mol. Biol. Evol, vol. 34, no. 11, pp. 2762-2772;
2. Avise J.C., 2000, Phylogeography - The History and Formation of Species, Harvard University Press, USA, vol. 447;
3. Bakos J., 1968, A ponty tenyészértékét meghatározó tulajdonságok és jelentőségük a szelekciós munkában, Halászat, vol. 14, no. 3, pp. 84-85;
4. Bakos J., Gorda S., Váradi L., Balogh J., 1997, Tenyésztő szervezetek szerepe a magyar pontyfajták fenntartásában és nemesítésében, XXI. Halászati Tudományos Tanácskozás, Szarvas, május 25-26, Összefoglalók, pp. 9-13;

5. Balon K., 1995, Origin and domestication of the wild carp, Cyprinus carpio: from Roman gourmets to the swimming flowers, Aquaculture, vol. 129, pp. 3-48;
6. Bártfai R., Egedi S., Yue G.H., Kovács B., Urbányi B., Tamás G., Horváth L., Orbán L., 2003, Genetic analysis of two common carp broodstocks by RAPD and microsatellite markers, Aquaculture, vol. 219, pp.157-167;
7. Bataillon T.M., David J.L., Schoen D.J., 1996, Neutral genetic markers and conservation genetics: simulated germplasm collections, Genetics, vol. 144, pp. 409-417;
8. Bernatchez L., Guyomard R., Bonhomme F., 1992, DNA sequence variation of the mitochondrial control region among geographically and morphologically remote European brown trout Salmo trutta populations, Molecular Ecology, vol. 1, pp. 73-161;
9. Brown W.M., George M., Wilson A.C., 1979, Rapid evolution of animal mitochondrial DNA, Proceedings of the National Academy of Sciences of the United States of America, vol. 76, pp. 1967-1971;
10. Brown J.H., Gillooly J.F., Allen A.P, Savage V.M., West G.B., 2004, Toward a metabolic theory of ecology, Ecology, vol. 85, pp. 1771-1789;
11. Carmona-Catot G., Benito J., García-Berthou E., 2011, Comparing latitudinal and upstream-downstream gradients: life history traits of invasive mosquitofish, Diversity and Distribution, vol. 17, pp. 214-224;
12. Carter R.E., Mair G.C., Skibinski D.O.F., Parkin D.T., Beardmore J.A., 1991, The application of DNA fingerprinting in the analysis of gynogenesis in tilapia, Aquaculture, vol. 95, pp. 41-52;
13. Chang Y., Huang F., Lo T., 1994, The complete nucleotid sequence and gene organization of carp (*Cyprinus carpio*) mitochondrial genome, J. Mol. Evol., 38, pp.138-155;
14. Chistiakov D.A., Voronova N.V., 2009, Genetic evolution and diversity of common carp Cyprinus carpio L., Central European Journal of Biology, vol. 4, no. 3, pp. 304-312;
15. Crooijmans R.P.M.A., Bierbooms V.A.F., Komen J., Van der Poel J.J., Groenen M.A.M., 1997, Microsatellite markers in common carp (Cyprinus carpio L.), Animal Genetics, vol. 28, no. 2, pp. 129-134;
16. Csizmadia Cs., Jeney Zs., Szerencsés I., Gorda S., 1995, Transferrin polymorphism of some races in a live gene bank of common carp, Aquaculture, vol. 129, pp. 193-198;
17. FAO, 2018, The state of world fisheries and aquaculture, Food and Agriculture organization of the United Nations;
18. Fésüs L., Komlósi I., Varga L., Zsolnai A., 2000, Molekuláris genetikai módszerek alkalmazása az állattenyésztésben, Agroinform Kiadó és Nyomda Kft. Budapest;
