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Macro-Hybrid and Micro-Hybrid of Fish

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ABSTRACT

This study reviews the progress in fish breeding, focusing on distant hybridization and gynogenesis, and introduces the theory of macro-hybrid and micro-hybrid. The macro-hybrid refers to the allo-progeny derived from distant hybridization, including the allo-progenies. The micro-hybrid refers to the auto-progenies derived from distant hybridization or heterologous sperm-induced gynogenesis, which possess a genome derived predominantly from the maternal but contain DNA fragments originating from the paternal. Macro-hybrids induce significant phenotypic changes, while micro-hybrids improve growth rate and stress resistance. Both hybridization and gynogenesis exhibit high selective pressure. This review elucidates how selective pressures (homozygosity + heterologous sperm + cold/heat shock) of the heterologous sperm-induced gynogenesis contribute to the generation of effective genetic variations. The study also presents the technologies of macro-hybrid and micro-hybrid. In macro-hybrids of distant hybridization, parental chromosome numbers are closely matched, enabling the formation of fertile allo-diploid and allo-tetraploid strains. In micro-hybrid of distant hybridization, equal or differing chromosome numbers between parents yield fertile auto-tetraploid and auto-diploid strains. In micro-hybrid of heterologous sperm-induced gynogenesis, equal or different chromosome numbers between parents yield auto-diploid strains. The integration of heterologous sperm-induced gynogenesis, back-cross, and self-cross strategies can address the issue of all-female progeny resulting from gynogenesis. A series of auxiliary breeding techniques is established to support the macro-hybrid and micro-hybrid breeding. Case studies of superior fish strains developed through macro-hybrid and micro-hybrid breeding are presented. The establishment of macro-hybrid and micro-hybrid theory and breeding technologies holds significant value for fish breeding.

1 | Overview of Breeding Techniques in China and Abroad

Aquatic products provide approximately one-third of the high-quality animal protein consumed by the Chinese population. Among them, fish account for 42% of aquatic products, making them the largest category and a vital source of protein [1, 2]. The seed industry contributes the most to the aquatic products value chain. Therefore, fish breeding techniques play a crucial role in aquaculture. The overall purpose of aquaculture breeding is to develop improved aquatic species with enhanced traits such as growth, disease resistance, and environmental adaptability to

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support sustainable and efficient production. The following is an overview and analysis of fish breeding techniques both in China and internationally:

1.1 | Selective Breeding

Selective breeding is one of the most commonly used breeding methods and holds an essential position in fish breeding [3]. Its primary goal is to identify and select individuals or populations with desirable traits from one or more groups. Traditional selective breeding approaches in fish include mass selection, family selection, parent selection, and combined selection [4–6], as well as BLUP (Best Linear Unbiased Prediction) based on estimations of breeding values [7–9]. These techniques have been applied in the selective breeding of various freshwater [10–12] and marine fish species [13–16]. Moreover, molecular marker-assisted selection (MAS) [17–32], genomic selection (GS) [33–41], and genome-wide association studies (GWAS) [42–47] have also been applied in fish breeding. Conventional selective breeding is simple, inexpensive, and has been widely applied to improve growth, yield, and adaptation by utilizing natural variation. However, it is slow, imprecise, and limited by available genetic diversity, with risks of inbreeding and trade-offs [48, 49]. MAS enhances precision by targeting specific genes or QTLs associated with important traits, accelerating genetic gain and reducing environmental bias. Yet, MAS is most effective for traits controlled by few major genes and may have limited impact on complex, polygenic traits [50–52]. GS overcomes this limitation by using genome-wide markers to predict breeding values, enabling faster, more accurate selection for both simple and complex traits. Although GS requires significant investment in genotyping, bioinformatics, and training populations, it provides the highest efficiency and long-term genetic improvement compared to conventional and MAS approaches [53, 54].

1.2 | Germ Cell Transplantation and Nuclear Transfer Breeding

Nuclear transfer has been applied to the development of nucleocytoplasmic hybrid fish and the generation of homozygous diploid fish. Experiments in teleost species, such as the goldfish (*Carassius auratus*) and the Chinese bitterling (*Rhodeus sinensis*), have demonstrated that blastula-stage nuclei possess totipotency, capable of directing enucleated eggs to develop into embryos and adults. For example, by transplanting the kidney cell nucleus of triploid crucian carp (*Carassius auratus*) into enucleated diploid crucian carp eggs, researchers successfully produced fertile cloned fish, confirming the genetic and developmental totipotency of differentiated fish somatic nuclei for the first time [55]. However, low survival rates in nucleocytoplasmic hybrid fish remain a challenge and require further research [56].

