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Innovation of carp germplasm and its research progress

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ABSTRACT

The artificial breeding of carp existed in China 8000 years ago. The breeding of carp played an important role in ancient Chinese history, and it still played a crucial role in modern aquaculture. The output of carp in China is very high, accounting for 8.42 % of the total output of freshwater products in 2023, ranking fifth in the total output of freshwater aquaculture fish. At the same time, carp is also the fish species with the highest number of new varieties bred in China. With the advent of the genomics era, breeding technologies have also made progress. This paper reviews the history and current status of carp farming, the germplasm resources of carp, and the application of fish genetic breeding technology in the germplasm innovation of carp.

1. History and current status of carp cultivation

The common carp (*Cyprinus carpio* L.), a taxonomic freshwater fish belonging to the genus *Cyprinus* in the Cyprinidae family, is long and flat. It has a round abdomen and a relatively small head. The dorsal surface is gray black or yellowish brown, the side of the body is golden yellow, and the abdomen is gray white. The dorsal and caudal fins are pale reddish yellow, while the other fins are golden yellow. However, the color often varies depending on the different habitats, and it has multiple varieties. The carp is a benthic omnivorous fish, which can not only eat plant food, but also prey on small aquatic animals. Moreover, the carp has strong adaptability to the environment, mild temperament, lively and good at jumping, and vigorous vitality. It is resistant to cold and low oxygen levels, as well as moderately tolerant to salinity and alkalinity. Its flesh is tender and tasty, containing a wealth of protein and various trace elements, making it a highly nutritious ingredient. In traditional Chinese medicine, carp also has certain medicinal values, such as diuretic detumescence, invigorating spleen and appetizing effects.

Carp is one of the traditional cultivated fish species in China. The carp culture in China has a profound historical heritage. Since ancient times, the dragon has always been a symbol of auspiciousness in traditional Chinese culture, and it is said that a carp can transform into a dragon once it leaps over the Dragon Gate. “The Carp Leaping Over the Dragon Gate” tells the story of the struggle of the carp against the current, daring to try to jump and finally leaping over the Dragon Gate. This classic tale has inspired generations of Chinese people and integrated into the spiritual totem of the Chinese nation. At the same time, the carp is also regarded as a representative of Chinese fish culture and the national fish.

According to the existing historical records, fish farming already existed in China during the Shang Dynasty 3000 years ago. Research by foreign scholars has found that the artificial cultivation of carp in China can be traced back to 8000 years ago [1]. The oracle inscriptions unearthed from the Yin Ruins of the Shang Dynasty (today’s Anyang City, Henan Province) are the earliest extant written records on fish farming in China. The first collection of poems in China, *the book of songs · Lingtai*, records the scene of King Wen of Zhou raising fish in Lingzhao and jumping fish in the pond. From the early Zhou Dynasty to the Warring States period (1046 BC - 221 BC), pond fish farming developed well. At that time, in Zheng, Song, Qi, Wu, Yue and other countries, fish farming became an important industry to enrich the country and strengthen the people. “The Classic of Fish Cultivation” written by Fan Li in the late Spring and Autumn period (about 460 BC) is one of the earliest Monographs on fish culture in the world, which details the methods of raising carp [2]. During the Han Dynasty (202 BC - 220 AD), large-scale pond aquaculture emerged, with people beginning to use natural or artificially excavated ponds for fish farming. Emperor Wu of Han Dynasty dug a Kunming pond with a radius of 40 miles in Chang’an for training sailors and fish farming. Additionally, fish farming in rice

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fields has also been carried out. During the Tang Dynasty (618 AD - 907 AD), the breeding objects expanded from carp to black carp (*Mylopharyngodon piceus*), grass carp (*Ctenopharyngodon idella*), silver carp (*Hypophthalmichthys molitrix*), and bighead carp (*Hypophthalmichthys nobilis*), forming the concept of the “Four Major Domestic Fishes”.

Carp farming plays an important role in ancient Chinese history, but in modern times, it is still an important aquaculture object. According to the rough statistics of vertebrate Encyclopedia of China and zoography of China, there are 1050 species of freshwater fish in China, including 420 species of Cyprinidae, accounting for 40 %. Among the more than 110 species of freshwater fish with high economic value in China, Cyprinidae is the majority, with the most common carp varieties (lineages), and many varieties such as Yellow River carp, Xingguo red carp (*C. carpio* var. xingguonensis), and Purse red carp (*C. carpio* Red var. wuyuanensis) are unique to China.

Aquaculture is one of the fastest growing industries in China’s fishery structure. The production of bulk freshwater fish in China has shown explosive growth since the 1950s, and its growth rate is higher than the world average. The production of bulk freshwater fish occupies a dominant position in the world [3,4]. According to the data of China fishery Statistical Yearbook in 2024, the total output of aquatic products in China was 71.16 million tons in 2023, an increase of 3.64 % over the previous year; among them, the output of freshwater products was 35.31 million tons, a year-on-year increase of 3.65 %. In 2023, the output of carp was 2.87 million tons, a year-on-year increase of 1.06 %, accounting for 8.42 % of the total output of freshwater products, ranking fifth in the total output of freshwater fish.

The existing wild carp populations in China have been highly inbred, or hybridized with hybrid carp varieties that have escaped into natural water, resulting in continuous degradation of their germplasm. The existing wild carp populations have exposed disadvantages such as small size, reduced disease resistance and stress resistance, and poor meat quality and taste. The current situation of wild Yellow River carp is one of the typical cases.

In the early stage of breeding in China, the wild germplasm resources were not paid enough attention, and the control of hybrids was not strict enough. The wild Yellow River carp and a variety of carp germplasm resources were mixed, which destroyed the original Yellow River carp germplasm resources, resulting in quality decline, body color difference, disordered scales, body shape change and other phenomena [5]. Furthermore, for a long time, the destruction of ecosystem, environmental pollution and over exploitation of fishery resources are the reasons for the further degradation of aquatic biological resources, and many species are in danger of extinction [6]. In addition to carp, black carp [7,8], grass carp [9] and other important cultured fish species are also facing similar predicaments.

In the context of the environmental protection policy emphasizing sustainable development, with the enhancement of environmental awareness, aquaculture is developing in the direction of large-scale and intensive. However, high-density aquaculture has also brought a series of problems. For example, problems such as the decline of carp germplasm, frequent diseases and various new microbial diseases are emerging in endlessly, which have become the problems faced by aquaculture at present. *Herpesvirus disease*, *carp hemorrhagic disease*, *carp spring viremia* and other fish infectious diseases have a serious impact on fishery production. The report on aquatic animal health in China in 2023 shows that the economic losses caused by diseases in aquaculture are about 50 billion yuan. Excellent varieties are the cornerstone of the sustainable development of aquaculture. In addition to promoting the standard breeding technology of carp, it is also necessary to cultivate excellent varieties of carp that adapt to the breeding environment, grow faster, produce higher yield and have stronger disease resistance, so as to help the high-quality development of carp breeding industry.

