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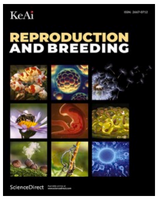

Germplasm innovation of large yellow croaker and its research progress

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ABSTRACT

Large yellow croaker is one of the species with the highest production of marine fish culture in China. Germplasm resources are the indispensable material basis for the healthy and sustainable development of large yellow croaker aquaculture industry. It is of great significance to systematically carry out the collection and preservation, identification and evaluation, and germplasm innovation of large yellow croaker germplasm resources. This paper summarizes the progress in the conservation and exploitation of large yellow croaker germplasm resources and germplasm innovation. Around the main line of conservation of large yellow croaker germplasm resources and the creation of good varieties, the development direction of creating major new varieties for complex economic traits (e.g., disease resistance, stress resistance, quality, and feed utilization efficiency, etc.) was proposed, which provided theoretical support for realizing the significant improvement of the coverage rate of improved varieties of large yellow croaker and the healthy development of large yellow croaker industry.

Large yellow croaker (*Larimichthys crocea*) is a critical fishery resource in the southeastern coastal regions of China, ranking first among the "Four Major Sea Products" of the East China Sea. It is the primary species for offshore fishing. In the 1970s, the fishery resources of large yellow croaker were rapidly depleted. With the unremitting efforts of Ningde aquatic science and technology workers with Mr. Liu Jiafu as an outstanding representative and the strong support of management departments at all levels, Ningde City, Fujian Province, successfully realized the artificial propagation and large-scale seed breeding of large yellow croaker in early 1990, gradually built a mature industrial technology support system, and fully realized the industrialization of large yellow croaker aquaculture. The rapid rise of large yellow croaker aquaculture industry has formed the largest core aquaculture area of large yellow croaker in China along the east coast of Fujian Province, driving the tide of artificial aquaculture of marine fish in China and becoming a model of "replacing fishing with aquaculture" in China. After more than three decades of rapid development, the large yellow croaker aquaculture industry has formed an annual output of 0.28 million tons in 2023, accounting for 13.66 % of the national marine fish aquaculture production [1]. The flourishing of the large yellow croaker farming industry has also driven the rapid development of various related industries, including farming equipment, bait and feed, product processing, domestic and international trade, tourism and leisure, hotels and catering in the upstream and downstream of the industrial chain, forming a group of national and provincial leading agricultural industrialization enterprises. This has made significant contributions to economic development, personnel employment and fishermen's poverty alleviation and prosperity [2]. With the rapid development of large-scale cultivation of large yellow croaker, artificial cultured large yellow croaker has generally appeared such phenomena as slower growth rates, smaller individual sizes, decreased muscle quality, weakened disease and stress resistance, as well as early

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maturation, have generally become prevalent in cultured large yellow croaker. These phenomena adversely affect the healthy development of the industry and may be closely related to the reduced genetic diversity of the farmed large yellow croaker. Therefore, research and protection of large yellow croaker germplasm resources is urgently needed. Germplasm resources are essential for the healthy and sustainable development of the large yellow croaker farming industry. The exploration and utilization of excellent germplasm resources are crucial for ensuring the supply of high-quality aquatic protein in China. The innovation of large yellow croaker germplasm resource is the material basis for ensuring a stable supply of high-quality protein, and the innovation of aquatic core breeding technologies is an important measure to enhance the competitive strength of seed industry power. The breeding of excellent new varieties of large yellow croaker is an important cornerstone for the sustainable development of the large yellow croaker aquaculture industry. This paper reviews the research progress of large yellow croaker in the protection and innovation of germplasm resources. It not only introduces the application of various genetic technologies such as selective breeding, hybrid breeding, gynogenesis breeding, molecular marker-assisted breeding, and genome-wide-selective breeding in germplasm innovation of large yellow croaker, but also discusses the effective measures for the protection of large yellow croaker germplasm resources, providing theoretical support for the healthy development of the large yellow croaker industry.

1. Conservation, development and utilization of large yellow croaker germplasm resources

1.1. *Taxonomic status, geographic distribution and populations of large yellow croaker*

Large yellow croaker belongs to Perciformes, Sciaenidae, *Larimichthys*. It is a significant economic fish species in the Northwest Pacific Ocean, particularly in China, North Korea, and South Korea. It is predominantly found in China's coastal waters, from the southern Yellow Sea, through the East China Sea and the Taiwan Strait, to the South China Sea near the Leizhou Peninsula, generally within the 60 m isobath. Historically, the main spawning, overwintering, and fishing grounds of large yellow croaker include Jiangsu Lvsiyang spawning ground in the Yellow Sea; the Yangtze River Estuary—Zhoushan outer overwintering ground, Zhoushan fishing ground, Zhejiang Daiquyang spawning ground, Zhejiang Maotouyang spawning ground, the Oujiang River—Minjiang River Estuary outer overwintering ground, and Fujian Guanjingyang inner Bay spawning ground in the East China Sea; in the South China Sea, the Nan'ao Island—Shanwei outer sea fishing ground east of the Pearl River Estuary in Guangdong, and the spawning grounds around Naozhou Island in western Guangdong [3]. Due to geographical distribution differences, large yellow croaker shows a series of geographical diversity in morphology, age of sexual maturity and other aspects, forming distinct populations and groups. To date, there is still academic debate regarding the division of geographical populations and spawning groups of large yellow croaker. Historically, the classification proposed by Tian Mingcheng [4] in 1962 has been widely used. This

