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Current status and application of largemouth bass (*Micropterus salmoides*) germplasm resources

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ABSTRACT

Largemouth bass (*Micropterus salmoides*, LB) is an important aquaculture and fishing species in the world. LB has been introduced into China since 1983, and its aquaculture production has increased year by year. The total yield of LB in China reached 802,486 tons in 2022, ranking seventh in China's freshwater fish aquaculture. However, the LB is facing threats such as degradation of germplasm resources and disease susceptibility due to limitations in the scale of introduction, coupled with the effects of high-density aquaculture, inbreeding, and species hybridization. This paper summarizes the current status of LB germplasm resources, variety genetic improvement, nutrition and fodder, aquaculture mode and diseases, and circulation and processing. This paper also provides recommendations on how to fully explore and utilize the existing germplasm resources of LB; culture new LB germplasm that combines excellent resistance and growth characteristics through innovations in breeding techniques; reduce the morbidity rate and improve the efficiency of cultured LB through the optimization of fodder formulations and innovation of aquaculture modes; and shift the processing of LB toward standardization, efficient nutrition and safety through the integration of high-tech and large-scale production. This paper provides a reference for the sustainable and healthy development of the LB industry.

Largemouth bass (*Micropterus salmoides*), also known as California bass, belongs to the genus *Micropterus* in the sunfish family Centrarchidae of Perciformes, which is native to the Mississippi River system in California, United States, and is now widely distributed in North American freshwaters [1]. According to the geographic distribution of origin and morphological differences, largemouth bass is divided into two subspecies: the northern subspecies of largemouth bass (*M. salmoides salmoides*), which is distributed in east-central United States, northeastern Mexico, and southeastern Canada, and the southern Florida subspecies of largemouth bass (*M. salmoides floridanus*) [2]. Largemouth bass prefers sandy or silty still water with low turbidity and particularly prefers to live in slow-moving currents; it is a typical carnivorous fish with strong predatory behavior. Largemouth bass reach

sexual maturity at more than 1 year of age, after which time it reproduces only once a year, spawning several times, with the spawning season lasting from February to July [3].

In the 1980s, the northern subspecies of largemouth bass was introduced to Taiwan and Guangdong, China [4,5], and its aquaculture was popularized. Due to the advantages of wide temperature adaptability, strong disease resistance, fast growth rate, short aquaculture cycle, tasty meat, and easy catching [5,6], largemouth bass have been favored by farmers and consumers. With the breakthrough of artificial compound fodder for largemouth bass, the culture scale of largemouth bass in China has expanded rapidly, and yield has also increased rapidly, reaching more than 800,000 tons by 2022 [7]. The rapid development of the largemouth bass aquaculture industry has not only brought more

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economic benefits to farmers but has also driven upstream and downstream industries such as fodder production and fish processing. However, in recent years, largemouth bass have faced problems such as degradation of germplasm resources, low seedling survival rates, reduced resistance, and disease susceptibility due to increased aquaculture density, inbreeding, and species hybridization [8]. As a result, there is an urgent need for the largemouth bass industry to breed fast-growing, resilient and high-quality varieties of largemouth bass, develop technologies suitable for large-scale aquaculture, optimize fodder formulations, and formulate standardized processing and production specifications. In this paper, the current status of largemouth bass germplasm resources, breeding, nutrition and fodder, aquaculture modes and diseases, circulation and processing and other aspects, as well as current problems in the largemouth bass industry, are reviewed. It is hoped that this paper will serve as a reference for the healthy and sustainable development of the largemouth bass industry.

1. Current status of research on largemouth bass germplasm resources

1.1. Morphological characteristics of largemouth bass

Largemouth bass has a fusiform body with flattened sides, a thicker dorsal surface, a large slit mouth, dense black spots arranged in bands on the head and back, a greenish-black dorsal coloration, and a grayishwhite belly [9]. It is difficult to distinguish the two subspecies of largemouth bass based on appearance alone, and in the past, the two subspecies were considered to be the same fish. It was not until 1949 that Bailey et al. [2] first compared the two subspecies in terms of morphology and found that the morphological differences between the two subspecies occurred mainly in localized characters, such as the number of lateral scales and the number of ribs. The northern subspecies had lateral scales ranging in number from 59 to 65 with 15 pairs of ribs, while the Florida subspecies had lateral scales ranging in number from 69 to 73 with 14 pairs of ribs. The study confirmed significant differences between the two subspecies only in the number of lateral scales and ribs but no significant differences in the number of other scales or vertebrae. Therefore, measurements of the number of lateral scales and ribs in largemouth bass can be an important basis for distinguishing between the two subspecies. Fan et al. [10] counted these characters in largemouth bass cultured in China by traditional measurement methods. and the results showed that the number of lateral scales and the number of ribs in the largemouth bass cultured in China were closer to the northern subspecies of largemouth bass, which confirmed the initial prediction that the largemouth bass cultured in China was a northern subspecies. Cai et al. [11] used the northern and Florida subspecies of largemouth bass as parents to establish four test populations through parental selfing and reciprocal crossing and found that there were significant differences between the heads and tails of the two subspecies using principal component analysis and discriminant analysis. Li et al. [12] used multivariate analysis to compare largemouth bass populations from Guangdong and Taiwan, China, and the results showed that the morphological differences between the populations from the two regions were concentrated in the middle of the body and the tail.