By 2023, there were 121 excellent freshwater fish breeding varieties suitable for promotion approved by the National Certification Committee for Aquatic Stocks and Varieties (NCCASV), including 33 new varieties of carp, accounting for 27.27 %. Carp is the fish with the largest number of new varieties bred in China. The rapid growth of the yield of carp is due to the application of its genetic improvement achievements. Almost every year, carp appears in the list of excellent cultured fish varieties suitable for promotion approved by the National Certification Committee for Aquatic Stocks and Varieties, which shows that China attaches great importance to the germplasm innovation of carp.

2. Germplasm resources of carp

There are a wide variety of carp. There are wild carp with excellent traits in nature, which generally have a certain breeding scale in the local area. Examples include the South China carp (*Cyprinus carpio rubrofuscus*), Yunnan carp (*Cyprinus yunnanensis*), Barbless carp (*Cyprinus pellegrini*), Heilongjiang carp (*Cyprinus carpio haematopterus* Tem. etSchl), Purse red carp, Xingguo red carp, Oujiang color carp (*C. carpio* var. color), Xiangjiang wild carp (*C. carpio* L.), and the Yellow River carp, among others. They are valuable germplasm resources with excellent genetic characteristics, and are often used as breeding parents to carry out germplasm innovation research [10]. Beyond the wild carp germplasm resources in China, China has introduced foreign varieties such as the German mirror carp (*Cyprinus carpio*), the scattered scale mirror carp (*Cyprinus carpio* var. specularis), and the Ukrainian scaled carp (*Cyprinus carpio*). These carp varieties have the same excellent traits as the existing wild carp in China, are also excellent breeding objects, and have high genetic and breeding value. They can enrich the carp germplasm resource bank, provide valuable parent resources for the research and development of new varieties of carp, and have produced many varieties (lineages) by using a variety of technical methods (Table 1).

It is a common method in carp genetic breeding to integrate and purify the excellent traits within the species by using intraspecific germplasm resources through close hybridization and selective breeding. Through distant hybridization, the reproductive isolation between species can be broken, the genetic material between species can be exchanged, the germplasm resources between species can be utilized, the germplasm resource bank of genetic breeding can be expanded, the phenotype and genotype changes can be generated, the species diversity can be increased, and the hybrid varieties (lineages) with excellent characteristics can be developed.

In the previous century, Chinese research teams utilized the diploid red crucian carp (*Carassius auratus* red var., $2n = 100$) as the maternal parent and the diploid Xiangjiang wild carp (*Cyprinus carpio* L., $2n = 100$) as the paternal parent to create a fertile allotetraploid hybrid lineage through intergeneric distant hybridization. This is the first vertebrate tetraploid lineage obtained through distant hybridization internationally, and its genome structure and characteristics have now been revealed [11,12]. The same research team also established two types of improved diploid carp lineages through subfamily distant hybridization between Xiangjiang wild carp ($2n = 100$) (♀) and blunt snout bream (*Megalobrama amblycephala*, $2n = 48$) (♂) [13], offering new perspectives for variety improvement.

Currently, researchers have cultivated many new germplasm of carp with different ploidy through distant hybridization technology, including diploid, triploid and tetraploid carp [14]. This advancement not only enriches the genetic diversity of carp species but also provides valuable germplasm resources for future breeding programs.

3. Advances in carp germplasm innovation

After being approved and announced by the National Certification Committee for Aquatic Stocks and Varieties, there are a total of 33 excellent varieties of cultured carp suitable for promotion, including 22 selective varieties (GS-01 series), 8 hybrid varieties (GS-02 series), and 3 introduced varieties (GS-03 series).

The goal of breeding work is to cultivate new varieties with excellent

Table 1
Excellent farming carp varieties in China.

Variety Name	Year	Registration Number	Category	Parental Source
Xingguo Red Carp	1996	GS-01-001-1996	Selective variety	Wild Xingguo Red Carp
Purse Red Carp	1996	GS-01-002-1996	Selective variety	Wild Purse Red Carp
Jian Carp (*Cyprinus carpio* var. Jian)	1996	GS-01-004-1996	Selective variety	Purse Red Carp × Yuanjiang Carp
Cold-resistant Lineage of Purse Red Carp	1996	GS-01-006-1996	Selective variety	Heilongjiang Wild Carp × Purse Red Carp
Selective Lineage of German Mirror Carp	1996	GS-01-007-1996	Selective variety	German Mirror Carp
Ying Hybrid Carp	1996	GS-02-003-1996	Hybrid variety	Scattered Scale Mirror Carp (♀) × Carp and Crucian Carp Nuclear Transplant Fish (♂)
Feng Hybrid Carp	1996	GS-02-004-1996	Hybrid variety	Xingguo Red Carp (♀) × Scattered Scale Mirror Carp (♂)
Heyuan Hybrid Carp	1996	GS-02-005-1996	Hybrid variety	Purse Red Carp (♀) × Yuanjiang Carp (♂)
Yue Hybrid Carp	1996	GS-02-006-1996	Hybrid variety	Purse Red Carp (♀) × Xiangjiang Wild Carp (♂)
Triple Hybrid Carp	1996	GS-02-007-1996	Hybrid variety	Heyuan Hybrid Carp (♀) × Scattered Scale Mirror Carp (♂)
Furong Hybrid Carp	1996	GS-02-008-1996	Hybrid variety	Scattered Scale Mirror Carp (♀) × Xingguo Red Carp (♂)
German Mirror Carp	1996	GS-03-009-1996	Introduced variety	Introduced from Germany in 1984
Scattered Scale Mirror Carp	1996	GS-03-010-1996	Introduced variety	Introduced from the former Soviet Union in 1958
Songpu Mirror Carp	1997	GS-01-002-1997	Selective variety	Heilongjiang Wild Carp, Purse Red Carp, German Mirror Carp, Scattered Scale Mirror Carp
Wan'an Glass Red Carp	2000	GS-01-002-2000	Selective variety	Wild Glass Red Carp
Xiangyun Hybrid Carp	2001	GS-02-001-2001	Hybrid variety	Feng Hybrid Carp (♀) × Allotetraploids of Red Crucian Carp × Common Carp (♂)
Songhe Carp	2003	GS-01-002-2003	Selective variety	Heilongjiang Carp, Purse Red Carp, Scattered Scale Mirror Carp
Ink Dragon Carp	2003	GS-01-004-2003	Selective variety	Koi Carp
Yuxuan Yellow River Carp	2004	GS-01-001-2004	Selective variety	Wild Yellow River Carp
Ukrainian Scaled Carp	2005	GS-03-001-2005	Introduced variety	Introduced from Russia in 1998
Jinxin Carp	2006	GS-01-003-2006	Selective variety	Jian Carp
Songpu Mirror Carp	2008	GS-01-001-2008	Selective variety	German Mirror Carp Selective Breeding Lineage F_4
Furui Carp	2010	GS-01-003-2010	Selective variety	Jian Carp and Wild Yellow River Carp
Songpu Red Mirror Carp	2011	GS-01-001-2011	Selective variety	Cold-Resistant lineage of Purse Red Carp and Scattered Scale Mirror Carp
Oujiang Color Carp "Longshen No. 1"	2011	GS-01-002-2011	Selective variety	Breeding Population of Carp in the Oujiang River Basin, Zhejiang Province
Easy caught Carp	2014	GS-01-002-2014	Selective variety	Barbless carp, Heilongjiang Carp, and Scattered Scale Mirror Carp
Jinxin Carp No. 2	2014	GS-02-006-2014	Hybrid variety	Ukrainian Scaled Carp ♀ × Jinxin carp ♂
Furui Carp No. 2	2017	GS-01-003-2017	Selective variety	Jian Carp, Yellow River Carp, and wild populations of Heilongjiang Carp
Jinxin Red Mirror Carp	2018	GS-01-002-2018	Selective variety	Cultured population of German Mirror Carp
Hehua Carp "Ruyuan No. 1"	2021	GS-01-002-2021	Selective variety	Rice field breeding population of South China Carp (commonly known as Hehua Carp), and wild population of Beijiang carp from the Pearl River system
Jian Carp No. 2	2021	GS-01-004-2021	Selective variety	Cultured population of Jian Carp
Mirror Carp "Longke No. 11"	2022	GS-01-001-2022	Selective variety	Selective lineage population of German Mirror Carp
Carp "Longke No. 12"	2023	GS-01-004-2023	Selective variety	Wild population of Barbless carp from Yunnan Jinning Reservoir, and wild population of carp from the Tailai section of the Nenjiang River