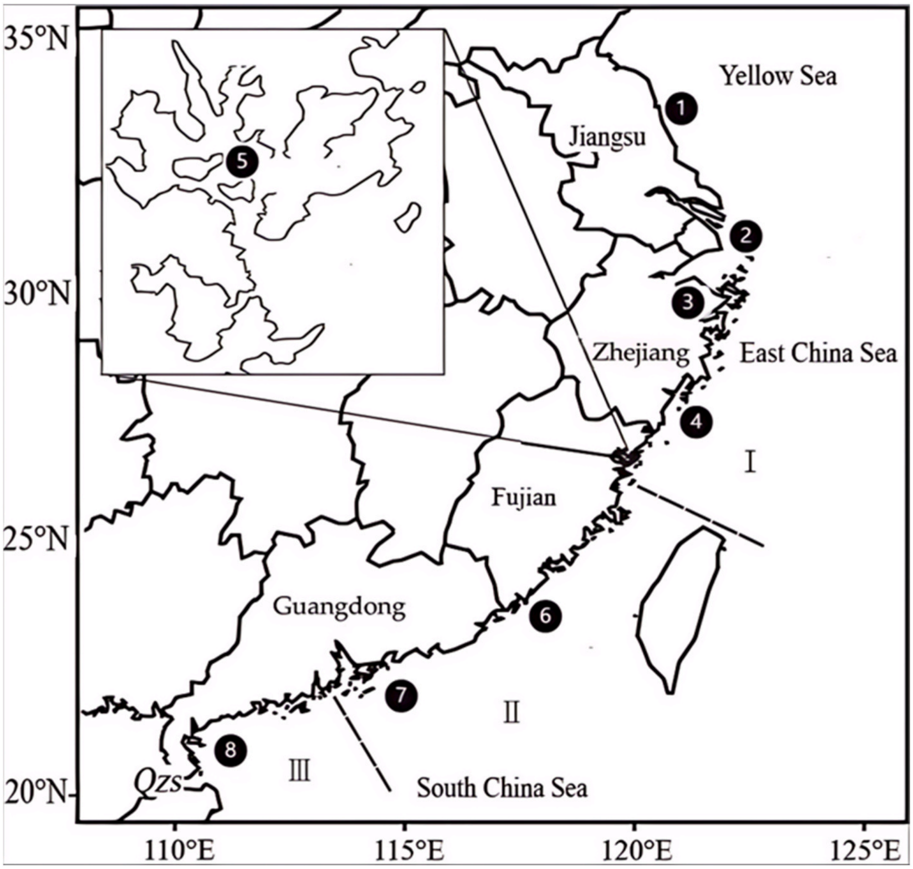

Fig. 1. Geographical population and distribution of spawning grounds of large yellow croaker
I. The Dai-qu stock; II. The Min-Yuedong stock; III. The Nao-zhou stock;
1. Jiangsu Lvsiyang spawning ground; 2. Zhejiang Daiquyang spawning ground; 3. Zhejiang Maotouyang spawning ground; 4. Zhejiang Dongtouyang spawning ground; 5. Fujian Guanjingyang spawning ground; 6. Fujian Jiulong River outer islands Spawning ground; 7. Guangdong Shanwei sea area Spawning ground; 8. Guangdong Naozhou Island near sea area Spawning ground.

classification divides large yellow croaker into three geographical populations from north to south: the Dai-qu stock, the Min-yuedong stock, and the Nao-zhou stock. The Dai-qu stock includes the groups in Lvsiyang in Jiangsu as well as Daiquyang, Maotouyang, and Dongtouyang in Zhejiang; the Min-yuedong stock includes the groups in Guanjingyang, Minjiang River Estuary, and in southern Fujian as well as Nan'ao, and Shanwei in Guangdong; and the Nao-zhou stock mainly includes the group near Naozhou Island in Guangdong. This geographical population classification of large yellow croaker has been adopted by the academic community to date (Fig. 1).

With the rapid development of morphology, ecology, and molecular biology, some scholars have put forward new ideas about the division of geographical populations of large yellow croaker in recent years. For instance, Xu et al. [5] analyzed the migration routes of large yellow croaker in the East China Sea and the Yellow Sea, combined with tagging and recapture data, suggesting that there were random mixed habitats and reproductive exchange between different geographical populations of large yellow croaker in the north of Taiwan. Chen et al. [6] based on the fishing statistics of large yellow croaker by more than ten major fisheries companies in mainland China from 1971 to 1982, and from the aspects of geographical isolation, quantitative dynamics and marine hydrology, they concluded that large yellow croaker in the eastern Fujian fishing ground (Guanjingyang) and those in the East China Sea and the Yellow Sea belong to the East China Sea-Yellow Sea population. Zhang et al. [7] proposed using Niushan Island in Pingtan, Fujian, as a boundary to divide large yellow croaker into the southern Yellow Sea-East China Sea geographical population and the Taiwan Strait-Eastern Guangdong geographical population. The original Nao-zhou stock was renamed the Western Guangdong geographical population. The southern Yellow Sea-East China Sea geographical population includes eight spawning groups in southwestern North Korea and in China, including Lvsiyang, Daiquyang, Damuyang Maotouyang, Dongtouyang, Guanjingyang, and Dongyin Islands in China. The Taiwan Strait-Eastern Guangdong geographical population includes four spawning groups, the Niushan Island, the Jiulong River outer Islands, Nan'ao Island, and Shanwei outer sea. The Western Guangdong geographical population includes two spawning groups: the sea area near Naozhou Island and the Xuwen sea area. Li et al. [8] based on population ecology, proposed dividing large yellow croaker into two geographical populations: the Southern Yellow Sea-East China Sea geographical population and the Taiwan Strait-South China Sea geographical population. The Southern Yellow Sea-East China Sea geographical population includes eight spawning groups in southwestern North Korea and in China, including Lvsiyang, Daiquyang, Damuyang, Maotouyang, Dongtouyang, Guanjingyang, and Dongyin Islands in China. The Taiwan Strait-South China Sea population comprises six spawning groups, including those in Niushan Island, the Jiulong River outer Islands, Nan'ao Island, Shanwei outer sea, the sea area near Naozhou Island, and the Xuwen sea area. YUAN et al. [9] made the most detailed analysis of the genetic structure of large yellow croaker by using the whole-genome resequencing data from a large number of samples including cultured and wild populations. The results showed no significant geographical distribution structure among the wild populations of large yellow croaker along China's coastal areas, which overturned the traditional view of dividing them into three geographical populations for a long time. The issue of geographical population and spawning group division for large yellow croaker is relatively complex and represents a weak link in germplasm resource protection. There is an urgent need to strengthen research on the biology and geographical ecology (including the analysis of migration routes) of each spawning group of large yellow croaker, using molecular biology methods combined with morphology, biochemical genetics, and variation regularity of each spawning population for comprehensive and systematic research.