1.2. Cytogenetic research on largemouth bass

The cytogenetics of largemouth bass have focused on the analysis of chromosome number, karyotype and DNA content. Hu et al. [13] investigated the chromosome number, karyotype and DNA content of largemouth bass and found that the chromosome number of largemouth bass was 2n=46, the karyotype formula was 2m+2st+42t and the number of chromosome arms (NF) was 48. Largemouth bass has one pair of metacentric chromosomes (chromosome 1), one pair of subtelocentric chromosomes (chromosomes 2, 4-23) with no submetacentric chromosome. Sun et al.

[14] found evidence via genomic analysis that chromosome 1 is a fusion chromosome: chromosome 1 of largemouth bass corresponds to chromosomes 20 and 24 of spotted seabass and chromosomes 18-21 and 24-25 of European seabass, respectively, and a region of high-density telomere elements was found at the 24th Mb region in the middle-upper part of chromosome 1 of largemouth bass, suggesting that chromosome 1 of largemouth bass is a fusion of two telocentric chromosomes and that one of them may be lost or degenerated.

1.3. Molecular population genetics research on largemouth bass

Lutz-Carrillo et al. [15] and Takagi et al. [16] used SSR technology to identify and evaluate the genetic diversity of wild largemouth bass in the United States and those introduced from Japan and concluded that the genetic diversity of the Florida subspecies was higher than that of the northern subspecies. Sun et al. [17], Liang et al. [18] and Su et al. [19] used microsatellite markers to analyze the genetic diversity of the cultured population of largemouth bass in China and found that the original species of largemouth bass in the United States had high polymorphism and a longer genetic distance than the cultured population. Hargrove et al. [20] and Li et al. [21] used the mitochondrial DNA D-loop region to analyze the population genetic variation of cultured largemouth bass populations, and the results showed that there was highly significant genetic differentiation between the northern subspecies of largemouth bass and the cultured population. Fu et al. [22] used microsatellite sequences of largemouth bass to design primers and construct multiple PCR systems, providing efficient research methods for population genetic analysis, lineage identification and genetic breeding of largemouth bass. Zhang et al. [23] applied isoenzyme detection techniques to completely distinguish the two subspecies of largemouth bass. Williams et al. [24] used RAPD molecular genetic marker technology to identify the two subspecies more sensitively. Lu et al. [25] used AFLP technology to compare and analyze the genetic structure of the selected population and cultured populations of the F₃ and F₄ generations of largemouth bass and concluded that largemouth bass were genetically stable and that the breeding effect was significant. Fan et al. [26] conducted an amplification analysis of largemouth bass populations from different sources and different geographical environments and established a microsatellite DNA fingerprint database of each largemouth bass population, which could clearly distinguish each hybrid species from its parents and effectively identify hybrid and pure largemouth bass populations. Yan et al. [27] used Roche 454 high-throughput sequencing technology to conduct transcriptome sequencing analysis of two subspecies of largemouth bass and establish an EST database, which can be used for molecular markers, construction of genetic maps and study of differential gene expression. Li et al. [28], Zhang et al. [29] and Nedbal et al. [30] sequenced and analyzed the complete mitochondrial genomes of the two subspecies of largemouth bass and found that the two subspecies could be effectively distinguished based on the COI sequences. A large number of scholars in China and abroad have carried out relevant research on the genetic variation of largemouth bass, and the results of these studies can provide a theoretical basis for the preservation of largemouth bass germplasm resources, identification of good varieties, breeding and improvement.

2. Current status of genetic improvement of largemouth bass

Research on the genetic improvement of largemouth bass is mainly focused on selective breeding, hybrid breeding, sex control breeding, polyploid breeding and molecular-assisted breeding (Table 1). The domestic cultured largemouth bass population has been cultivated for many years with severe inbreeding and low genetic diversity, resulting in the currently uneven quality level of varieties [8]. Therefore, breakthroughs and innovations in breeding technology provide an important theoretical basis for the genetic improvement of largemouth bass and make great contributions to promote the healthy development of the

Table 1The new varieties of largemouth bass.

Number	Name	Type	Formation time	Parental origin	District	Breeding unit
1	Micropterus salmoides "Youlu No. 1"	Selective breeding	2010	Four breeding groups of largemouth bass in China	Guangdong, China	PearlRiver Fisheries Research Institute
2	Micropterus salmoides "Youlu No. 3"	Selective breeding	2018	Micropterus salmoides "Youlu No. 1"and the northern subspecies of largemouth bass introduced to the United States in 2010	Guangdong, China	PearlRiver Fisheries Research Institute、Guangdong Liangshi Aquatic Seed Industry Co., Ltd
3	Micropterus salmoides "Wanlu No.1"	Selective breeding	2018	Introduced population of largemouth bass from Missouri region, USA	AnHui, China	Anhui Zhang Lin Fisheries Co., Ltd.
4	Micropterus salmoides "Jia Defeng No.1"	Selective breeding	2023	Micropterus salmoides "Youlu No. 1", largemouth bass breeding population in Taiwan and Guangdong	Guangdong, China	Xinrong Aquatic Products Co., Ltd
5	Hybrids derived from Micropterus and Lepomis	Hybrids	1977	Micropterus salmoides $(\mathfrak{P}) \times$ Lepomis cyanellus (\mathfrak{S})	American	Department of Genetics and Development, University of Illinois
6	Hybrids derived from Micropterus and Lepomis	Hybrids	2020	Micropterus salmoides (\mathfrak{Q}) \times Lepomis macrochirus (\mathfrak{F})	Guangdong, China	PearlRiver Fisheries Research Institute
7	Gynogenic largemouth bass	Gynogenesis	2022	Micropterus salmoides $(\mathfrak{Q}) \times Siniperca$ chuatsi (\mathfrak{F})	Hunan, China	Hunan Normal University
8	Triploid largemouth bass	Polyploid species	1992	Wild Micropterus salmoides	American	Heart of the Hills Research Station

largemouth bass aquaculture industry.