traits, and in this process, it is necessary to select target traits from the germplasm gene bank. Therefore, in order to achieve the desired target trait, the first step is to have the gene exist in a selectable gene pool. In this regard, breeding workers have adopted methods such as distant hybridization and nuclear transfer to promote gene exchange between species, greatly enriching the gene pool of fish breeding.

In actual breeding work, the development of many new varieties is based on discovering variant lineages that exhibit specific traits, such as the Wan'an Glass Red Carp, Ink Dragon Carp, and Jinxin Red Mirror Carp, etc., which target special body colors. With the advent of the era of gene editing, the use of gene editing technology to precisely and selectively modify the receptor genome, achieving the addition and deletion of specific DNA fragments, or the deletion and replacement of specific DNA bases, can create mutant lineages that do not exist in nature in a short period of time, achieving the goal of genetic trait modification.

With the continuous development of biotechnology, fish genetic breeding technology has gradually evolved from conventional best linear unbiased estimation (BLUP), to molecular marker assisted breeding using modern molecular biology techniques, and now to genome-wide selection (GS) breeding technology using informatics methods in the genome era. In addition, there are methods such as sex-controlled breeding, hybrid breeding, gynogenesis breeding, polyploid breeding, and transgenic technology (Table 2).

3.1. Advances in traditional selective breeding of carp

Varieties with stable and excellent characters can be obtained through artificial system selective breeding, which can be used as parents for hybrid breeding or other genetic improvement breeding. As of 2023, the data approved and published by the National Certification Committee for Aquatic Stocks and Varieties showed that the suitable carp breeding varieties for promotion include Xingguo red carp [15],

Table 2
Carp breeding technology and its progress.

breeding techniques	start time[a]	process	representative of varieties
selective breeding techniques	Over 1800 years ago, the discovery of red or golden mutants of crucian carp and the selective breeding of goldfish (*Carassius auratus*) [118]	Best linear unbiased prediction (BLUP) method based on the theory of linear mixed models.	Furui Carp No. 2 (Variety Registration Number: GS-01-003-2017); Carp "Longke No. 12" (Variety Registration Number: GS-01-004-2023)
hybrid breeding techniques	In 1920, the hybridization of the ocean sunfish (*Mola mola*) [119]	Using allotetraploids of red crucian carp (♀) × common carp (♂) as the paternal parent and crossbred with diploid carp resulted in allotriploid offspring. Their sterile characteristics can avoid gene contamination and their growth rate is faster than that of the parents.	Xiangyun carp (Variety Registration Number: GS-02-001-2001); Jinxin carp No. 2 (Variety Registration Number: GS-02-006-2014)
gynogenesis breeding techniques	In 1932, experiments on the Amazon molly (*Mollienesia formosa*) [120]	Rapid purification of varieties, sex control, and screening of recessive pathogenic traits in genetic breeding	Jian carp (Variety Registration Number: GS-01-004-1996)
molecular marker assisted breeding techniques	In 1987, a high-body allogynogenetic silver crucian carp was selected from isoenzyme markers and other markers [121]	Mapping the genetic structure of complex traits through genome-wide association studies (GWAS)	Mirror carp "Longke No. 11" (Variety Registration Number: GS-01-001-2022); Jian carp No. 2 (Variety Registration Number: GS-01-004-2021)
genome-wide selective breeding techniques	In 2000, the genome sequencing of the first aquatic animal, the Tiger Puffer (*Takifugu rubripes*), was completed [122]	Construction of SNP map and high density genetic linkage map in carp	None
sex-controlled breeding techniques	In 1960, all-male tilapia was developed using interspecies hybridization [78]	A new method for producing all-female carp without exogenous hormones	None
polyploid breeding techniques	In 1959, the successful induction of polyploidy in *Gasterosteus aculeatus* [106]	The allotriploid carp was obtained by crossing the allotetraploid fish developed by distant hybridization breeding technology as male parent and female diploid fish	Xiangyun carp (Variety Registration Number: GS-02-001-2001)
transgenic techniques	In 1985, the world's first transgenic fish was born [123]	Successful development of genetically modified carp	None
gene editing techniques	In 2011, the myostatin gene (*mstn*) was knocked out in yellow catfish (*Pelteobagrus fulvidraco*) [124]	Knockout of bone related genes and muscle inhibitor genes in carp has been achieved	None

[a] The inception period applied in fish breeding technology.