1.2. History and current status of utilization of large yellow croaker fishery resources

The large yellow croaker is a unique and local marine fish species in China. It holds a crucial position in the structure of marine fish fauna in China. It has been ranked first in China's marine fishing for a long time, and once occupied an important position in the marine fisheries in China and even the Western Pacific Ocean. As early as over 1700 years ago, the working people in China began to catch large yellow croaker as a kind of food fish. The large yellow croaker is a traditional delicacy of the people in the southeastern coastal regions of China, leading to the development of diverse processing and cooking methods that are deeply embedded in the local folk culture of Fujian and Zhejiang provinces. Before the 1970s, the average annual catch of large yellow croaker in China was about 120,000 tons, with renowned fishing grounds such as Lvsiyang in Jiangsu, Daiquyang in Zhejiang, Maotouyang in Zhejiang, and Guanjingyang in Fujian. However, in the 1950s–1960s, the prevalent "Qiaogu" fishing method in the southeastern coastal areas of China once led to the depletion of large yellow croaker resources. The destructive encirclement fishing with "motorized large seine nets" from the 1970s to early 1980s completely cut off the fishing season of large yellow croaker in the southeast coastal area. During the 1973–1974 winter-spring fishing season, the catch in the outer wintering ground of Dasha was as high as 250,000 tons, but by the 1979–1980 winter-spring fishing season, the catch in the outer wintering ground of Minjiang River Estuary had drastically dropped to only 60,000 tons [3]. Since then, the wild populations and fishery resources of large yellow croaker have experienced a steep decline. Although after the realization of artificial breeding, various places continue to strengthen the stock enhancement by releasing large yellow croaker fry, the natural fishery resources of large yellow croaker have yet to recover.

1.3. Development of artificial breeding and cultivation industry of large yellow croaker

In order to restore the natural fishery resources of large yellow croaker, Fujian Province established the "Guanjingyang Large Yellow Croaker Breeding Reserve" in 1985. Concurrently, fishery scientists in Ningde City began technical research on artificial breeding and the cultivation of large yellow croaker. Supported by various levels of government and the efforts of scientists, a series of breakthroughs have been made in the artificial breeding and aquaculture technology of large yellow croaker. From 1980 to 1985, they overcame challenges in the survival, domestication, and cultivation of wild broodstock, achieving initial success in artificial insemination and indoor artificial breeding of large yellow croaker. From 1986 to 1990, the large-scale artificial batch breeding techniques were realized, laying the foundation for the subsequent industrialization of large yellow croaker farming. In the 1990s, the large-scale cage farming models were gradually implemented, driving the fourth wave of marine fish farming in China, represented by a variety of cultured fish such as large yellow croaker. The large yellow croaker farming industry also radiated from east Fujian to Zhejiang, Jiangsu, Guangdong, and beyond [2]. Since the beginning of the 21st century, the farming industry of large yellow croaker has rapidly developed. The supporting systems and standardization for industry technologies, including the breeding of original and improved varieties, fish disease prevention and control, environmental monitoring, quality safety and aquatic product processing, have become increasingly mature and perfect. The annual yield of farmed large yellow croaker has steadily increased year by year, growing from 85,800 tons in 2010 to 281,000 tons in 2023 (Fig. 2), maintaining the first place in the output of marine farmed fish in China for nine consecutive years from 2014 to 2022 [1]. Large yellow croaker has consistently ranked among the top aquatic commodities by export value under China's general trade practices. Over the long term, its export performance has exhibited a distinctive "volume decline with revenue growth" phenomenon. The export volume

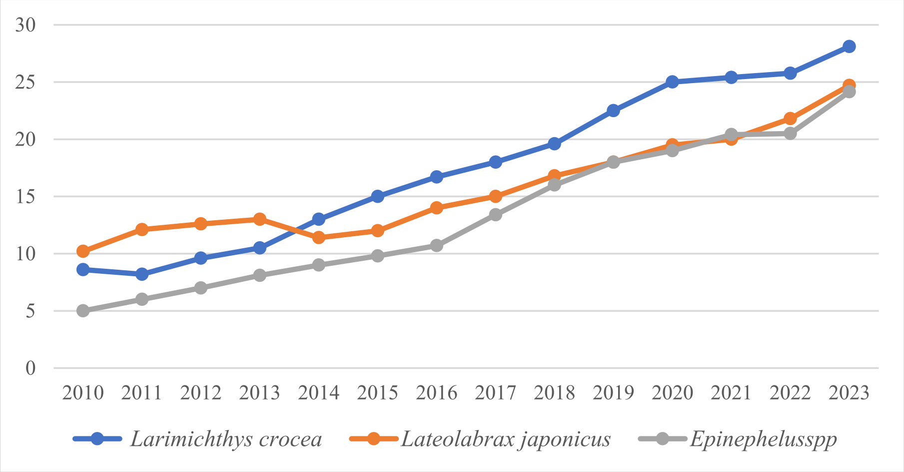

Fig. 2. 2010–2023 Production of major marine farmed fish species.

declined from 55,000 tonnes in 2004 to 34,400 tonnes in 2020, reflecting an average annual contraction rate of 2.89 %. The export value, however, rose from USD 140 million in 2004 to USD 261 million in 2020, achieving a compound annual growth rate (CAGR) of 3.96 %. This divergence underscores sustained unit price appreciation, driven by enhanced product quality and market premiumization strategies. The species has emerged as a cornerstone of China's export-oriented fisheries, contributing significantly to the marine trade network and demonstrating high economic value [10]. In terms of the construction of the original and improved variety breeding engineering system of large yellow croaker, it has established the State Key Laboratory of Mariculture Breeding, Fujian Guanjingyang National Original Variety Farm for Large Yellow Croaker, the Ministry of Agriculture and Rural Affairs Genetic Breeding Center for Large Yellow Croaker, the National Fishery Seed Industry Demonstration Farm, Fujian Provincial Large Yellow Croaker Improved Variety Farm, and Fujian Provincial Engineering Technology Research Center for Large Yellow Croaker Improved Variety Breeding Enterprises, etc.

1.4. Conservation and multiplication of germplasm resources of large yellow croaker

In view of the current situation that large yellow croaker is facing the depletion of germplasm resources, governments at all levels are very concerned about the protection and restoration of wild resources of large yellow croaker. The Ministry of Agriculture and Rural Affairs, Fujian Province, and Ningde City have successively established Guanjingyang large yellow croaker spawning grounds and its germplasm resources protection areas with different protection categories, promulgated relevant protection regulations, and established Fujian Guanjingyang National Original Variety Farm for Large Yellow Croaker [2]. The primary goal is to protect germplasm resources through the preservation, domestication, original variety cultivation and propagation of wild large yellow croaker. Additionally, they are conducting sea area multiplication and release, and resource restoration for the first-generation seedlings of original variety.