2.1. Selective breeding of largemouth bass

Selective breeding, as an important breeding method, has made significant progress in the breeding of largemouth bass and has produced several excellent varieties. Based on four selective breeding populations of northern largemouth bass in China, the Pearl River Fisheries Research Institute used traditional breeding techniques combined with modern molecular biology techniques to cultivate the first domestic largemouth bass through artificial selection, producing the new variety "Youlu No. 1." [9,31], with the growth rate as the main indicator. The growth rate of "Youlu No. 1" is faster than that of common largemouth bass, and the deformity rate of high back and short tail is lower. In 2012, the Pearl River Fisheries Research Institute and other organizations jointly conducted selective breeding to establish a basic breeding population with the largemouth bass "Youlu No. 1" and the northern largemouth bass as the parents. With growth characteristics under the conditions of ingestion of artificial fodder and easy domestication as the main indicators of selective breeding, the largemouth bass "Youlu No. 3" was bred [32]. The success rate of domestication for "Youlu No. 3" was significantly higher than that of "Youlu No. 1", and the growth rate was faster. In addition, there are many domestic units conducting selective breeding of largemouth bass, such as Foshan Xinrong Aquatic Company Limited, and other units have been jointly breeding a new variety of largemouth bass "Jia Defeng No. 1" since 2015, with growth rate and survival rate as the target traits, and it is currently in the pilot breeding stage [33]. Zhang Lin Fishery and other units carried out selective breeding research on the largemouth bass "Wanlu No. 1" with growth rate and disease resistance as the breeding objectives. The F₁ and F₂ generations have already been produced at present, which have obvious advantages in terms of growth rate, body size and survival rate [34]. However, selective breeding has shortcomings, such as a long breeding cycle and insufficient number of breeding target traits. Therefore, in terms of germplasm innovation for largemouth bass, it is necessary to innovate on the basis of selective breeding and advance the genetic improvement of largemouth bass.

2.2. Hybrid breeding of largemouth bass

Close hybridization studies of largemouth bass have focused on the northern largemouth bass, the Florida largemouth bass, and their offspring. Although there are numerous reports on this topic, researchers

have failed to reach a consensus on their growth rates thus far [35]. Some scholars believe that the growth rate of parents is faster. For example, Zolczynski et al. [36], Williamson et al. [37] and Philipp et al. [38] studied the northern subspecies of largemouth bass, the Florida subspecies and their offspring from reciprocal crossings in terms of growth traits and found that the northern largemouth bass grew significantly faster than the Florida subspecies and its offspring.

Moreover, some researchers concluded that hybrids have more significant growth advantages [35]. For example, Kleinsasser et al. [39] conducted a hybrid breeding experiment with largemouth bass and found that the growth rate of the offspring group of the hybridization of 2-year-old Florida largemouth bass $(9) \times$ northern largemouth bass (3)was the fastest, and that of the Florida subspecies was the slowest. Neal et al. [40] also conducted similar experiments and found that initially, the growth rate of the Florida largemouth bass and hybrid offspring was fast until it began to slow when the total length reached approximately 275 mm. The average body weights of the hybrid offspring were significantly higher than those of the Florida largemouth bass at 1 year and 2 years of age. Recently, Wang et al. [41] analyzed the F₁ offspring of hybrids between the northern largemouth bass (N), Florida largemouth bass (S), and "Youlu No. 3" (T) and found that the growth performance of "Youlu No. 3" (\mathfrak{P}) (T) \times Florida largemouth bass (\mathfrak{F}) (S) (TS) outperformed that of the remaining two subpopulations. This shows that different subspecies have different hybrid advantages, and the above studies also provide insights for subsequent genetic breeding of largemouth bass.

There are few studies on the distant hybridization of largemouth bass. The most distant hybridization of largemouth bass is intergeneric hybridization. Parker et al. [42] used Florida largemouth bass as the female parent and 10 fish of different genera in the same family as the male parent and found that the closer the genetic distance between the two parents was, the higher the success rate of normal development of hybrid offspring embryos. Whitt et al. [43] performed an intergeneric hybridization experiment between largemouth bass and green sunfish (Lepomis cyanellus) and found that the embryos of the largemouth bass (2) × green sunfish (3) hybrid showed a normal morphology and developmental process, whereas the embryos of the green sunfish (9) × largemouth bass (3) hybrid were abnormal in development, and almost all of them died by the time they hatched. Li et al. [44] analyzed the hybrid F_1 of largemouth bass $(\mathfrak{P}) \times$ bluegill sunfish (Lepomis macrochirus) (3) and found that their hybrid embryos developed normally and that the growth rate and fodder utilization of hybrid F₁ were significantly higher than those of the males, while there were no significant

differences with the females. Moreover, interspecific hybridization between largemouth bass and smallmouth bass (*Micropterus dolomieu*) has been studied extensively [45]. Wheat et al. [46] conducted hybridization and backcrossing experiments between largemouth bass and smallmouth bass and found that the increased heterozygosity of some dehydrogenase sites was related to the growth rate of the hybrid offspring. There is an obvious correlation, hybrid vigor is closely related to the genetic material in the egg cell. Although fish distant hybridization can significantly change the genotype and phenotype of offspring [47,48], there has been no report of a new fish with significant heterosis resulting from distant hybridization using largemouth bass as the parental species.