19. Flajs'hans M., Hulata G., 2006, Common carp - Cyprinus carpio. Genimpact final scientific report University of South Bohemia, Vodnany, pp. 109-116;
20. Freyhof J., Kottelat M., 2008, Cyprinus carpio. The IUCN Red List of Threatened Species 2008: e.T6181A1 2559362;
21. Froufe E., Magyary I., Lehoczky I., Weiss S., 2002, mtDNA sequence data supports and Asian ancestry and single introduction of the common carp into the Danube Basin, Journal of Fish Biology, vol. 61, no. 1, pp. 301- 04;
22. Ghelichpour M., Shabani A., Shabanpour B., 2013, Microsatellite variations and genetic structure of common carp (Cyprinus carpio) populations in Gomishan bay and Gorganroud River (Southeast of the Caspian Sea), International Journal of Aquatic Biology, vol.1, pp. 22-27;

23. Gorda S., 2012, Vízi genetikai erőforrások - a magyar pontytenyésztési program, NACEE Workshop, 2012. május 4., Sáregres – Rétimajor;
24. Gorda S., Borbély T., 2014, Ponty teljesítményvizsgálat eredménye, pp. 1-27;
25. Gross R., Kohlmann K., Kersten P., 2002, PCR-RFLP analysis of the mitochondrial ND-3/4 and ND-5/6 gene polymorphisms in the European and East Asian supspecies of common carp (Cyprinus carpio L.) Aquaculture, vol. 204, pp.507-516;
26. Heibo E., Magnajagen C., Vøllestad L.A., 2005, Latitudinal variation in life-history traits in Eurasian perch, Ecology, vol.86, pp. 3377-3386;
27. Heino J., Virkkala R., Toivonen H., 2009, Change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions, Biological Reviews Climate, vol. 84, pp. 39-54;
28. Jeppesen E., Mehner T., Winfield I.J., Kangur K., Sarvala J., Gerdeaux D., Rask M., Holmgren P., Romo S., Eckmann R., Sandstrom A., Blanco S.L., Kangur H., Ragnarsson A., Tarvainen M., Ventela A.M., Søndergaard M., Lauridsen T.L., Meerhoff M., 2012, Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes, Hydrobiologia, vol. 694, pp. 1-39;
29. Johns G.C., Avise J.C., 1998, A Comparative Summary of Genetic Distances in the Vertebrates from the Mitochondrial Cytochrome b Gene, Molecular Biology and Evolution, vol. 15, pp. 1481-1490;
30. Kánainé S.D.I., 2019, Mikroszatellit markerek izolálása hal populációk genetikai variabilitás vizsgálatának és nemesítésének megalapozásához, Doktori (PhD) értekezés, Gödöllő;
31. Kirpichnikov V.S., 1972, Methods and effectiveness of ropsha carp breeding. Communication I. Breeding Amis, Original Forms and Cross System, Russian Journal of Genetics, vol. 8, pp. 65-72;
32. Kohlmann K., Gross R., Murakaeva A., Kersten P., 2003, Genetic variation and structure of common carp populations throughout the distribution range inferred from allozyme, microsatellite and mtDNA marker, Aquatic Living Resources, vol. 16, pp. 421-431;
33. Kohlmann K., Kersten P., 2013, Deeper insight into the origin and spread of European common carp (Cyprinus carpio carpio) based on mitochondrial D-loop sequence polymorphisms, Aquaculture, vol. 97 - 104, pp. 376-379;
34. Kongchum P., Palti Y., Hallerman E.M., Hulata G., David L., 2010, SNP discovery and development of genetic markers for mapping innate immune response genes in common carp (Cyprinus carpio), Fish, Shellfish Immunol., vol. 29, pp. 356-361;