Regarding the construction of the germplasm resources protection area for large yellow croaker, in October 1985, Fujian Province established the "Guanjingyang Large Yellow Croaker Breeding Reserve", This reserve includes the original Guanjingyang large yellow croaker spawning ground and its juvenile feeding and fattening ground, large yellow croaker migration channel and other adjacent offshore areas in Sandu Bay, Ningde City, and the "Guanjingyang Large Yellow Croaker Proliferation Station" was established in Ningde to manage the reserve. In August 2008, the Ministry of Agriculture announced the list of the first batch of 40 national aquatic germplasm resources protection zones in China, including the Guanjingyang Large Yellow Croaker National Aquatic Germplasm Resources Protection Zone in Ningde City, Fujian Province. This protection zone is located within Sandu Bay, Ningde City, overlapping with the original provincial "Guanjingyang Large Yellow Croaker Breeding Reserve", covering a total area of 190 km^2, with a core area of 35 km^2 and an experimental area of 155 km^2. The core special protection period is from March to December each year, with the primary focus on protecting large yellow croaker. Additionally, it also considers other aquatic species inhabiting the sea area, such as *Scylla*, *Scomberomorus* spp., and *Muraenesox* spp., it has effectively protected the germplasm resources of large yellow croaker in Guanjingyang, East Fujian [3].

In terms of the construction of the original and improved variety farm of large yellow croaker, in order to protect the wild germplasm resources of large yellow croaker, preserve and maintain the original variety of large yellow croaker, realize the proliferation of wild fishery resources, and strengthen the utilization of excellent large yellow croaker germplasm resources to support the large yellow croaker aquaculture industry, etc. In recent years, it has approved the construction of one national large yellow croaker original variety farm and three national large yellow croaker improved variety farms. The national large yellow croaker original variety farm has a marine living germplasm resource bank of large yellow croaker, an original variety domestication workshop, a breeding workshop and a supporting laboratory, which specifically carries out the collection, arrangement, preservation, development and utilization of wild large yellow croaker original variety, and annually carries out the expansion and breeding of the first generation of original variety and the cultivation of seedlings, which will be used for the proliferation and release of large yellow croaker and the restoration of wild germplasm resources. At the same time, it can also provide germplasm resources with higher genetic diversity for the selection and breeding of improved varieties of large yellow croaker and support the development of large yellow croaker aquaculture industry.

Following the realization of large-scale artificial breeding of large yellow croaker, Fujian Province and Zhejiang Province have organized annual activities to multiplication and release large yellow croaker into the wild. In Fujian, these activities primarily occur within the Guanjingyang Large Yellow Croaker Breeding Reserve in Sandu Bay, and also extend to the Minjiang Estuary, Luoyuan Bay, and Shacheng Bay. In Zhejiang, these release activities primarily occur in Xiangshan Harbor, Nanjiushan Islands, Zhoushan Islands, and Nanji Islands. With the continuous expansion of artificial breeding scale of large yellow croaker, the frequency and quantity of released seedlings have increased annually. According to incomplete statistics, the number of large yellow croaker released by government departments in 2019 was more than 30 million, and the number of large yellow croaker released by private voluntary organizations in Ningde reached 1.6 billion. Over the past decade, most of the released fry in Fujian have come from the Guanjingyang National Large Yellow Croaker Original Variety Farm. From 2012 to 2022, this farm produced over 300 million original variety first-generation fry for release, primarily fish larger than 5 cm, mainly in areas including Guanjingyang, Sansha Bay, Huangqi Bay, and Luoyuan Bay.

2. Progress of germplasm innovation in large yellow croaker

With the breakthrough of the large yellow croaker artificial aquaculture technology and the rapid development of the large yellow croaker farming industry, the identification and evaluation, and genetic breeding of large yellow croaker germplasm resources have also gradually unfolded and become increasingly active. With the continuous development of biotechnology, fish genetic breeding techniques have evolved from traditional breeding technologies such as selective breeding, hybrid breeding, and gynogenesis breeding to modern biological breeding technologies, including sex control breeding, molecular marker-assisted selective breeding [11], and genome-wide selective breeding. On this basis, the genetic breeding and germplasm innovation of large yellow croaker have also progressed rapidly. Many domestic research teams have successively cultivated a number of new lineages and varieties of large yellow croaker by using technologies such as population selective breeding, family selective breeding, gynogenesis, and genome-wide selective breeding (Table 1).

2.1. Progress in traditional selective breeding of large yellow croaker

Through artificial systematic selective breeding, we can obtain lineages (varieties) with excellent traits, which can be further used as parents for hybrid breeding or other genetic improvement breeding. As of 2023, a total of 283 new aquatic varieties have been approved by the National Certification Committee for Aquatic Stocks and Varieties, with only four new varieties of large yellow croaker have been approved.

In 2001, Jimei University and other units bred the variety “Minyou No.1” after five generations with the growth rate, body shape, and survival rate as key indicators, using wild large yellow croaker caught in Guanjingyang as the basic population, and through conventional population selective breeding technology combined with gynogenesis breeding technology. In 2010, it was approved as a new breeding variety suitable for promotion by the National Certification Committee for Aquatic Stocks and Varieties (Variety Registration No.: GS-01-005-2010). This variety showed a 23.90 % increase in growth rate and a 13.70 % increase in survival rate compared to the common populations without selective breeding. The large yellow croaker “Donghai No. 1” was developed by Ningbo University and other units, using wild large yellow croaker collected from Daiquyang, Zhejiang Province in 2000, as the basic population. It was obtained by population selective breeding technology with the growth rate and cold tolerance as key indicators after more than ten years and five generations of breeding. It was approved as a new breeding variety suitable for promotion by the National Certification Committee for Aquatic Stocks and Varieties in 2013 (Variety Registration No.: GS-01-001-2013). The weight growth rate of 19-month-old seedlings of the new variety was 15.57 % faster than that of local commercial seedlings, and the survival rate of 10-month-old seedlings at 6 °C water temperature was 22.50 % higher than that of local commercial seedlings [12]. The large yellow croaker “Yongdai No. 1” was bred by Ningbo Marine and Fisheries Research Institute and other units, was approved in 2020 (Variety Registration No.: GS-01-001-2020). This variety, selected for growth rate and body shape over five generations, showed a 16.36 % higher growth rate at 21 months compared to the common populations without selective

Table 1
Large yellow croaker breeding technology and its progress.