2.3. Sex-controlled breeding of largemouth bass

Studies show that female largemouth bass typically grow faster and live longer than males [49]. Therefore, many researchers have conducted exploratory experiments to generate single-sex groups and increase the ideal sex ratio. For example, a research team led by academician Shaojun Liu in the laboratory of the author induced gynogenesis in largemouth bass with sperm from Mandarin fish (Siniperca chuatsi) and obtained gynogenetic largemouth bass with a faster growth rate and better meat quality than the common largemouth bass. Garrett et al. [50] controlled the sex of largemouth bass by injecting steroid hormones, feeding fodder soaked in hormones and feeding live brine shrimp containing hormones, all of which successfully masculinized females. Arslan et al. [51] found that oral administration of 17β-estradiol slightly increased the incidence of females during all periods, whereas largemouth bass were unresponsive to exogenous androgens at 40 days of age when female differentiation had already occurred. Yan et al. [52] found that the Dmart1 gene showed obvious sexual dimorphism in largemouth bass and other fish. These results suggest that Dmart1 plays an important role in sex determination and differentiation in largemouth bass. Based on the discovery by Du et al. [53] that deletion of two male-specific genes could distinguish females from males by agarose gel electrophoresis of PCR, Wen et al. [54] further found that the sex determination system of largemouth bass was male heterogametic (XX/XY). Male-specific genetic markers were successfully developed based on the discovery of a large sex-differentiation region on chromosome 7 of largemouth bass. These series of sex determination studies play a great role in both sex identification and aquaculture applications of largemouth bass.

2.4. Polyploid breeding of largemouth bass

Polyploid breeding of largemouth bass has been little studied, and only triploid largemouth bass have been bred thus far. Garrett et al. [55] treated eggs with different hydrostatic pressures at 5 min after fertilization, and the results showed that 100 % artificially induced triploids of largemouth bass could be obtained at a high pressure of 8000 psi for a duration of 1 min with relatively low mortality. Neal et al. [56] found that there was no difference in the average daily growth rate of diploid and triploid largemouth bass when they were juveniles, but the reproductive development of triploid largemouth bass was later than that of diploid largemouth bass. In the future, further research on triploid largemouth bass over 1 year old should be undertaken to determine whether sterile triploids have a growth advantage over reproducing diploid adults.

2.5. Molecular-assisted breeding of largemouth bass

Sun et al. [57] sequenced the whole genome of varieties of large-mouth bass, combined PacBio single-molecule real-time sequencing with Hi-C technology, and detected certain genes associated with improved traits, such as growth, development and immunity. In addition, Sun et al. [14] also performed a genome assembly at the

chromosome level and identified eight gene families associated with ion channels, providing the molecular mechanisms of largemouth bass adaptation to fresh and brackish water. Li et al. [58] conducted a breeding study of multigene aggregation and found that the number of aggregated growth-related dominant genotypes in an individual was positively correlated with growth traits. Ma et al. [59] obtained three SNP loci associated with bait domestication, which were closely related to the ability of largemouth bass to utilize artificial compound fodder. Zhao et al. [60] developed SNP markers using sequencing platforms such as GBS and demonstrated that a small number of SNP subgroups were sufficient for kinship identification of largemouth bass. The results of the molecular studies carried out can be applied to breeding research to provide a scientific basis for breeding efficiency, feeding domestication and trait improvement.

3. Research on the nutritional needs and fodder preparation of largemouth bass

Largemouth bass is a typical carnivorous fish. Food intake in juveniles can reach 50 % of the body weight, and that in adults can reach 20 % of the body weight under good growing conditions in the 30 days after hatching, whose food is mainly rotifers and small crustaceans in zooplankton [61]. When the full length of juveniles reaches approximately 5 cm, they will be fed fry and aquatic insects; when they reach 10 cm in full length, they can be fed small fish [62]. As the fish grow, frogs, snakes and turtles can also become their prey. When food sources are insufficient, members of the same species often kill each other. In an aquaculture situation, the food provided to largemouth bass during the fry period is mainly animal fodder, such as surimi, fish pulp, small fry, and small shrimp. When largemouth bass fry reach approximately 3 cm in length, they can be domesticated with artificial compound fodder, and then, they can successfully ingest compound fodder after domestication. The main raw materials of fodder are fish meal, enzymatic fish pulp, soybean meal, flour, protein powder, tapioca starch, seawater fish oil, and soybean oil. The proportion of each component is often different.

3.1. Nutritional requirements of largemouth bass

The protein requirement in fodder of largemouth bass increases or decreases depending on the period of growth. In general, the protein requirement of largemouth bass is more than 40 % in the fodder, and 46.0-49.0 % is appropriate, of which fishmeal should contribute no less than 50 % of the protein [63]. Largemouth bass have a low capacity to utilize sugars, and high sugar levels can predispose to fat accumulation in muscle. Gou et al. [64], Tan et al. [65] and Li et al. [66] showed that the carbohydrate content in largemouth bass fodder should not exceed 20 %. According to the study of Xu et al. [67], the specific growth rate of largemouth bass increased significantly when the sugar-fat ratio was 0.32, and its apparent digestibility of protein and energy decreased significantly with increasing sugar-fat ratio. In general, the fat content should be kept at 11.5–14 %. In addition to fat requirements, the content and composition of essential fatty acids in fodder are equally critical. Tidwell et al. [68] suggested that the content of essential fatty acids in largemouth bass diets should be approximately 1 %. However, the optimal ratio of both linoleic and linolenic acids is still under investigation. The cellulose requirement of largemouth bass was reported by Qian et al. [69]. It is suggested that its content should not be higher than 3.5 %. Moreover, a high concentration of vitamin C can improve the ability of largemouth bass to resist diseases, but there is currently no relevant report on the requirement of vitamin in fodder [70]. Zhang et al. [71] found that compound fodder additives such as Astragalus polysaccharides, bile acids, and L-carnitine added to basal fodder could effectively promote the growth of largemouth bass and improve the antioxidant capacity of the liver.