Purse red carp [16], Jian carp [17], Cold-resistant lineage of Purse red carp [18], Selective lineage of German mirror carp [18], Songpu carp (*Cyprinus carpio* Songpu), Wan'an glass red carp, Songhe carp (*Cyprinus carpio* Songhe), Ink Dragon carp, Yuxuan Yellow River carp, Jinxin carp, Songpu mirror carp [19], Furui carp, Songpu red mirror carp, Oujiang color carp "Longshen No. 1", Easy caught carp, Furui carp No. 2, Jinxin red mirror carp, Hehua carp "Ruyuan No. 1", Jian carp No. 2, Mirror carp "Longke No. 11", and Carp "Longke No. 12", totaling 22 carp breeding varieties [20,21].

After long-term artificial selective breeding, most varieties have achieved the aggregation of excellent traits such as disease resistance, fast growth rate, and high nutritional value. However, the genetic diversity of some varieties has decreased, and breeding for complex traits has encountered genetic bottlenecks. Directional selection of traits is an indispensable part of breeding work. The main purpose of traditional selective breeding is to screen out individuals or populations with excellent genetic traits and enable them to inherit stably, which is the cornerstone for the multi generational utilization of excellent traits.

The common methods of fish selective breeding include population selective breeding, family selective breeding, and BLUP (Best linear unbiased prediction) based on the best linear unbiased prediction of breeding value. BLUP technology has been applied in the development of Furui carp and Furui carp No. 2. The premise of using BLUP Method is that the population is an open system. If there are not enough ponds and only a few families are produced, it is easy to cause inbreeding and germplasm decline, which will offset the advantages of BLUP method. Similarly, inbreeding decline is easily caused by inbreeding after multiple generations of selective breeding in family selective breeding and population selective breeding. In the development process of Jian carp, the combination of inbred mating and gynogenesis technology can quickly purify genes, stabilize genetic traits, eliminate the genes of recessive and harmful traits, and speed up the whole breeding process. In order to eliminate or reduce inbreeding decline caused by continuous selective breeding of multiple generations, the vitality can be significantly improved by establishing multiple families and crossing among multiple families [22].

3.2. Advances in hybrid breeding of carp

The excellent traits of parents can be integrated through hybrid breeding among different varieties, and most of the hybrids have obvious heterosis. According to the data approved and published by the National Certification Committee for Aquatic Stocks and Varieties, there are 33 kinds of excellent carp breeding varieties suitable for promotion, of which 8 are hybrids, accounting for 24.24 %. Hybrid breeding is one of the most basic and widely used breeding methods, which can exchange genes between parents. The purpose of hybridization is to integrate the excellent traits of parents and obtain heterosis. It plays an important role in the creation of fish germplasm.

Due to the characteristics of hybrids, self-crossing of their own species or escape to natural waters to hybridize with other fish may cause serious genetic pollution, which will have an unexpected impact on the natural environment and genetic diversity of wild varieties [23]. A typical example is the germplasm degradation of the Yellow River carp. Therefore, it is absolutely necessary to prevent the escape of hybrids in the farming process, and strengthen the awareness of biological prevention in the use and promotion, and protect the germplasm gene bank. However, if the offspring are sterile triploid fish, such as "Xiangyun crucian carp", "Xiangyun carp", and "Xiangyun crucian carp No. 2", etc., there will be no such problem, which will solve the problem that hybrid carp cannot be put into natural water.

According to the distance of the genetic relationship between the hybrid parents, hybridization can be divided into close hybridization and distant hybridization. Close hybridization is intraspecific hybridization. Under the influence of different environments, the traits of the same species of fish are also very different. Carp is the only species with obvious lineages and varieties. Distant hybridization refers to the hybridization between species, genera and even between biological types with more distant relationships. Because of the close genetic relationship, intraspecific hybridization does not produce offspring infertility or inability to mate, which is a commonly used method in hybrid breeding. Because carp is a species with different varieties, its intraspecific hybridization is very successful [24].

A large number of hybrid breeding of carp have been carried out in China, and 8 new varieties have been approved by the National Certification Committee for Aquatic Stocks and Varieties, including Ying hybrid carp, Feng hybrid carp, Heyuan hybrid carp, Yue hybrid carp, Triple hybrid carp, Furong hybrid carp, Xiangyun carp, and Jinxin carp No. 2, as well as Songpu mirror carp, Songpu red mirror carp [25], and Easy caught carp, which have been obtained by combining hybrid breeding technology with selective breeding technology. The variation range of offspring produced by close hybridization is not large, but if the parents are properly selected and the mating group is reasonable, the ideal results can be obtained.

Since the late 1950s, China has also carried out a large number of fish distant hybridization experiments, most of which are between subfamilies or genera, and many hybrid combinations have heterosis (hybrid vigor) [26]. In addition to heterosis, distant hybridization can also produce polyploidy, especially in hybridization between different subfamilies of Cyprinidae, polyploid phenomenon is common. For instance, polyploidy has been obtained in hybrid combinations such as grass carp (♀) × topmouth culter (*Culter alburnus*) (♂) [27], Japanese white crucian carp (*Carassius auratus cuvieri*) (♀) × blunt snout bream (*Megalobrama amblycephala*) (♂) [28], red crucian carp (♀) × common carp (♂) [29], and common carp (♀) × blunt snout bream (♂) [30]. Examples include allotetraploids of red crucian carp (♀) × common carp (♂) lineages [29], and autotetraploids of common carp (♀) × blunt snout bream (♂) lineages [31], etc.

Currently, only fish have been reported to establish distant hybridization lineages among animals, as most other animals cannot produce fertile offspring through distant hybridization. Among them, the developed triploid hybrids usually have heterosis. They integrate the favorable genes of both parents, show better growth traits and stronger disease resistance, and show stronger vitality than diploid parents [32]. The gene redundancy caused by the introduction of additional chromosome sets can protect them from harmful recessive mutations [33]. Domestic scholars [26] developed allotetraploids of red crucian carp (♀) × common carp (♂) with stable genetic traits using red crucian carp as maternal parent and Xiangjiang wild carp as paternal parent. In production, the allotetraploid hybrids was used as the paternal parent to hybridize with the female diploid Japanese white crucian carp and Feng hybrid carp respectively, and the allotriploid offspring with large-scale infertility, good growth traits and rich nutritional value were bred [34], which were named "Xiangyun crucian carp" and "Xiangyun carp", respectively. Their growth traits and stress resistance were better than their parents. Because it is sterile triploids, it does not need to consider the damage to the natural environment and genetic diversity of wild varieties caused by escape, which is of great significance in fish genetic breeding.