Breeding techniques	Research process	Representative of varieties
selective breeding techniques	Four new varieties were obtained through continuous multi-generational breeding using population selection techniques, with growth rates, body size, and body weight as breeding indicators. However, new varieties with composite traits such as disease resistance, stress resistance, and quality have not been successfully created.	“MinYou No.1” Large yellow croaker (Variety Registration No.: GS-01-005-2010) “Donghai No.1” Large yellow croaker (Variety Registration No.: GS-01-001-2013) “Yongdai No.1” Large yellow croaker (Variety Registration No.: GS-01-001-2020) “Fufa No.1” Large yellow croaker (Variety Registration No. GS-01-006-2022)
hybrid breeding techniques	Chinese scholars have conducted hybrid breeding experiments between large yellow croaker, yellow drum, and brown croaker. The research results showed that the survival rate of their hybrid offspring is extremely low, and some offspring have been identified by molecular biology experiments as heterospermic gynogenetic individuals. Additional, Chinese scholars have also conducted interspecific hybridization between large yellow croaker and small yellow croaker, and successfully obtained hybrid offspring that can survive and develop normally.	None
gynogenesis breeding techniques	The teams led by Academician Shaojun Liu from Hunan Normal University and Professor Xinhua Chen from Fujian Agriculture and Forestry University collaborated to induce gynogenesis in large yellow croaker using genetically inactivated sperm of yellow drum (*Nibea albiflora*), improved the artificial induction conditions and gynogenesis technology processing conditions, ultimately forming a population of about 5000 gynogenetic large yellow croaker.	None
molecular marker assisted breeding techniques	In 2007, Chinese scholars constructed the first genetic linkage map of large yellow croaker. QTL mapping was conducted on the resistance to *Cryptocarya irritans* trait of large yellow croaker, and four QTL loci and candidate genes (*IFNAR1*, *ifngr2*, *IKBKE*, and *CD112*) related to disease resistance traits were identified.	None
genome-wide-selective breeding techniques	In 2015, Chinese scholars used high-throughput whole genome sequencing technology to complete the	None

(*continued on next page*)

Table 1 (*continued*)

Breeding techniques	Research process	Representative of varieties
	world's first physical map of the whole genome of large yellow croaker. GWAS analysis was used to obtain SNP polymorphic loci, candidate genes and QTL information related to growth traits, disease resistance traits, gonadal development, muscle quality, sex index traits, and high temperature tolerance traits of large yellow croaker.	
gene editing techniques	Knockout of the *mstn* gene in *Larimichthys crocea*.	None

breeding under the same farming conditions. The large yellow croaker "Fufa No. 1", developed by Ningde Fufa Aquatic Farm Co., Ltd. and other units, was approved in 2022 (Variety Registration No.: GS-01-006-2022). This variety, selected for body weight over five generations, demonstrated a 23.60 % increase in average body weight at 18 months compared to the common populations without selective breeding under the same farming conditions. Currently, the selective breeding traits of new varieties of large yellow croaker are relatively limited, primarily focusing on growth traits, body shape, and body weight, while new varieties with complex traits such as disease resistance, stress tolerance, and quality have yet to be developed.

2.2. Progress in hybrid breeding of large yellow croaker

Distant hybridization is an important technology widely used in fish genetics and breeding. Distant hybridization can combine the whole genome of parent species, which may lead to phenotypic and genotype changes in offspring. In terms of phenotype, offspring from distant hybridization usually show heterosis in growth, resistance, quality and yield [13]. Liu et al. [14] conducted the hybridization test between large yellow croaker (♀) and yellow drum (*Nibea albiflora*) (♂), finding no barriers to fertilization but an extremely low survival rate of the offspring (0.17 %). The AFLP results indicated that the F_1 hybrid fry contained genes from both parents, with no significant selective loss of paternal or maternal genes. Wang et al. [15] conducted intergeneric hybrid between large yellow croaker (♀) and brown croaker (*Miichthys miiuy*) (♂), obtained hybrid progeny with fertilization rate of 56.25 %, hatching rate of 45.24 %, and fry survival rate of 0.65 %. The comparative analysis of microsatellite and AFLP markers between parents and hybrid offspring showed that the hybrid offspring and maternal parent had high genetic homogeneity, and belonged to heterospermic gynogenetic individuals. Liu et al. [16] conducted hybridization experiments between small yellow croaker (♀) and large yellow croaker (♂). The results showed that the embryonic development time and hatching rate (61 h 50 min and 90.5 %) of hybrid F_1 were similar to those of small yellow croaker at 18.5 °C constant temperature. The results of microsatellite marker identification of F_1 showed that all F_1 produced the same bands as their parents, indicating that F_1 was a hybrid of small yellow croaker and large yellow croaker. Liu et al. [17] used biochemical analysis methods to analyze the muscle nutrient composition of hybrid offspring of small yellow croaker (♀) × large yellow croaker (♂) and their parents. The results showed that the muscle moisture content of hybrid offspring was lower than that of their parents, and the contents of crude protein, essential amino acids, flavor amino acids, and saturated fatty acids (SFA) were higher than that of their parents, and the contents of crude fat, monounsaturated fatty acids (MUFA), and polyunsaturated fatty acids (PUFA) were between their parents, and their muscle nutritional value was better than that of their parents. Yang et al. [18] observed the process of sex differentiation and gonadal development in the hybrid offspring of small yellow croaker (♀) × large yellow croaker (♂). The results showed that the hybrids had normal sex differentiation and gonadal development, successfully producing both male and female gametes.

2.3. Progress in gynogenesis breeding of large yellow croaker

Large yellow croaker has different growth rates between males and females. Female individuals usually grow faster than male individuals. We can apply a combination of gynogenesis and sex-reversal techniques to devise a method for obtaining large numbers of all-female large yellow croaker individuals. That is, after obtaining gynogenetic large yellow croaker, we can breed all-female large yellow croaker by transforming genetically female fish (XX, ♀) into physiologically male fish (XX, ♂) through exogenous hormone treatments, and physiologically male fish (XX, ♂) are next mated with common female large yellow croaker (XX, ♀) [19]. By combining the techniques of gynogenesis and sex-reversal, we are able to breed all female offspring to achieve the goals of the industrial production practice of gynogenesis breeding techniques, which is important to improve the breeding efficiency and economic benefits of large yellow croaker.