3.2. Fodder domestication of largemouth bass

In conventional cultured production, largemouth bass are mainly fed chilled fish or small miscellaneous fish. However, due to factors such as high aquaculture costs and susceptibility to disease, the use of artificial compound fodder is imperative. Conventional domestication refers to the domestication of largemouth bass with a body length of approximately 3 cm. Initially, during the 1st-10th day, largemouth bass will be fed mixed bait consisting of copepods, red worms and fish slurry, and the amount of water flea feeding will be gradually reduced until only fish slurry is fed. On the 11th-20th day, after successful conversion to fish slurry, small-pellet compound fodder is added to the fish slurry, and the feeding amount of fish slurry is reduced day by day until the fry are only fed artificial compound fodder [72]. The addition of food attractants to fodder can accelerate domestication. Researchers found that the survival rate of conventionally domesticated fry up to the ponding specification of 5 cm was 68.4 %. Additionally, it was found that after 10-14 days of domestication, most fry can be successfully domesticated and transferred to artificial diets [73]. Some scholars have proposed effective programs for the domestication of largemouth bass on compound fodder. Zhang et al. [72] designed a domestication device using flowing water to optimize the shortcomings of traditional domestication techniques; it can feed fry uniformly through flowing water feeding to achieve regular and fixed feeding.

In addition, factory domestication in large-scale aquaculture of largemouth bass has become more popular in recent years. Different from the traditional domestication method based on outdoor pond domestication, factory domestication is carried out in an indoor factory recirculating water aquaculture system, which is easy to manage and has a high degree of control [74]. The fry are in a fully enclosed environment, and phototropism or knocking sounds are used to make the fish cluster, which is conducive to centralized domestication [75]. In the early stage of domestication, the fish are fed fairy shrimp, in the middle stage they are fed copepods, and in the late stage, all the fish are fed artificial fodder, and the size of the fodder is gradually increased starting from powdered fodder. To avoid affecting the water quality, the principle of a small number of times must be followed during the feeding process. There are several key technical points in the domestication method: the choice of the time of fry feeding domestication [76], the feeding method, the choice of domestication bait, the domestication process [77], and water quality management.

4. Largemouth bass aquaculture and diseases

4.1. Aquaculture distribution and yield

In 1983, Guangdong Province took the lead in introducing largemouth bass from Taiwan. In 1985, artificial breeding was successfully carried out. Since then, largemouth bass has ushered in rapid development in China [5]. The COVID-19 pandemic has had an enormous impact on all industries, but the yield of largemouth bass is increasing annually. According to the 2023 China Fisheries Statistics Yearbook, in 2022, the annual yield of largemouth bass in China exceeded 800,000 tons [7]. Except for Hainan, Heilongjiang and Qinghai, there are no statistical data for largemouth bass; 28 provinces and cities in the country's 31 regions have cultured largemouth bass, of which 11 provinces and cities have an aquaculture yield of largemouth bass exceeding 10,000 tons. In the past decade, the annual aquaculture production of largemouth bass in China increased from 240,000 tons in 2012 to 800,000 tons in 2022 (Fig. 1). Currently, largemouth bass aquaculture yield has reached a new high and is still showing a high linear growth trend. Largemouth bass has become an important freshwater aquaculture species in aquaculture areas throughout South China, East China, Central China, Southwest China and other regions, with Guangdong, Zhejiang, Jiangsu and Hunan as the main production areas.

4.2. Aquaculture modes

At present, the aquaculture mode of largemouth bass is mainly based on pond culture. Largemouth bass can consume artificial compound fodder, but the high protein content in fodder also tends to cause water quality deterioration and induce fish diseases, so the aquaculture mode of largemouth bass will also be changed according to local conditions [78]. The sustainable development of the largemouth bass aquaculture industry can only be achieved by exploring new and efficient aquaculture modes. Several important largemouth bass aquaculture modes are described below:

(1) Pond culture

Culture ponds is currently the most widely used aquaculture mode, and it is a medium-to-high-density aquaculture mode, which is convenient for production management [79]. The water depth of the large-mouth bass culture pond is recommended to be approximately 1.5–2.5

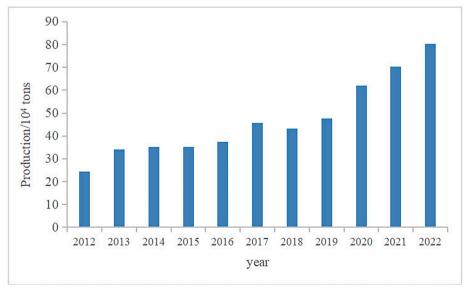


Fig. 1. Changes in the production of largemouth bass in China from 2012 to 2022.

m. Generally, the fry are released and the fish are marketed in the same year. This method has a low bait coefficient and a high aquaculture yield. The yield in the Jiangsu and Zhejiang regions is $1.5{\text -}2.2~{\rm kg/m^2}$, and the yield in the Guangdong region can reach $4.5{\text -}6.0~{\rm kg/m^2}$. However, in pond culture, the impact of high density is first the increase in water quality deterioration, followed by the mutation of harmful microorganisms and the rapid spread of diseases. Therefore, fish should be fed in small quantities many times to reduce fodder waste, and regularly monitoring the values of dissolved oxygen, pH, ammonia nitrogen, nitrite and other indicators in the water, as well as the application of control measures at different stages, is helpful for disease prevention and control.