Researchers have also transplanted primordial germ cells from rainbow trout into the peritoneal cavity of newly hatched masu salmon fry, resulting in masu salmon producing rainbow trout offspring, demonstrating the feasibility of germ cell transplantation in fish [57, 58]. Subsequent studies successfully established spermatogonial stem cell lines (e.g., SG3) and haploid embryonic stem cell lines in species such as medaka and rainbow trout, creating germ cell transplantation systems and applying semi-clonal techniques to produce fertile individuals [59–61]. Germ cell transplantation in fish can be classified into intra-species, inter-species, and triploid recipient transplantation. Among them, interspecific transplantation has shown that donor cells can undergo accelerated differentiation in heterologous recipients. Triploid recipients have also successfully produced purebred offspring, highlighting the mechanism and potential applications of environmentally regulated reproductive development [58, 62–64]. Both germ cell transplantation and nuclear transfer techniques continue to play important roles in fish breeding research [60, 63, 65–80]. While nuclear transplantation has demonstrated the totipotency of fish somatic cells, immune rejection of donor cells remains a significant obstacle in cross-species transplantation, significantly affecting chimeric survival and the efficiency of germ cell colonization [81]. Although germ cell transplantation transcends species barriers, the long-term reproductive viability of donor-derived gametes is questionable-heterologous microenvironments may induce epigenetic dysregulation or aberrant differentiation in germline stem cells [82]. From a technical perspective, challenges in achieving precise microsurgical manipulation and synchronizing recipient embryos represent major procedural bottlenecks, restricting large-scale implementation. Existing methodologies function mainly as proof-of-concept [83], while meaningful application in sustainable aquaculture requires advances in immunocompatibility, automation, and thorough long-term safety evaluation.

1.3 | Physical and Chemical Induction of Polyploidy

Artificial polyploid breeding can be achieved through physical or chemical induction. Physical methods primarily involve heat or cold shock and hydrostatic pressure to induce triploid or tetraploid individuals [84–90], while chemical induction methods use agents such as colchicine to achieve the same results [91–95]. These approaches differ from the polyploid populations obtained via distant hybridization. To date, no reports have successfully established bisexual fertile tetraploid fish lines using these methods, possibly due to difficulties in achieving exact tetraploid chromosome numbers.

We further posit that while physical or chemical polyploid induction can achieve high success rates, they carry significant limitations, including challenges in establishing stably fertile tetraploid lines [93], residual chemical inducers (e.g., colchicine), and elevated teratogenic risks from physical stressors. At the same time, escaped sterile individuals may compete with wild conspecifics, whereas fertile tetraploid escapees pose a risk of genetic pollution through introgression [96]. Currently, these techniques are primarily used in experimental settings. For their broader application in scalable breeding, it is essential to integrate them with complementary strategies and to conduct systematic evaluations of their long-term health and ecological impacts.

1.4 | Transgenic and Gene Editing

The world's first transgenic crucian carp was produced in China [97], followed by several related studies [97–102]. The use of transgenes to introduce exogenous genes for the enhancement of desirable traits has achieved notable success in multiple fish species [98, 103–107]. Aquaculture research primarily focuses on enhancing growth, disease resistance, cold tolerance, and exploring life mechanisms [98, 108–119]; however, concerns about the ecological risks of transgenic fish remain. The genetically modified Atlantic salmon, developed in the United States, became the world's first approved transgenic fish for commercial sale [120–122].

Gene editing enables direct manipulation of DNA and has been widely applied in model organisms such as zebrafish [123–132] and in economically important fish species [133–137]. Recently, the knockout of the *cntd1* gene enabled the production of unreduced gametes and polyploid zebrafish, offering new avenues for creating triploid and tetraploid fish [138]. Furthermore, gene editing has shown promising results in reducing intramuscular bones in fish [139–146]. Although significant progress has been made in transgenic and genome editing for aquaculture breeding, their systemic risks remain insufficiently evaluated. To prevent the pitfalls of unchecked technological optimism, it is essential to couple these advancements with thorough life-cycle ecological risk assessments, ethical oversight, and consideration of societal acceptance.