At present, there are mainly two kinds of studies on the genetic effects of hybrid breeding: heterosis and the molecular mechanism of distant hybridization. Heterosis refers to the phenomenon that hybrid offspring are superior to their parents' average in growth, survival, reproductive ability or production performance [35]. In the past, the understanding of heterosis was mainly based on phenotype, and models such as dominance hypothesis, super dominance hypothesis, and epistasis hypothesis were produced. Some scholars believe that these hypothetical models essentially limit the interpretation of data, and these terms should be abandoned [36]. With the advancement of molecular biology, epigenetics and genomics, scientists began to use these studies to explain the mechanism at the molecular level. These data will facilitate the establishment of genetic and mathematical models to explain the vitality phenotypes at different developmental stages [37]. At present, it is considered that heterosis is the result of genome interaction [38].

The selection of hybrid parents is crucial to the success of hybridization. Some scholars have summarized the genetic and reproductive laws of fish distant hybridization [26]. The success rate of distant hybridization is related to the number of chromosomes, karyotype, genetic composition and the coordination between nuclear-nuclear and nuclear-cytoplasmic.

Due to the existence of interspecific reproductive isolation, it is difficult to form fertile lineages by distant hybridization. Therefore, in the study of distant hybridization of fish, the creation of bisexual fertile hybrid lineages is a highly exploratory and innovative research work. Previously, there was a lack of genetic and reproductive laws for reference to guide the directional breeding of distant hybridization, and it was difficult to predict what type of offspring might appear in the offspring of distant hybridization. If breeding merely based on phenotypic advantage complementation is blind, it will easily lead to the death of hybrid offspring, no heterosis, and it is difficult to form lineages and other adverse results. To explore the genetic and reproductive laws of fish distant hybridization, and to summarize the goal of complementary phenotypic characteristics into an orderly genetic basis track, has an important guiding role for the research of fish genetics and breeding [26].

3.3. Advances in gynogenesis breeding of carp

Gynogenesis is a reproductive mode in which the egg is activated by sperm and the development is mainly controlled by maternal genetic material. The gynogenesis of fish can be divided into natural gynogenesis and artificially induced gynogenesis. There are more than ten species of fish in nature that can undergo natural gynogenesis [39].

Artificially induced gynogenesis refers to a breeding technique in which eggs are activated by the genetic material inactivation of sperm, and zygotes are mainly controlled by female pronucleus to develop into embryos. In the past, it was believed that sperm only activated the development of egg cells and did not participate in inheritance. However, with the deepening of research, Jiang et al. (1983) found the rapid growth response of the population and some individuals with paternal genetic traits in the gynogenetic offspring of silver crucian carp. They believed that in the gynogenetic reproduction of silver crucian carp, heterologous sperm could not only stimulate the development of eggs, but also make the DNA fragments of the paternal parent (red carp) randomly incorporated into the genome of the maternal parent, resulting in the allogynogenetic effect, which accelerated the growth of the offspring and appeared paternal traits [40].

Artificial gynogenesis technology can rapidly purify varieties, control sex, and screen recessive pathogenic traits. Some gynogenetic populations also exhibit enhanced disease resistance [41]. Currently, artificial gynogenesis technology has been successfully applied in the breeding of many new varieties, including Jian carp, Xingguo red carp gynogenetic lineage, Jian carp No. 2, Cold-resistant lineages of Purse red carp, Songpu carp, Songhe carp and so on, which are used for rapid purification to obtain genetically stable new varieties, and the all-female Jinxin carp is also cultivated in combination with sex reversal technology.

There are also a certain proportion of male individuals in some gynogenetic fish such as Amazon molly (*Poecilia formosa*) and red crucian carp developed from natural gynogenesis caused by distant hybridization [42–44]. Silver crucian carp is a naturally gynogenetic fish [45]. Male individuals account for 10 %–20 % of the self-crossing offspring of silver crucian carp. However, when red crucian carp sperm is used to activate the gynogenetic development of silver crucian carp eggs, males only account for 2.5 %. If activated by Xingguo red carp sperm, all the gynogenetic offspring of silver crucian carp are female. This indicates that the sex of silver crucian carp is determined by the paternal genetic material [40].

Artificial induction of gynogenesis was first demonstrated by Oppermann in 1913 [46]. However, even after more than a century, its molecular mechanisms remain unclear. The low survival rate of gynogenesis and the difficulty in evaluating gynogenesis still limit the application of gynogenesis technology, which makes it difficult to obtain enough gynogenetic population to meet the actual breeding needs, and it is difficult to determine whether there are hybrid individuals in gynogenetic population. However, if the gynogenesis is activated by distant sperm with different chromosome numbers from the egg donor, the gynogenetic offspring can be determined by observing the chromosome numbers [41].

3.4. Advances in molecular marker-assisted breeding of carp

Molecular marker assisted breeding uses the characteristics of close linkage between molecular markers and genes that determine target traits. Through DNA molecular markers, specific genes or genomes can be tracked to achieve the purpose of selecting target traits, making the breeding process more accurate and efficient. At present, molecular marker technology has developed to the third generation, single nucleotide polymorphism (SNP) marker [47]. These technologies can be used not only for genetic relationship analysis [48], lineages identification [48], and genetic map construction [49], but also for marker-assisted selection (MAS) [50]. Currently, SNPs have gradually replaced low-throughput molecular markers such as AFLP (Amplified Fragment Length Polymorphism), RAPD (Random Amplified Polymorphic DNA), microsatellite markers, and has become the mainstream [51], playing an important role in the construction of high-density gene linkage map.

In 2004, the first genetic linkage map of carp was constructed [52]. The genetic linkage map is the basis for further mapping quantitative trait loci (QTLs) related to important economic traits. The high-density genetic linkage map will promote the fine mapping of QTLs for important economic traits in carp. In China, researchers have constructed genetic linkage maps of carp with different densities. The Yellow River carp is one of the four famous freshwater fishes in China. Domestic scholars have carefully mapped the growth related QTLs of the Yellow River carp [53]. Additionally, domestic scholars have also made fine mapping of QTLs for growth related traits in Yangtze carp [54].