(2) Polyculture in ponds

Putting largemouth bass together with filter-feeding silver carp and bighead carp into pond polycultures will help control the density of plankton and maintain good water quality [80]. In addition, the polyculture mode of largemouth bass and river crabs [81] has also brought new economic benefits to farmers. Largemouth bass are active in the middle and upper layers of the water body, and crabs are active in the middle and lower layers of the water body. The excrement generated by largemouth bass provides nutrients to river snails, which in turn can purify the water body and provide fresh food for crabs. While improving the efficiency of ponds and reducing the risk of traditional monoculture, polyculture also promotes green culture. The polyculture of largemouth bass and river crab not only does not increase the burden of crab ponds but also increases biodiversity, thereby reducing nutrient loss and increasing aquaculture income. This mode can achieve yields of 0.75–0.9 kg/m² for largemouth bass and 0.09 kg/m² for crab.

(3) Land-based factory recirculating aquaculture

Land-based factory recirculating aquaculture [82,83] has the advantages of complete control, recycling, green environmental protection and efficient yield. This technology is suitable for the promotion of aquaculture throughout the country, and there are such farming modes in Guangdong, Jiangsu and Zhejiang. Based on the comprehensive consideration of the growth performance of largemouth bass and the economic benefits of culture, it is most appropriate to maintain the density of adult fish at 65 fish/m² using barrels with an inner diameter of 4 m and a height of 2 m, with the yield of a single barrel being 500–600 kg; while with the flow tank as the aquaculture area of the pond engineering recirculating aquaculture mode, the flow tank aquaculture area yield is 80–100 kg/m². The combination of land-based industrial recirculating aquaculture with rice-fishery integrated culture or aquaponics [84] can promote resource recycling and effectively achieve environmental emission reduction.

(4) Cage culture

Cage culture [85] is mainly concentrated in regions with abundant water resources, and largemouth bass cage culture can be carried out in pollution-free reservoirs and lakes. When largemouth bass grow to a certain stage, there will be a disparity in size, and it is necessary to frequently divide the cage [86]. The cage culture mode of largemouth bass generally adopts a cage frame size of 5 m \times 5 m \times 2.5 m, and when the fry stocking density (depending on the size of the fish body) is approximately 3 cm, the stocking density is 1000–1500 fish/m²; when the size is 7–10 cm, the stocking density is 600–800 fish/m². With the growth of largemouth bass, the stocking density should gradually decrease; when the fish grow to 20 cm or 150–200 g, the stocking density is 80–120 fish/m², and this density can be maintained until the commercial fish reach a size of 450–750 g, and the yield can reach 50–70 kg/m² [87]. In addition, because some farmers are keen to pursue the short-term economic benefits brought by cage culture, they throw a

large amount of bait, blindly expanding the scale of cage culture, resulting in the deterioration of the environment of aquaculture waters, water quality eutrophication and other adverse consequences; some areas have begun legislation to restrict cage culture in lakes and reservoirs and prohibit fertilization and feeding [88].

4.3. Aquaculture disease problems

In recent years, largemouth bass have become susceptible to many diseases due to feeding on unquarantined wild fish, unreasonable use of fodder, high culture density and other reasons. Basic research on various diseases of largemouth bass is not sufficient, and prevention and control measures are lacking, which seriously hinders the development of the largemouth bass aquaculture industry. There are three main types of common diseases in largemouth bass, namely, bacterial diseases, viral diseases and parasitic diseases (Table 2).

5. Circulation and processing of the largemouth bass industry

5.1. Circulation mode

At present, there are approximately 120 largemouth bass circulation enterprises, mainly distributed in the Pearl River Delta region. Guangdong, the province with the highest yield of largemouth bass aquaculture in China, produced 381,900 tons in 2022, accounting for 47.6 % of the national yield. Calculated with a circulation ratio of 90 %, the trading volume of largemouth bass in Guangdong in 2022 was 343,700 tons, with a transaction volume of approximately 10.25 billion yuan [7]. The circulation ratio share of largemouth bass in the main production areas is changing, and the share from Guangdong Province is decreasing, while the share of other provinces is increasing [89]. The circulation direction of largemouth bass changed from mainly "south-to-north fish diversion" to partly "north-to-south fish diversion", and the circulation period also changed from May to October to the whole year, with only the circulation volume differing between the two circulation directions. In general, the overall circulation of largemouth bass will continue to increase, and the circulation industry will be closely integrated with the catering industry. With the development of circulation technology, the circulation of largemouth bass live fish has gradually developed from individual transportation to cold chain transportation. The high-density and low-temperature temporary culture of live fish and pure oxygen cold chain remote transportation technology have gradually covered the consumption field of largemouth bass throughout China, and the processing yield value will exceed 10 billion.