1.5 | Distant and Close Hybridization Breeding

Hybrid breeding not only produces heterosis but also creates progeny that combine superior traits from both parents, surpass parental traits, or exhibit novel characteristics. This method has become a widely applied, effective, and rapid approach to introduce genetic variation [147–158]. Through hybridization, advantageous genes from different parents can be combined, significantly improving the overall performance of the offspring [159–161]. As of 2024, hybridized fish varieties account for 32% of all new fish breeds approved in China, among which distant hybrids constitute 68%. Some of these new varieties have already shown excellent performance in commercial applications, such as *Channa argus*×*Channa maculata*, *Carassius auratus cuvieri*×*Carassius auratus red var*, and *Megalobrama amblycephala*×*Culter alburnus* [162–164].

Since the first report on distant hybridization in fish in 1558, studies have been conducted on over 1080 fish species across 56 families worldwide, with a primary focus on orders such as Centrarchiformes [165, 166], Cypriniformes [167–172], Poeciliidae [173], and Salmonidae [174, 175]. Since the late 1950s, breeding research using hybridization has resulted in a series of high-quality fish varieties, promoting the development of aquaculture [176–183].

Our team has conducted extensive research on fish distant hybridization, overcoming the three major challenges: low survival rate, reproductive difficulties, and identification challenges. They have elucidated the main genetic and reproductive patterns in distant hybrids, established both one-step and multi-step breeding strategies, and successfully cultivated fertile tetraploid lines, naturally gynogenetic strains, and improved triploid fish varieties [155, 159, 184–188]. Among seven distant hybridization combinations, seven naturally gynogenetic fish types have been developed [149, 150, 153, 189–193].

Nonetheless, more precise breeding through distant hybridization remains a topic for further investigation. Building on previous work, our team has integrated distant hybridization with heterologous sperm-induced gynogenesis, establishing the concepts and technologies of macro-hybridization and micro-hybridization, thereby enhancing the accuracy and applicability of these breeding approaches [155]. While distant hybridization demonstrates significant efficacy in developing novel germplasm (e.g., allopolyploids, gynogenetic lines) and advancing commercial cultivar development (accounting for 32% of new aquatic varieties in China), its potential risks remain systematically unassessed. Hybrid progeny frequently exhibit genetic instability leading to trait segregation [194], and large-scale adoption exacerbates genetic homogenization within farmed populations. Escaped hybrids may compromise the genetic integrity of wild relatives through introgression [195]. Current regulatory frameworks lack sufficient ecological risk assessment for the environmental release of hybrids, with reproductive barriers in inter-familial/genus crosses (e.g., fertility fluctuations, offspring deformities) persisting as technical constraints. Integrating genomic surveillance to quantify introgression risks and establishing an interdisciplinary evaluation framework are imperative to reconcile breeding benefits with ecological sustainability [196].

1.6 | Gynogenetic (and Androgenetic) Breeding

Gynogenesis can be classified into artificial and natural types. Artificial gynogenesis is often achieved through heterologous sperm-induced activation. In this process, eggs are activated by sperm from a different species, but the resulting offspring inherit genetic material almost exclusively from the maternal genome, leading to highly homozygous populations. Cold (or heat) shock treatment is applied to prevent the extrusion of the second polar body and achieve chromosome doubling.

Since the 1960s, scientists worldwide have successfully induced gynogenesis and androgenesis in various fish species [197–207].

Over the years, we have developed multiple superior artificially gynogenetic fish [208–217] and naturally gynogenetic strains [184, 218–221], many of which exhibit excellent or unique traits and constitute novel germplasm resources. For instance, gynogenetic mrigal carp exhibit enhanced cold tolerance [210], gynogenetic mandarin fish exhibit accelerated embryonic development [208], gynogenetic bluntnose black bream show increased hypoxia tolerance [214, 222], and gynogenetic northern snakehead shows faster growth [217]. Additionally, gynogenetic white crucian carp demonstrate improved disease resistance and growth [212], and gynogenetic koi exhibit more vivid coloration [223]. Naturally gynogenetic grass carp exhibit higher amino acid content in muscle tissues [191], while naturally gynogenetic bluntnose black bream exhibit superior nutrition and muscle characteristics [224].

Androgenesis refers to the development of embryos initiated by inactivated eggs fertilized by normal sperm, with the paternal genome guiding development. Although rare in nature, cases of androgenesis have occasionally been observed in fish hybrids [225–227] (for example, carp and grass carp hybrid, white crucian carp, and bream hybrid). Artificial induction of androgenesis has been successfully achieved in several species [228–232]. Notably, the use of diploid sperm from tetraploid fish can bypass the need for chromosome doubling treatments and significantly improve success rates [159, 204, 205, 233–235].