During the development of Jian carp No. 2, mirror carp “Longke No. 11” and other varieties mentioned above, molecular marker assisted breeding technology was also used to select the genes that controll their target traits. During the development of Jian carp, domestic scholars used DNA fingerprint analysis and allele variable analysis to assist in the analysis of genetic relationship and identification of lineages [22]. By using SNP markers for the growth-related genes of Jian carp, Jian carp No.2 was bred with an average growth rate of 17.70 % higher than that of Jian carp. In the breeding process, simple sequence repeats (SSR) loci were also used to determine the genetic distance of parents, reducing the risk of inbreeding [55]. During the development of Jian carp No. 2, the growth related genes of Jian carp were isolated, and the SNP loci were searched and screened, so as to select and retain the offspring. During the development of mirror carp “Longke No. 11”, aiming at the pathogen of herpes virus type III (CyHV-3) and scaleless traits, the domestic scientific research team analyzed the genetic mechanism of resistance to CyHV-3 in carp, screened the genetic markers related to disease resistance [56], and bred mirror carp “Longke No. 11″ with significant disease resistance advantage by using population selective breeding combined with molecular marker assisted breeding technology. Under the same culture conditions, compared with the German mirror carp selective breeding lineage, the survival rates of 24-month-old pond and cage culture increased by 14.80 % and 31.50 %, respectively. The proportion of scaleless individuals increased by 23.30 %, accounting for 60.0 %. Mirror carp “Longke No.11″ is the first new variety of carp with disease resistance in China with disease-resistant traits as the breeding target. Disease resistance cannot be judged by phenotype, so it is of great significance to develop lineages with disease resistance related genes by developing gene markers controlling disease resistance and molecular marker assisted breeding.

3.5. Advances in genome-wide selection breeding of carp

In 2001, Meuwissen et al. [57,58] first proposed the method of genomic selection (GS). The genome-wide selection breeding technology is marker assisted selection within the whole genome, which can accurately estimate the genetic estimated breeding value (GEBV) based on the whole genome genetic markers. The biggest difference from the traditional marker assisted selection is that genome-wide selection not only depends on a set of gene loci, but also jointly analyzes the information of the whole genome, so as to predict the value of individual sports species more accurately. GS not only uses linkage disequilibrium (LD) and additive genetic relationships, but also uses co segregation to capture QTL relationships [59]. With the progress of sequencing technology and high-throughput SNP genotyping technology, genome-wide selective breeding technology has been rapidly developed and applied in aquaculture. At present, the genome-wide selection breeding of aquatic animals is mainly aimed at the resistance to infectious diseases, ketone yield and meat yield [60–64].

Through MAS and GS methods, modern selective breeding can go deep into the gene level of controlling target traits rather than traditional phenotypic selection. Both methods require determining the genetic structure of the target traits.

In 2009, Chinese scientific research institutions launched the “Carp Genome Project” and completed the whole genome sequencing of carp in 2011 [65]. Additionally, as of 2023, the National Center for Biotechnology Information (NCBI) has recorded genome data for over 40 species of Cyprinidae fish.

Genome-wide association studies (GWAS) is a method used to identify associations between the genome and traits/diseases. The technology of QTL mapping based on co-separation of QTL and linkage markers has been developed for nearly a century. As a rising star, GWAS has only developed for more than 20 years, but it has also become an important means to study the genetic structure of complex traits, and has had a significant impact in many fields, such as population genetics, complex trait genetics, epidemiology, social science and medicine [66]. Nowadays, GWAS has been used to identify genes related to important economic traits and pathogenic characteristics of cultured aquatic animals, which plays an important role in the development of molecular markers.

Since the construction of the first genetic linkage map of carp, a large number of QTL mapping studies have been carried out [67], such as the important economic quantitative trait loci related to the pathogenic gene of abnormal red skin color of Yellow River carp [68], the resistance to Aeromonas hydrophila infection [69], growth traits [54], feed conversion efficiency [70], head size [71], cold tolerance traits [72], and muscle fiber have been identified [73], many of which are located by GWAS, and some of these loci have been applied in the actual molecular marker assisted breeding.

Because the growth traits in transgenic Yellow River carp are still significantly separated, domestic scholars have identified the growth related genes of transgenic Yellow River carp through GWAS, and used this for molecular marker assisted selection to cultivate a transgenic Yellow River carp lineages with stable production performance and uniform phenotype, which is named Guan carp [74].

The genomic selection (GS) of carp is mainly used in the study of growth traits [67]. Some scholars used the GS methods to predict the drug resistance genes of koi carp herpesvirus disease. The accuracy of correctly identifying koi carp herpesvirus disease resistant animals is 8 %–18 % higher than the best linear unbiased prediction of pedigree (pBLUP) [75]. GS has great potential in genetic improvement of carp, especially in improving breeding efficiency [76]. Although the genome maps of a large number of Cyprinidae fishes have been deciphered, there are few reports on the application of genome-wide selective breeding technology in carp breeding [77].

3.6. Advances in sex-controlled breeding of carp

Sex control refers to the technology that enables female animals to produce the desired sex offspring or change the gender of the receptor through human intervention in the normal reproductive or developmental process of animals. Its purpose is to obtain the desired sex offspring or individuals. Sex control of fish can be achieved through a variety of ways, such as classic reproductive endocrine regulation, interspecific hybridization to control sex [78,79], artificially induced gynogenesis to control sex, temperature to control sex [80] and so on. With the in-depth study of the genetic mechanism of fish sex, sex marker assisted breeding and genetic engineering have become possible to control sex. In the sex-controlled breeding of carp, sex control is mainly through reproductive endocrine regulation and artificial induction of gynogenesis. In recent years, genetic engineering technology has been used to control the sex of carp [81].

Many fish have obvious sexual dimorphism in growth rate and individual size, which is closely related to a variety of important economic traits. Through gender control, the dominant unisexual population can be cultivated to give full play to the advantages of production traits affected by gender and obtain higher economic benefits. The sexual dimorphism in growth rate results from the difference in gonadal maturation time between male and female individuals. In general, the growth rate is slow when gonads develop early, and fast when gonads develop late. This is because most nutrients are used for gonadal growth during gonadal development.

Fish have diverse sex determination systems, and there are unique ways of sex differentiation such as natural sex reversal [82]. In teleosts, sex determination is generally the result of the joint action of genetic factors and environmental factors, and is easily affected by environmental factors [83,84]. A variety of environmental factors such as hormones, temperature, pH, density, light intensity, hypoxia and so on may affect the sex determination pathway. Sex differentiation in fish is regulated by the reproductive endocrine system. Exogenous steroid hormone treatment at the early stage of gonadal development can induce sex reversal in fish [85]. Since the 1960s, sex reversal based on hormones has been successfully tested in a variety of fish and has been widely used [86–88], including carp [89]. Considering that the direct use of exogenous hormones to produce unisexual fish fry may cause environmental risks and potential food safety hazards [90], and the sex of unisexual fish produced by this method may restore genetic sex, at present, aquaculture no longer uses this technology to directly cultivate unisexual fish, but uses the sex reversal parent fish induced by exogenous hormones to produce fry [80]. Using sex reversal parent fish to produce all-female offspring and super male offspring has been applied in aquaculture breeding [91,92]. In addition, some scholars have successfully developed a new method of producing all-female carp without using any exogenous hormones by using genetic engineering technology [81].