In recent years, consumers' demand for fast and convenient food has increased, as has the maturity of prefabricated fish processing technology. The consumption form of largemouth bass has also gradually shifted from predominantly live fish consumption to parallel development of live fish and processed products [90]. At present, the varieties of preprocessed largemouth bass dishes are mainly boiled fish fillets and pickled fish fillets, which can greatly preserve the restaurant taste through rapid freezing and sealing technology. Scholars are also committed to optimizing cold chain logistics. For example, Ju et al. [91] found that green tea polyphenols combined with packaging can effectively inhibit the increase in the total colony count of largemouth bass during the entire logistics period while allowing the fish to maintain good color and high sensory scores.

5.2. Processed product

There has been less research on deep-processing products of large-mouth bass in recent years, which mainly focus on pickled and air-dried bass. Zhang et al. [92] and Liu et al. [93] used largemouth bass as the raw material for primary processing to investigate the effects of the pickling and air-drying process on the oxidative degradation of its lipids, the hydrolysis of proteins and the formation of flavor characteristics. Li

Table 2
Common diseases of largemouth bass and prevention and control methods.

Disease type	Pathogen	Susceptible period	Symptoms of infection	Prevention and control method
Bacterial disease	Flavobacterium columnare	April–June and September–October	The gills of juvenile fish are rotten, and the gills of adult fish are infected and turn yellow and gradually become necrotic	Disinfection of the whole pool and oral administration of antibacterial drugs
	Nocardia	June-September	Extensive necrotic white nodules appear on the body surface and internal organs of sick fish	Disinfect in time, feed scientifically, and oral administration of antibacterial drugs
Viral disease	Largemouth bass ranavirus	May-August	There are no obvious symptoms and the virus is recessive	No effective drugs, scientific feeding, timely disinfection
	Micropterus salmoides rhabdovirus	March–April	Organs are enlarged, the body color is black, the body is curved, and swimming irregularly in a spiral shape	No effective drugs, comprehensive prevention and treatment
Parasitic disease	Trichodina	March–May	The body color is darker, the fish body is thin, there is mucus on the body surface, and the gills are white and rotten	Disinfect the whole pond and soak the fish in glacial acetic acid for 1 h to effectively prevent trichozoa
	Ichthyophthirius multifiliis	March–May	Swimming slowly, the fish body is thin, and the body surface and gills are covered with white dot-like cysts	Disinfection of the whole pool, scientific feeding

et al. [94] developed the technology of tea flavoring lighted salted largemouth bass to improve the defects of hard texture and high salt content of traditional salted fish, which can be used as precooked and ready-to-eat aquatic products after vacuum packaging. Wei et al. [95] also conducted a similar study to explore the application of hurdle technology in light pickled semidry processing of largemouth bass. Wang et al. [96] explored a new processing technology to process largemouth bass into fish floss products with a unique flavor. Zhou et al. [97] innovatively combined largemouth bass with Shanghai smoked fish, with reference to the processing of traditional Shanghai smoked fish, and produced a new type of Shanghai smoked fish by improving raw materials and processing technology. To solve the problems of losses caused to farmers and restrictions to the development of the industry caused by the slow sales of adult largemouth bass after they are concentrated in the market, it is necessary to optimize and enrich the deep processing technology of largemouth bass, with a view to achieving the industrial production of largemouth bass products.

In terms of industry and brand building, many culture areas are dominated by individual farmers. Because of the volatility of seed prices, individual competitiveness is weak, and farmers do not have the ability to resist risks, resulting in very limited development. Coupled with the lack of good processing routes and relatively backward production links, these factors lead to the existence of a single major product type in the largemouth bass industry. Moreover, the lack of a well-known largemouth bass brand and a short industrial chain hinder the further development of the industry.

6. Recommendations and prospects

With the maturity of largemouth bass aquaculture technology and breakthroughs in compound fodder technology, the scale of largemouth bass aquaculture has expanded rapidly, and the yield has increased annually. However, as the largemouth bass industry prospers, it is also facing many problems, which limit its development. In view of this, countermeasures and recommendations are given for the constraints that exist in the largemouth bass industry.

(1) Breeding and promotion of improved varieties

The contribution rate of improved varieties to the aquaculture industry is increasing, so it is imperative to strengthen the management and conservation of largemouth bass germplasm resources. First, it is necessary to establish the germplasm bank of largemouth bass as soon as possible, optimize the germplasm quality, accelerate the cultivation and promotion of improved varieties, pay attention to parental selection, adopt high-quality parental breeding, expand the construction of fish farms, and make full use of local advantages to carry out the localization of seedling breeding technology to promote the upgrading of

largemouth bass breeding varieties. Second, it is necessary to innovate breeding methods. Traditional selective breeding has limitations, and the target traits of breeding are single traits. Therefore, a variety of breeding methods can be combined to carry out comprehensive breeding for multiple traits, such as growth and stress resistance, with the aim of breeding a new variety of largemouth bass with better traits. Third, it is also necessary to improve laws and regulations, strengthen supervision and management capabilities, improve the related standards of seedling breeding, seedling quality testing and information technology, establish a controllable germplasm performance and information traceability system, and realize the effective combination of improved varieties and good methods. Fourth, the state should give full play to the leading role of the government in the development of the improved variety aquaculture industry, support the cultivation, production and promotion of improved varieties from both policy and financial aspects, encourage enterprises to carry out research and development of new varieties, carry out promotion work such as improved variety breeding demonstration, large-scale breeding technology training and guidance, and expand the contribution rate and coverage rate of improved varieties.