35. Ladoukakis E.D., Zouros E., 2017, Evolution and inheritance of animal mitochondrial DNA: rules and exceptions, J. of Biol. Res. Thessaloniki, vol. 24, no. 2;
36. Lane N., Martin W., 2010, The energetics of genome complexity, Nature, vol. 467, pp. 929-934;
37. Lang B.F., Gray M.W., Burger G., 1999, Mitochondrial genome evolution and the origin of eukaryotes, Annu. Rev. Genet., vol. 33, pp. 351-397;
38. Lehoczky I., Magyary I., Hancz C., Weiss S., 2005a, Preliminary studies on the genetic variability of six Hungarian common carp strains using microsatellite DNA markers, Hydrobiologia, vol. 533, no.1, pp. 223-228;
39. Lehoczky I., Jeney Zs., Magyary I., Hancz Cs., Kohlmann K., 2005b, Preliminary data on genetic variability and purity of common carp (Cyprinus carpio L.) strains kept at the live gene bank at Research Institute for Fisheries, Aquaculture and Irrigation (HAKI) Szarvas, Hungary, Aquaculture, vol. 247, pp. 45-49;

40. Lehoczky I., 2006, A HAKI ponty élő génbankjának populációgenetikai vizsgálata mikroszatellit DNS markerekkel és PCR-RFLP módszerrel, Doktori (PhD) értekezés, Kaposvári Egyetem, Állattudományi Kar, vol. 108;
41. Lehoczky I., Nagy Z.T., Bakos J., Jeney Zs., 2010, Jelentősebb hazai vadponty fajtáink genetikai változatosságának fenntartása a HAKI ex situ génbankjának, valamint a faj természetes vizeinkben élő populációinak segítségével, Halászat, vol. 103, no. 3, pp. 104-109;
42. Lehoczky I., Kovács B., Kovács G., Gorda S., Péteri A., Bakos J., 2018, A ponty genetikája és erőforrásai, Vármédia-Print Kft. Gödöllő, 9-34; In: A ponty (Cyprinus carpio L.) biológiája és tenyésztése, Csorbai B., Urbányi B., Szent István Egyetem, Mezőgazdaság- és Környezettudományi Kar, Akvakultúra és Környezetbiztonsági Intézet, Halgazdálkodási Tanszék megbízásából Vármédia-Print Kft. Gödöllő, vol. 203;
43. Li O., Cao D., Zhang Y., Gu Y., Zhang X., Lu C., Sun X., 2009, Studis on feed conversion ratio trait of common carp (Cyprinus carpio L.) using EST-SSR marker, J. Fisheries China, vol. 33, pp. 624-631;
44. Li W.H., 1997, Molecular Evolution, Sinauer, Sunderland;
45. Liu Z.J., Cordes J.F., 2004, DNA marker technologies and their applications in aquaculture genetics, Aquaculture, vol. 238, pp. 1-37;
46. Mabuchi K., Miya M., Senou H., Suzuki T., Nishida M., 2006, Complete mitochondrial DNA sequence of the Lake Biwa wild strain of common carp (Cyprinus carpio L.) further evidence for an ancient origin, Aquaculture, vol. 257, pp. 68-77;
47. Magnuson J.J., Meisner J.D., Hill D.K., 1990, Potential changes in the thermal habitat of Great Lakes fish after global climate warming, Transactions of the American Fisheries Society, vol. 119, pp. 254-264;
48. Márián T., Krasznai Z., Bakos J., 1984, Transzferrin polimorfizmus vizsgálat eredménye magyarországi pontypopulációkban, Halászat, vol. 30, no. 4, pp. 112-113;
49. Mondol Md.R.K., Islam Md.S., Alam Md.S., 2006, Characterization of different strains of common carp (Cyprinus carpio L.) (Cyprinidae, Cypriniformes) in Bangladesh using microsatellite DNA markers, Genetics and Molecular Biology,, vol. 29, no. 4, pp. 626-633;