In the sex-controlled breeding of carp, Chinese scholars have combined artificial gynogenesis and sex reversal technology to establish a breeding technology for rapid production of all-female fish [93]. With the in-depth study of the existence of sexual dimorphism in fish, X-chromosome and Y-chromosome linked genetic marker assisted fish sex control biotechnology has been developed, which provides a technical route for fish sex-controlled breeding [94,95]. At present, the research on sex-controlled mainly focuses on the sex determination system (SDS) and the genetic and molecular mechanisms of sex differentiation [96–99]. Artificial gynogenesis is also a means to prove the sex determination system [100]. During artificial gynogenesis, if it is a fish with XY sex determination system, it will get XX all-female offspring. In ZW sex determined fish, in theory, only ZZ males and WW females can be produced, and it is impossible to produce all-female offspring.

3.7. Advances in polyploid breeding of carp

Polyploid is an organism with three or more complete sets of chromosomes. It exists widely in animals and plants and is an important way of speciation [101,102]. Salmon (*Salmo salar*) and trout (*Oncorhynchus mykiss*) are ancient autotetraploids [103,104], while carp and crucian carp are ancient allotetraploids [105]. These ancient tetraploids have completed the diploid transformation in their evolutionary process. Compared with its diploid ancestors or related species, polyploids often show excellent economic traits such as fast growth, strong adaptability and disease resistance [33].

Polyploid breeding refers to the use of artificially induced chromosome doubling or natural chromosome doubling and other methods to obtain polyploid breeding materials through cell genome doubling, so as to select excellent varieties that meet people's needs. The genome of fish has great plasticity and is easy to double. There are many applied researches on fish polyploidization. The first report of successful induction of artificial polyploid fish was *Gasterosteus aculeatus* in 1959 [106]. So far, successful induction has been reported in a variety of salmon and trout, carp, crucian carp, grass carp, silver carp, *Paramisgurnus dabryanus*, *Paralichthys olivaceus*, *Pagrosomus major*, *Monopterus albus*, etc. [107]. In addition, distant hybridization is also an important way to induce polyploidy. A domestic research team has developed an allotriploid fish varieties, named Xiangyun carp, with diploid Feng carp as maternal parent and allotetraploids of red crucian carp (♀) × common carp (♂) as paternal parent by combining cell engineering technology and sexual hybridization. It was approved by the National Certification Committee for Aquatic Stocks and Varieties in 2001, and the variety registration number is GS-02-001-2001.

Because of the sterility of allotriploid fish, it is of great significance in protecting natural germplasm resources and preventing gene hybridization. Triploid fish can provide more niche for donor reproductive stem cells due to their infertility, which is widely used in germ cell transplantation technology, and also a way to prevent gene pollution of wild germplasm caused by transgenic fish.

3.8. Advances in the application of transgenic technology in carp germplasm innovation

The essence of fish genetics and breeding is to combine the excellent genes in the gene pool, and then make the excellent genes can be stably inherited. Transgenic breeding provides a way to realize gene transportation and has become an effective means of character improvement. Transgenesis refers to the technology that uses gene transfer technology to introduce foreign genes into the genome of the recipient, enabling stable integration and inheritance to offspring. Fish is a relatively primitive group of vertebrates, with large genetic plasticity, large amount of eggs, easy access to fertilized eggs, rapid in vitro development of embryos, convenient microscopic operation, and good economic value. Therefore, fish has become a good material for the development of transgenic animals and the cultivation of excellent varieties.

China was the first country to start the breeding research of transgenic fish. In 1985, Zhu Zuoyan and others developed the world's first transgenic fish. Since then, they have also established several theoretical models of transgenic fish [108,109]. Subsequently, countries all over the world have carried out the research on transgenic fish. In 1991, Zhu Zuoyan constructed an “all-fish” gene construct consisting of all the genetic elements of Chinese Cyprinidae fish. He introduced the grass carp growth hormone gene driven by the carp β-actin promoter into fertilized eggs of Yellow River carp. The transgenic Yellow River carp grew fast and had high feed conversion efficiency. Under the same breeding conditions, the average growth rate of transgenic carp was 52.93–114.92 % faster than that of the control Yellow River carp. In that year, it could reach the market specification, shorten the breeding cycle by half, reduce the breeding cost and risk, and greatly reduce the labor intensity. This transgenic fish was named Crown carp. In 2000, the Crown Carp [110] transformed with “all-fish” growth hormone gene (GH) completed a pilot test, including food safety and ecological safety evaluation [111]. The triploid transgenic Ji carp with rapid growth, high food utilization rate and sterility was developed by allotetraploids of red crucian carp (♀) × common carp (♂) crossing with Crown Carp, thus fundamentally solving the ecological risk problem [112]. Some scholars believe that from a scientific point of view, the industrialization conditions of fast-growing transgenic “all-fish” GH gene carp are fully mature.

The most important feature of transgenic technology is that it can break the barrier between species, expand the range of available genes, and accurately select and operate a gene, which is unmatched by traditional breeding. However, if the transgenic species escape, it will cause serious genetic pollution to the nature, and may produce potential ecological risks. The consequences are unimaginable. It is particularly important to control the risk of transgenic species. Limiting the terminal products of transgenic fish to sterile triploid fish can fundamentally solve the ecological safety problem of transgenic fish, and using “all-fish” gene as exogenous gene can minimize the food safety risk of transgenic fish.

3.9. Advances in the application of gene editing technology in carp germplasm innovation

Genome editing, also known as genome engineering or gene editing, is a type of genetic engineering, which refers to a technology of DNA insertion, deletion, modification or replacement in the living genome. From the first in vitro validation of zinc finger nucleases (ZFNs) in 1996 to the emergence of CRISPR (Clustered Regularly Interspaced Short Palindromic Repeats)/Cas9 (CRISPR-associated 9) technology in 2012 [113,114], gene editing technology has advanced rapidly, editing efficiency and accuracy have been continuously improved, and the application field has been continuously expanded. It makes it relatively simple to carry out functional genome research in fish, and makes it possible to accurately edit the specific position of the target genome.