(2) Disease prevention and control

The frequent occurrence of pests and diseases is also one of the key factors leading to the decline in yield and quality of largemouth bass. Therefore, it is necessary to achieve good disease prevention and control results from the following four aspects. First, for the selection of healthy and high-quality largemouth bass seedlings, it is best to ensure that the specifications are uniform and effective virus detection is carried out. Before the release of seedlings, quicklime or bleaching powder should be used to disinfect the pond, kill germs and reduce the occurrence of fish disease; after disinfection, enough fertilizer water and water transfer work should be performed. Second, a good aquaculture environment should be selected and an environmentally friendly aquaculture mode should be established; the aquaculture area should ensure sufficient water sources, convenient drainage and irrigation, and location away from toxic and harmful places and pollution sources or pollutants. In addition, large-size silver carp and bighead carp can be raised in the aquaculture pond of largemouth bass to regulate the water quality and achieve a suitable environment for the growth of largemouth bass. When in polyculture, largemouth bass and river crab can move in different habitat spaces, times and water layers. The feces excreted by largemouth bass can serve as a nutrient source for aquatic grasses needed by crab culture, effectively reducing water pollution and improving the ecological environment, which is conducive to the healthy growth of largemouth bass. Third, compared with feeding frozen fish, feeding high-protein compound fodder can effectively reduce water pollution and reduce aquaculture costs. The immunity and disease resistance of largemouth bass can be enhanced by adding immune polysaccharides and vitamins B and C to daily feeding. In the epidemic season or after the occurrence of disease, it is also possible to prevent the occurrence and spread of disease by changing the feeding method, reducing the amount of feeding and changing the location of feeding. Fourth, for the standardized and rational use of fishery drugs, Chinese herbal preparations are preferred because they have the advantages of high safety, low toxicity, less residue, etc. The drug should meet the requirements of healthy aquaculture and pollution-free production when considering factors such as the largemouth bass itself and human health, but is also conducive to consider resource protection. In summary, it is necessary to strengthen the monitoring and prevention of diseases of largemouth bass. Based on ecological prevention and control technology, it is important not abuse the use of drugs and firmly grasp the concept of "prevention is more important than cure".

(3) Improve artificial compound fodder

At present, the problems of mixed quality and a low utilization rate of compound fodder products cannot be ignored. The use of compound fodder is the key technology of largemouth bass aquaculture, and highquality largemouth bass fodder formulations should have the characteristics of being science-based, safe, with good palatability, amino acid balance and high performance cost ratio. First, the formula should be scientific and reasonable; the fodder formula should be based on feeding standards to meet the nutritional needs of largemouth bass in different growth stages and different aquaculture modes. Next, fodder quality and safety must meet the quality and safety standards stipulated by the state and legal compliance. Furthermore, for high efficiency and environmental protection, environmentally friendly fodder can significantly improve the aquaculture environment and fodder utilization rate, which is beneficial to the health of largemouth bass. Last, fodder should be green and healthy; the development and application of green fodder can provide rich vitamins and various amino acids for largemouth bass, enhance immune function, promote growth and development, reduce morbidity and reduce fodder costs. In the future, the research and development of largemouth bass fodder should be more accurate, sustainable, efficient, healthier and environmentally friendly. Additionally, processing technology should optimize the fodder formula, strengthen the promotion and application of artificial compound fodder, promote healthy, efficient and safe high-quality fodder to replace frozen fish, and improve the economic efficiency of aquaculture.

(4) Strengthen industry and brand building

The market price of largemouth bass fluctuates with the change in the relationship between supply and demand. When the fish are listed in the peak season, the supply exceeds the demand, and the price is very low. However, the current development of the largemouth bass processing industry is still very slow, and it is impossible to effectively rely on the sale of processed products to alleviate the enormous losses to farmers caused by unsellable fresh fish. Therefore, it is necessary to speed up the research and development of deep-processed largemouth bass products, diversify the types of largemouth bass products, and process them into leisure foods such as fish floss, dried fish, and pickled fish fillets to increase the added value of products and promote the food culture of largemouth bass. Furthermore, it is also necessary to establish the largemouth bass brand, promote green and high-quality products to enter the market, and gradually increase its influence. Last but not least, it is also essential to help farmers establish professional cooperatives to solve the problems of scattered aquaculture and low professional level, strengthen the cooperation between individual farmers and related enterprises, and establish the business mode of "enterprise + farmer". Enterprises should rely on their advantages in technology, capital and other aspects to drive the development of individual farmers. Industrial management is the key to the stable development of the largemouth bass

industry.

In summary, the largemouth bass, as a fish with important ecological and economic significance, is deeply loved by farmers and consumers. With the optimization and improvement of all aspects of the largemouth bass industry chain, such as promoting the revitalization of the seedling industry, the improvement of compound fodder, and the change of aquaculture modes, the largemouth bass industry is moving toward healthy, efficient, low-consumption and sustainable development. Greater promotion of the largemouth bass freshwater aquaculture fishery is necessary to achieve more significant economic and social benefits.

CRediT authorship contribution statement

Pengfei Yu: Writing – original draft, Data curation. Hong Chen: Data curation. Mingli Liu: Data curation. Haitao Zhong: Visualization. Xueyan Wang: Visualization. Yilin Wu: Visualization. Yu Sun: Resources, Data curation. Chang Wu: Visualization. Shi Wang: Visualization. Chiye Zhao: Methodology, Data curation. Chaoying Luo: Investigation, Data curation. Chun Zhang: Funding acquisition, Conceptualization. Fangzhou Hu: Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Conceptualization. Shaojun Liu: Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. Shaojun Liu is the editor-in-chief for Reproduction and Breeding and was not involved in the editorial review or the decision to publish this article. All authors declare that there are no competing interests.

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