50. Mooij W., Janse J., De Senerpont Domis N., lsmann H., Ibelings B.W., 2007, Predicting the effect of climate change on temperate shallow lakes with the ecosystem model PCLake, Hydrobiologia, vol. 584, pp. 443-454;
51. Napora-Rutkowski Ł., Rakus K., Nowak Z., Szczygieł J., Pilarczyk A., Ostaszewska T., Irnazarow I., 2017, Genetic diversity of common carp (Cyprinus carpio L.) strains breed in Poland based on microsatellite, AFLP, and mtDNA genotype data, Aquaculture, vol. 473, pp. 433-442;
52. O'Connell M., Wright J.M., 1997, Microsatellite DNA in fishes, Rev. Fish. Biol. Fish, vol. 7, pp. 331-363;
53. Pintér K., 1989, Magyaroszág halai, Akadémiai Kiadó, Budapest, pp. 109-116
54. Power M., Dempson J.B., Reist J.D., Schwarz C.J., Power G., 2005, Latitudinal variation in fecundity among Arctic charr populations in eastern North America, Journal of Fish Biology, vol. 67, pp. 255-273;
55. Pujolar J.M., De Leo G.A., Ciccotti E., Zane L., 2009, Genetic composition of Atlantic and Mediterranean recruits of European eel Anguilla anguilla based on EST-linked microsatellite loci, Journal of Fish Biology, vol. 74, pp. 2034-2046;
56. Schindler D.W., 1997, Widespread effects of climate warming on freshwater ecosystems in North America, Hydrological Processes, vol. 11, pp. 1043-1067;

57. Sharma S., Jackson D.A., Minns C.K., Shuter B.J., 2007, Will northern fish populations be in hot water because of climate change?, Global Change Biology, vol. 13, pp. 2052-2064;
58. Szerencsés I., Bakos J., Jeney Zs., 1990, Transzferrin (Tf) polimorfizmus vizsgálat a szarvasi ponty-fajtagyűjteményben, Halászat, vol. 36, no. 83, pp. 1-2;
59. Tang F., Santos A., Bessert M., Lu C., Liu W., 2016, On the occurrence of mirror carp, an aquaculture breed of Cyprinus carpio Linnaeus, 1758, in the Songhua River, the largest tributary of the Amur River, Wiley, DOI: 10.1111/jai.13185
60. Teletchea F., Fontaine P., 2014, Levels of domestication in fish: implications for the sustainable future of aquaculture, Fish and Fisheries, vol. 15, pp. 181-195;
61. Thai B.T., Burridge C.P., Pham T.A., Austin C.M., 2004, Using mitochondrial nucleotide sequences to investigate diversity and genealogical relationships within common carp (Cyprinus carpio L.), International Society for Animal Genetics, Animal Genetics, vol. 36, pp. 23-28;
62. Thai B.T., Pham T.A., Austin C.M., 2006, Genetic diversity of common carp in Vietnam using direct sequencing and SSCP analysis of the mitochondrial DNA control region, Aquaculture, vol. 258, pp. 228-240;
63. Thai B.T., Burridge C.P., Austin C.M., 2007, Genetic diversity of common carp (Cyprinus carpio L.) in Vietnam using four microsatellite loci, Aquaculture, vol. 269, pp. 174-186;
64. Tóth B., Bagi Z., Kézi T., Kusza Sz., 2019, Mikroszatellit markerek optimalizálása magyarországi ponty (Cyprinus carpio L.) tájfajtákon, Előzetes közlemény Állattenyésztés és takarmányozás, vol. 68, no. 4, pp. 302-312;
65. Tóth B., Khosravi R., Ashrafzadeh M.R., Bagi Z., Fehér M., Bársony P., Kovács Gy., Kusza Sz., 2020, Genetic diversity and structure of common carp (Cyprinus carpio L.) in the Centre of Carpathian Basin: implications for conservation, Genes, vol. 11, no. 11, pp. 12-68;