Some scholars knocked out bone-related genes such as *SP7*, *bmp2a*, *Runx2*, and the muscle growth inhibitor gene myostatin (*mstn*) in carp, and obtained bone defect carp and carp with more muscle [115]. In 2022, some domestic scholars achieved the elimination of intermuscular spines in blunt snout bream through gene editing technology [116], and developed blunt snout bream without intermuscular spines. In 2023, a research team developed the spineless crucian carp [117]. This achievement is expected to be applied in carp, black carp, grass carp, silver carp, bighead carp and other important Cyprinidae fishes. Even if genetically modified varieties cannot enter the market for the time being due to food safety and ecological risks, when relevant problems are solved, the rapid and accurate character changes brought by genetically modified varieties will effectively improve the breeding speed and quality.

Compared with transgenic technology, gene editing technology only edits the existing genes of organisms, which is relatively accurate and does not introduce foreign genes, and is relatively more reliable in terms of genetic stability.

4. Prospects for germplasm innovation in carp

After entering the 21st century, the role of aquaculture in the supply of aquatic products in the world has become a consensus, and germplasm innovation determines the quality and yield of aquatic products. After long-term efforts, fish breeding has been combined with modern life sciences, and a variety of breeding technologies have been established, especially with information technology to develop genome-wide selection technology.

The goal of breeding is to improve yield and quality. In terms of improving the yield, the existing new varieties of carp are basically around the growth related, disease resistance, feed conversion efficiency and other traits to improve the yield. In terms of improving quality, few varieties have been bred around quality related traits such as flavor amino acid content, number of intermuscular spines, and meat quality or muscle fiber, but these traits seriously affect the edible and processing value of carp, making the price and sales of carp perform poorly in the consumption field.

The output of carp accounts for 8. 42 % of the total output of freshwater products. “Sweet and sour carp” is widely known in northern China, but it is very rare on the table in southern China. Carp is fat, tender and nutritious. However, carp have many intermuscular spines, rough meat and heavy earthy smell, which are the most important factors affecting carp consumption. The yield of carp is very high, but if we want to further improve the output value of carp, on the basis of the increase in yield, the breeding of taste, intermuscular spines and other traits that affect consumption is the direction of carp breeding in the future. The common growth of quantity and quality will effectively improve the status of carp in the field of consumption.

The economic losses caused by diseases in aquaculture are huge, but the first disease-resistant variety of carp in China did not appear until 2022. Breeding new varieties with disease-resistant traits is important to reduce production costs and labor burdens and improve carp production.

Among the new varieties of fish, the number of new varieties cultivated by modern breeding technologies (such as sex-controlled breeding, marker-assisted selection breeding and genomic selection breeding technology) is far lower than that cultivated by traditional and classical breeding technologies (such as selective breeding, hybrid breeding, gynogenesis breeding and polyploid breeding). According to the data approved and released by the National Certification Committee for Aquatic Stocks and Varieties, there were 33 common carp varieties from 1996 to 2023. However, only the easy catch carp (Variety Registration Number: GS-01-002-2014), Jian carp No. 2 (Variety Registration Number: GS-01-004-2021), and mirror carp “Longke No. 11” (Variety Registration Number: GS-01-001-2022) used modern breeding techniques in the breeding process, and all of them were molecular marker assisted breeding techniques, indicating that the practical application of these modern breeding techniques was not much, and the degree of combination of traditional and classical breeding techniques with modern biological techniques was not close.

Looking back at the germplasm innovation process of carp and other fish species, we found that there are still many genetic laws and molecular mechanisms that need to be utilized in breeding techniques that have not been studied.

In terms of hybrid breeding, the success rate of distant hybridization is related to the chromosome number of hybrid parents [26]. When the chromosome numbers of two kinds of fish are the same or similar, hybrid breeding technology may break the reproductive isolation and obtain viable offspring. The degree of chromosome matching of hybrid parents and the matching relationship of chromosome number of hybrid parents will affect the coordination of nucleus-nucleus and nucleus-cytoplasm of hybrid F_1. The coordination of nucleus-nucleus and nucleus-cytoplasm is related to the survival rate of hybrid F_1, and the molecular mechanism behind this law remains to be studied. The study of such laws will avoid the blindness of the death of hybrid offspring. Many studies on nuclear-cytoplasmic hybridization and gynogenesis have suggested that the mitochondrial genome of paternal lineages has an important impact on the traits of offspring. Clarifying its mechanism can provide new ideas for breeding.

Additionally, the mechanism of gynogenesis breeding technology has not been clarified. At present, gynogenesis is faced with the problem of low fertilization rate and lower emergence rate in practical application. The farther the paternal and maternal relationship of gynogenesis is, the lower the fertilization rate and emergence rate are. This trend is the same as that of hybridization, suggesting that the success rate of gynogenesis may be related to sperm egg recognition. The research on the mechanism of gynogenesis can improve the success rate of gynogenesis technology and enhance its practicability. Studies on gynogenesis technology have shown that the traits of offspring may be controlled by the paternal genome, but the mechanism remains unclear, which may be due to a small amount of paternal DNA entering the egg cell during fertilization.

Finally, molecular marker-assisted selection (MAS) and genomic selection (GS) breeding techniques, which have higher relative cost and technical threshold, are rarely used, especially GS. The application of these techniques will enhance the accuracy of breeding. However, the new germplasm of cultured fish obtained by using transgenic technology and gene editing technology has not been legally approved for marketing, and there are few researches on carp in this aspect. Gene editing technology is of great significance in reverse genetics. At the same time, a large number of growth-related genes and disease-resistant related genes have been identified. Gene editing for these genes is of great significance to the germplasm innovation of carp.

Overall, there are relatively few studies on disease-resistant and quality related traits of carp varieties, but the future is promising. The basic research of fish genetics and breeding and the comprehensive application of genetic breeding technology are the direction of future efforts.

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CRediT authorship contribution statement

Zhipeng Yang: Conceptualization, Writing – original draft, Writing – review & editing. **Qinglin Xu:** Data curation, Formal analysis. **Xin Wang:** Data curation, Formal analysis. **Huan Liu:** Data curation, Formal analysis. **Yalan Zhang:** Data curation, Formal analysis. **Wei Chen:** Data curation, Formal analysis. **Sijin Fan:** Data curation, Formal analysis. **Junfeng Wu:** Data curation, Formal analysis. **Yaohui Li:** Data curation, Formal analysis. **Huan Zhong:** Data curation, Formal analysis. **Fangzhou Hu:** Data curation, Formal analysis. **Ming Wen:** Data curation, Formal analysis. **Kaikun Luo:** Data curation, Formal analysis. **Shi Wang:** Conceptualization, Writing – original draft, Writing – review & editing, Funding acquisition.

Declaration of competing interest

All authors declare that there are no competing interests.

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