Gynogenesis is a special mode of sexual reproduction. In this mode of reproduction, genetically inactivated sperm enters the egg to activate embryonic development, but the sperm nucleus does not fuse with the egg nucleus to form a zygote, so gynogenetic individuals usually only have the genetic information of the maternal parent. 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 [20]. In terms of artificially induced gynogenesis breeding of large yellow croaker, the research team of Jimei University successfully bred the first generation (G_1) and second generation (G_2) of gynogenetic large yellow croaker, and identified the genetic composition of the gynogenetic offspring using microsatellite markers and AFLP markers [21–23]. Chen et al. [24] induced gynogenesis in large yellow croaker using genetically inactivated sperms from *Oplegnathus fasciatus*, and detected the ploidy of fertilized eggs by flow cytometry. The experimental results showed that all fertilized eggs without cold shock treatment were haploid, while those treated with cold shock were diploid, indicating that sperm heritage inactivation was effective. The gonadal tissue sections showed that all gynogenetic populations were female. The teams led by Academician Shaojun Liu from Hunan Normal University and Professor Xinhua Chen from Fujian Agriculture and Forestry University collaborated to induce gynogenesis in large yellow croaker using genetically inactivated sperm of yellow drum (*Nibea albiflora*), improved the artificial induction conditions and gynogenesis technology processing conditions, ultimately forming a population of about 5000 gynogenetic large yellow croaker.

2.4. Progress in molecular marker-assisted breeding of large yellow croaker

In the development and application of genetic markers, as early as the 1990s, the research teams of Xiamen University began using isoenzyme biochemical markers to analyze the population genetic structure and genetic diversity of wild and farmed large yellow croaker in Guanjingyang, Fujian. They discovered that both populations exhibited low levels of genetic diversity [25]. In addition to biochemical genetic markers, there have been many studies on the development and application of DNA molecular markers in large yellow croaker. Different research teams in China have successively developed molecular markers such as Amplified Fragment Length Polymorphism (AFLP) and Simple Sequence Repeat (SSR) markers of large yellow croaker, which have been used to analyze the genetic structure and diversity of different geographical populations of large yellow croaker, revealing that farmed populations generally have lower genetic diversity than wild populations [26,27]. In the development of molecular markers for mitochondrial DNA, Li et al. [28] constructed a restriction endonuclease map of the mitochondrial DNA of large yellow croaker, and Cui et al. [29] completed the sequencing of the whole mitochondrial genome of large yellow croaker, which provided an important foundation for the study of population genetics and evolution of large yellow croaker. Currently, it is also very active to carry out population genetic analysis, germplasm resource identification and molecular systematics of large yellow croaker using part or all of the mitochondrial genome sequences [30–32]. With the advancement of molecular biology research techniques, the study on functional genes related to important economic traits of large yellow croaker has also become increasingly abundant, and several research teams in China have also successively cloned a number of functional genes related to growth, stress resistance, and disease resistance of large yellow croaker, and have analyzed their gene expression and regulatory mechanism.

Genetic map is a map constructed by gene linkage and recombination exchange value, showing the relative position of genetic markers associated with traits. To date, high-density genetic linkage maps have been constructed for over 40 species of aquatic animals, and most of them are based on Single Nucleotide Polymorphisms (SNP) or SSR markers [33]. As early as 2007, Ning et al. [34] constructed the first genetic linkage map of large yellow croaker. Over the past decade, research on the linkage map of large yellow croaker has gradually increased in China, which has laid a solid foundation for the molecular breeding of large yellow croaker. Ye et al. [35] constructed a genetic linkage map based on two half sib families of large yellow croaker, found 289 microsatellite loci, which were integrated into 24 linkage groups, and detected seven QTL loci in five linkage groups. Ao et al. [36] constructed the genetic linkage map of large yellow croaker, with a total length of 5451.3 cM and an average distance between loci of 0.54 cM. Kong et al. [37] mapped QTLs for resistance to *Cryptocarya irritans* in large yellow croaker and found four QTL loci and candidate genes (*IFNAR1*, *ifngr2*, *IKBKE* and *CD112*) related to resistance traits. These above studies provided effective sequence information for the selective breeding of genetic markers for growth and disease resistance traits in large yellow croaker. High-density genetic linkage maps have provided important data support for precise localization, gene editing, and genome-wide selective breeding of large yellow croaker.

A large number of studies have shown that economic traits are mostly quantitative traits and controlled by multiple genes. Traditional breeding methods struggle to achieve accurate selection. Therefore, constructing high-density genetic linkage map and QTL localization can develop genetic markers that can effectively control economic traits. The phenotype of a quantitative trait is mostly controlled by multiple genes, and the aim of QTL localization is to determine the corresponding gene loci that cause variation in that quantitative trait. So far, QTL localization has been carried out for nearly 100 species of domestic and foreign aquaculture animals, including fish, molluscs, crustaceans, and echinoderms, with the main traits related to growth, morphological traits, disease resistance, stress response, temperature tolerance, meat quality, and sex determination [38–41].

Single nucleotide polymorphism chips (SNP chips), also known as single nucleotide polymorphism chips, is a high-throughput genotyping technology. SNP chips use DNA chip technology to detect and analyze SNP. The basic principle is to fix specially designed probes on the chip that can be matched to a particular SNP sequence. After amplification and labeling, the sample DNA was hybridized with the probe on the chip, and the signal was detected by fluorescence and other methods. According to the intensity of the signal, the SNP type at each locus can be determined. At present, it is widely used in genomics research and individual genetic variation detection. Recently, Wang et al. [42] completed the research and development of a high-throughput gene chip-large yellow croaker “Ningxin No. 3” high-density SNP typing chip, which realized the comprehensive “chip” of large yellow croaker genome breeding, effectively promoted the rapid development of the breeding of improved varieties of large yellow croaker, and provided standardized and high-precision massive genotype data for the genetic location of important economic traits, genome-wide selective breeding.

2.5. Progress in genome-wide selective breeding of large yellow croaker

Genome-wide association study (GWAS) is a large-scale, multi-sample, and repeatedly verified association analysis technology between gene sequences and target traits at the genome-wide level, and then to find the research methods of genetic factors related to target traits, so as to determine the inheritance genes related to traits. GWAS can be used to analyze quantitative and qualitative traits, including identifying new variant traits and detecting trait information controlled by single or multiple genes [43]. With the decreasing cost of whole-genome sequencing, GWAS technology has been widely applied in the genetic improvement of economic traits in aquaculture animals. The main traits involved include gonad differentiation in *Oreochromis niloticus*, muscle production [44] and disease resistance traits [45] in *Oncorhynchus mykiss*, growth traits in *Litopenaeus vannamei* [46], and shell color in *Patinopecten yessoensis* [47].