66. Tsipas G., Tsiamis G., Vidalis K., Bourtzis K., 2009, Genetic differentiation among Greek lake populations of Carassius gibelio and Cyprinus carpio carpio, Genetica, vol. 136, pp. 491-500;
67. Udvari Zs., 2017, Magyarországon elismert pontyfajták, Földművelésügyi Minisztérium, Horgászati és Halgazdálkodási Főosztály, iktatószám: HHgF vol.268
68. Vandeputte M., 2003, Selective breeding of quantitative traits in the common carp (Cyprinus carpio): A review. Aquatic Living Resources, vol. 16, no. 5, pp. 399-407;
69. Váradi L., Szilágyi G., Horváth L., 1993, Egynyaras pontyállomány genetikai és morfológiai elemzése a Dinnyési Ivadéknevelő Gazdaságban, Halászat, vol. 86, pp. 46-48;
70. Vos P., Hogers R., Bleeker M., Reijans M., van de Lee T., Homes M., Frijters A., Pot J., Peleman J., Kuiper M., Zabeau M., 1995, AFLP: a new technique for DNA fingerprinting, Nucleic Acids Research, vol. 23, pp. 4407-4414;
71. Wang J., Xia D., 2002, Studies on fish heterosis with DNA fingerprinting, Aquaculture, vol. 33, pp. 941-947;
72. Wang J., He A., Ma Y., Wang C., 2012, Genetic map construction and quantitative trait locus (QTL) analysis on growth-related traits in common carp (Cyprinus carpio L.), Afr. J. Biotechnol., vol. 11, pp. 7874-7884;
73. Xiao W., Zhang Y., Liu H., 2001, Molecular Systematics of Xenocyprinae (Teleostei: Cyprinidae): Taxonomy, Biogeography, and Coevolution of a Special Group Restricted in East Asia, Molecular Phylogenetics and Evolution, vol. 18, no. 2, pp. 163-173;
74. Xu P., Zhang X., Wang X., Li J., Liu G., Kuang Y., Xu J., Zheng X., Ren L., Wang G., Zhang Y., Huo L., Zhao Z., Cao D., Lu C., Li Ch., Zhou Y., Liu Z., Fan Z., Shan

G., Li X., Wu S., Song L., Hou G., Jiang Y., Jeney Zs., Yue D., Wang L., Shao Ch., Song L., Sun J., Ji P., Wang J., Li Q., Xu L., Sun F., Feng J., Wang Ch., Wang S., Wang B., Li Y., Zhu Y., Xue W., Zhao L., Wang J., Gu Y., Lv W., Wu K., Xiao J., Wu J., Zhang Z., Yu J., Sun X., 2014, Genome sequence and genetic diversity of the common carp, Cyprinus carpio, Nature Genetics, vol. 46, no. 11, pp. 1212-1219;
75. Zhang Y., Liang L., Jiang P., Li D., Lu C., Sun X., 2008, Genome evolution trend of common carp (Cyprinus carpio L.) as revealed by the analysis of microsatellite loci in a gynogentic family, Journal Genetics and Genomics, vol. 35, no.2, pp. 97-103;
76. Zhang Y., Wang S., Li J., Zhang X., Jiang L., Xu P., Lu C., Wan Y., Sun X., 2013, Primary genome scan for complex body shape-related traits in the common carp Cyprinus carpio. J. Fish. Biol., vol. 82, pp. 125-140;
77. Zhou J.F., Wu Q.J., Ye J.Z., Tong J.G., 2003, Genetic divergence between Cyprinus carpio carpio and Cyprinus carpiohaematopterus as assessed by mitochondrial DNA analysis, with emphasis on origin of European domestic carp, Genetica, vol. 119, pp. 93-97;
78. Zhou J., Wu Q., Wang Z., Ye Y., 2004, Genetic variation analysis within and among six varieties of common carp (Cyprinus carpio L.) in China using microsatellite markers, Genomics, vol. 40, pp. 1389-1393.

Received: November 16, 2020
Revised: February 04, 2021
Accepted and published online: May 31, 2021