Zhao et al. [48] also carried out GWAS analysis on the disease resistance traits of large yellow croaker against *Cryptocaryon irritans*, and identified 15 QTLs and 2 candidate genes (*casp8* and *traf6*) in two populations. Xiao et al. [49] completed the world’s first genome-wide physical map of large yellow croaker by using high-throughput whole-genome sequencing, and assembled the whole-genome maps of large yellow croaker into 686 maps with a total length of 727 Mb and an N50 length (126 maps) of 1.7 Mb, which has laid a solid foundation for in-depth research on the genetic mechanisms of growth, disease resistance, stress resistance and other traits of large yellow croaker. In addition, many domestic scholars have used GWAS analysis to obtain SNP polymorphic loci, candidate genes and QTL information associated with growth traits, disease resistance traits, gonadal development, muscle quality, sex index traits, and high temperature tolerance traits of large yellow croaker [50–60]. These findings provide important molecular tools for the subsequent genetic improvement of economic traits in large yellow croaker. Through the polymerization and selection of gene loci or alleles for economic traits in large yellow croaker, the production performance of cultured large yellow croaker can be comprehensively improved to promote the sustainable development of large yellow croaker aquaculture industry.

The whole genome resequencing (WGR) technology can sequence the whole genome of different individuals, comprehensively interpret the variation information on the genome, and calculate the correlation between the variation information and economic traits. In recent years, with the whole genome of many aquaculture animals being deciphered one after another, WGR is widely used in the aquaculture field to detect the genetic information of the target traits, the mechanism of environmental adaptation and the verification of selective breeding effect, including the adaptive genetic differentiation of *Leuciscus waleckii* [61], the genetic diversity of *Cyprinus carpio* [62], the development of sex linked molecular markers of *Silurus meridionalis* [63], the male development of *Salmo salar*, the disease resistance characteristics of *Scophthalmus maximus* [64] and the ammonia nitrogen tolerance of *Epinephelus coioides* [65] and so on. Kon et al. [66] used WGR technology to analyze the genetic population structure of large yellow croaker from Ningde, Fujian Province and Zhoushan, Zhejiang Province, and found the genetic difference gene loci of large yellow croaker in different water bodies, and revealed the genetic differences due to adaptive domestication. Wan et al. [55] carried out WGR analysis on resistance traits of visceral white spot disease caused by *Pseudomonas plecoglossicida* in large yellow croaker. Based on 254110 SNPs information, three candidate regions related to resistance were found on chromosomes 3, 5 and 20, and candidate genes for resistance traits (*IL10*, *THBS1*, *IGSF21*, *IGR*, *IGH*, *IRF8*, *TRAIL*, *CC*, *TNF* and *LINGO1*) were found.

Genome selection (GS) is to use genome-wide markers and phenotypic data to estimate the effect values of each molecular marker or chromosome segment, and comprehensively estimate the genetic effect of genome-wide loci of species. A variety of analysis methods are used to generate an equation to predict the genome estimated breeding value (GEBV). Finally, GEBV is compared with the actual phenotypic values, and the accuracy of the prediction equation is evaluated using a validation population with both genotype and phenotypic data. Liu et al. [67] analyzed the heritability of growth traits in over 3000 populations of the yellow drum, achieving an accuracy of 80 %. Qiu et al. [68] estimated the genetic parameters of nine quantitative traits based on SNP markers and found a high phenotypic and genetic correlation between body length, body height, body width, and visceral weight. Dong et al. [69] evaluated the heritability values of body weight, body length, and meat quality (such as n-3 HUFA index) of large yellow croaker. They compared the prediction accuracy of different calculation models, assessed the effectiveness of SNPs required by GS, and believed that it was entirely feasible to utilize GS for the breeding of growth and meat quality traits. Dong et al. [70] developed two new computational strategies for genome prediction methods and a new FBayesC prediction method. These genome prediction methods were applied to the genetic improvement of economic traits in large yellow croaker. At the same time, they also conducted comparative GWAS studies on economic traits of large yellow croaker using single-marker analysis and Bayesian models. The research results not only provided a method to save the cost of genome breeding, but also helped to advance the process of genome selective breeding of large yellow croaker.

2.6. Application of gene editing technology in germplasm innovation of large yellow croaker

Gene editing is a process of modifying specific sequences of the genome of organisms, which can efficiently and accurately achieve gene insertion, deletion, or replacement, thereby altering their genetic information and phenotypic characteristics [71]. The CRISPR/Cas9 system has become the most commonly used gene editing tool due to its simplicity and efficiency. Its basic principle is that the Cas9 protein and single guide RNA (sgRNA) form a Ribonucleoprotein (RNP) complex, which cleaves the target site to create a DNA double-strand break (DSB). Subsequently, the host cells primarily repair the damage through non-homologous end joining (NHEJ) and homology-directed repair (HDR) [72]. The research team of Xiamen University successfully knocked out the *mstn* gene of large yellow croaker using the CRISPR/-Cas9 system [73]. Li et al. [74] applied CRISPR/Cas9 gene editing technology for large yellow croaker, introducing the recombinant plasmids encoding green fluorescent protein (GFP) into the fertilized eggs of large yellow croaker via microinjection before the egg membrane hardened, achieving a high survival rate of 40 % and a GFP expression positive rate of 81.8 %, indicating that the microinjection technology for large yellow croaker has been successfully established. On this basis, Cas9 mRNA and sgRNA (Lc-tyra) targeting the tyrosinase a gene of large yellow croaker were co-injected into the fertilized eggs of large yellow croaker, and resulting in the detection of mutant individuals with Lc-tyra insertion and deletion mutations. Relevant experimental results show that the CRISPR/Cas9-based gene editing technology can efficiently introduce mutations at specific sites within the large yellow croaker genome, which provides potential applications for genetic improvement and functional genome research of this species. To date, the primary target traits for gene editing in aquaculture animals include infertility, growth, and disease resistance traits. Gene editing is widely used in aquaculture. The main advantage is that fish can easily obtain thousands of in vitro fertilized embryos, and these embryos are large enough for manual microinjection. At present, polygenic traits continue to pose a significant challenge for gene editing technology. It is necessary to edit multiple alleles associated with the same trait at the same time to achieve the purpose of optimizing traits. Therefore, it is still necessary to develop and improve gene editing technology.

3. Summary and prospect

After entering the 21st century, the role of aquaculture in the global aquatic product supply has become a consensus, and germplasm innovation particularly determines the quality and yield of aquatic products [75]. After long-term efforts, fish breeding has been integrated with modern life sciences, establishing various breeding technologies, especially the genome-wide selective breeding technology developed in conjunction with bioinformatics technology. The objective of breeding is to increase yield and enhance quality. Regarding yield enhancement, current research on new varieties of large yellow croaker has focused primarily on traits related to growth, disease resistance, and stress tolerance. Regarding quality enhancement, there are virtually no varieties selected based on flavor and texture-related traits such as flavor amino acid content and muscle fiber quality, yet these traits significantly impact the economic value of large yellow croaker.

The economic losses caused by diseases in large yellow croaker farming are great, but no new disease-resistant varieties of large yellow croaker have been developed in China until now. In actual breeding work, genetic diversity may be unconsciously reduced in order to improve growth rate, body size, and other economic traits. Genetic diversity means that the large yellow croaker population has more genotypes, which increases the number of individuals in the population that may have disease-resistant traits, thus improving the overall adaptability and viability of the population. Breeding new varieties with disease-resistant traits is of great significance in reducing production costs and increasing the yield of large yellow croaker.

In the research and development process of new fish varieties, the number of new varieties cultivated by modern breeding technologies (such as sex control breeding, molecular marker-assisted selective breeding, genome-wide selective breeding, etc.) is far lower than that bred by traditional and classic breeding technologies (such as selective breeding, hybrid breeding, gynogenesis breeding, etc.). This indicates that the practical application of these modern breeding technologies is not wide, and the degree of combination of traditional and classic breeding technologies with modern biological technology is not close [76].

Looking back on the process of germplasm innovation of large yellow croaker, we found that there are still many genetic laws and molecular mechanisms that need to be analyzed in breeding technology have not been studied. In terms of hybrid breeding, the success rate of distant hybridization is related to the chromosome number of hybrid parents. When the chromosome numbers of parents are the same or similar, hybrid breeding technology may break the reproductive isolation between species and obtain viable offspring. For example, the hybridization between large yellow croaker and small yellow croaker can successfully cultivate bisexual fertile hybrid offspring [77]. The degree of chromosome matching of hybrid parents will affect the nuclear-nuclear and nuclear-cytoplasmic (cytoplasmic) coordination of hybrid F_1. The nuclear-nuclear and nuclear-cytoplasmic coordination is related to the survival rate of hybrid F_1. For example, the hybrid offspring of *Larimichthys crocea* and *Miichthys miiuy* or *Nibea albiflora* have very low survival rates, which may be related to nuclear-nuclear and nuclear-cytoplasmic incompatibility. The molecular mechanism behind this phenomenon remains to be investigated. By revealing these molecular mechanisms, the blindness of death of hybrid offspring will be avoided. In addition, many studies on nucleocytoplasmic hybridization and gynogenesis have suggested that the paternal mitochondrial genome has an important impact on the traits of offspring [78]. Clarifying its molecular mechanism can provide new ideas for genetics and breeding. At present, the molecular mechanism of gynogenesis breeding technology has not been fully clarified. The gynogenesis breeding of large yellow croaker faces the problems of low fertilization rate and lower hatching rate in practical application. The farther the paternal-maternal relationship in terms of gynogenesis, the lower the fertilization rate and the hatching rate. This trend is the same as that in hybrid breeding, suggesting that the success rate of gynogenesis may be related to sperm-egg recognition. The research on the molecular mechanism of gynogenesis breeding 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. Finally, molecular marker-assisted breeding (MAS) and genome-wide selective breeding (GS), which have higher relative cost and technical threshold, are rarely used, especially genome-wide selective breeding. The application of this technology will improve the accuracy of breeding. However, new germplasm from cultured fish obtained through transgenic techniques and gene editing techniques have not yet been successfully marketed, and there have been relatively few studies on this aspect of large yellow croaker. At the same time, a large number of genes associated with growth and disease resistance have been identified. Gene editing for these genes is of great significance to the germplasm innovation of large yellow croaker.

In summary, based on the current situation of protection and utilization of large yellow croaker germplasm resources and the development needs of large yellow croaker aquaculture industry, it is necessary to investigate the “family background” of large yellow croaker germplasm resources in China as soon as possible in the future. Strengthening the protection and restoration of these resources, and cultivating a system of protection and innovative utilization of large yellow croaker germplasm resources with seed industry enterprises as the main body and the participation of government, industry, university and research. At present, the research on important economic traits such as disease resistance, feed utilization efficiency, and taste and flavor of excellent lineages (or varieties) of large yellow croaker is still in its early stages. Economic traits of fish are controlled by quantitative trait loci (QTL) of multiple genes, most of which have minor effects, but a few may have decisive influences [79]. These complex economic traits are often controlled by multiple genes that are difficult to locate and exhibit genetic linkage [80]. But looking forward to the future, by continuously deepening the research on the molecular mechanism of germplasm improvement and the formation of dominant traits of large yellow croaker, integrating excellent germplasm resources, and integrating the modern breeding technology system that combines traditional and classical breeding techniques with modern molecular biology techniques, we can break through the barriers to the sustainable development of large yellow croaker seed industry and aquaculture industry, which not only lays a solid foundation for the genetic breeding research of large yellow croaker, but also provides excellent germplasm guarantee for the healthy and sustainable development of the large yellow croaker aquaculture industry, which is of great significance in fish genetic breeding and aquaculture.

CRediT authorship contribution statement

Huan Liu: Writing – original draft, Data curation, Conceptualization. **Sijin Fan:** Formal analysis. **Qinglin Xu:** Formal analysis. **Xin Wang:** Formal analysis. **Yalan Zhang:** Formal analysis. **Wei Chen:** Formal analysis. **Yu Hu:** Formal analysis. **Xinyue Deng:** Formal analysis. **Hanyu Liu:** Formal analysis. **Chongzhi Yang:** Formal analysis. **Fangle Tong:** Formal analysis. **Zehong Wei:** Formal analysis. **Shi Wang:** Writing – review & editing, Supervision. **Shaojun Liu:** Writing – review & editing.

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Declaration of competing interest

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