For instance: In Cypriniformes with buoyant eggs (e.g., grass carp [236], silver carp, bighead carp, mrigal carp [210]), the optimal cold shock duration is 10–15 min; for adhesive eggs (e.g., carp, crucian [212], blunt snout bream [214], culter), it is 20–40 min; for Perciformes (e.g., largemouth bass [211], mandarin fish [208], northern snakehead [217]) and Siluriformes (e.g., channel catfish, native catfish, yellow catfish), the ideal cold shock duration is 15–20 min; empirical evidence from extensive experimental results underscores the necessity of establishing protocols with quantifiable survival rates. Although androgenesis/gynogenesis has successfully generated diverse elite lines, its application faces persistent bottlenecks: artificially induced survival rates typically fall below 5%, and ploidy manipulation techniques frequently induce teratogenic effects. These inherent limitations represent critical priority areas for future optimization.

2 | Comparison of Breeding Techniques

From 1996 to 2024, a total of 306 new aquaculture varieties were approved in China. Among them, 43% were developed through selective breeding, 35% through hybridization (distant and close), and 5% through gynogenesis. Techniques such as germ cell transplantation, nuclear transfer, transgenics, and gene editing have yet to be reflected in newly approved varieties, mainly due to regulatory and technical constraints [237].

Selective breeding, hybridization, and gynogenesis have distinct characteristics. From a phenotypic perspective, offspring derived from selective breeding or gynogenesis generally resemble the paternal and maternal phenotypes (especially in heterologous sperm-induced gynogenesis). Genetically, these two methods also result in relatively minor changes. In contrast, distant hybridization tends to induce greater changes in both phenotype and genetic composition. This comparison provides a framework for selecting breeding methods: for minimal genetic and phenotypic alteration, selective breeding and gynogenesis are appropriate; for significant innovation in phenotype and genetics, distant hybridization is preferable.

Furthermore, selective pressure plays a significant role in both distant hybridization and gynogenesis. For example, in heterologous sperm-induced gynogenesis, low survival rates due to strong selection pressure act as a powerful screening mechanism [238]. Thus, in addition to its inherent genetic effects, heterologous sperm-induced gynogenesis also exhibits selection effects. Selective breeding, therefore, can either be applied independently or integrated with other breeding techniques for enhanced outcomes.

While selective breeding and gynogenesis maintain phenotypic stability, they neglect the adaptive decline caused by inbreeding depression and the fixation of deleterious alleles [239, 240]. Although the innovative potential of distant hybridization is often highlighted, insufficient attention is given to its inherent reproductive barriers (e.g., hybrid sterility), trait segregation, and ecological risks (e.g., genetic pollution from escaped hybrids). Claims regarding the "broad applicability" of heterologous sperm-induced gynogenesis lack empirical support-survival rates below 5% and high deformity rates across multiple species challenge its technical universality [241]. Crucially, the synergistic potential between modern biotechnologies (e.g., gene editing, germ cell transplantation) and traditional methods remains systematically overlooked. Future breeding strategies should integrate these complementary approaches rather than relying on a single technique.

3 | Theory and Technologies of Macro-Hybrid and Micro-Hybrid

We present the theory and technologies of macro-hybrid and micro-hybrid systems, based on extensive practical experience with distant hybridization and gynogenesis.

Macro-Hybrid: The macro-hybrid refers to the allo-progenies derived from distant hybridization, including the allo-diploid and allo-tetraploid progenies (Figure 1). In macro-hybrids of distant hybridization, parental chromosome numbers are closely matched, enabling the formation of fertile allo-diploid and allo-tetraploid strains. In micro-hybrid breeding of distant hybridization, equal or different chromosome numbers between parents yield fertile auto-tetraploid or auto-diploid strains (Figure 1).

Micro-Hybrid: The micro-hybrid refers to the auto-progenies derived from distant hybridization or heterologous sperm-induced gynogenesis, which possess the genome from the maternal parent predominantly but contain DNA fragments originating from the paternal (Figure 2a,b). In the micro-hybrid of distant hybridization, equal or different chromosome numbers between parents yield fertile auto-tetraploid or auto-diploid strains. In the micro-hybrid of heterologous sperm-induced gynogenesis, equal or different chromosome numbers between parents yield auto-diploid strains. The integration of heterologous sperm-induced gynogenesis, back-cross, and self-cross strategies can address the issue of all-female progeny resulting from gynogenesis when the maternal parent possesses an XX sex determination system, thereby enabling rapid expansion of the breeding population (Figure 3). Amplification of the micro-hybrid effect was achieved through repeated crossings of multiple populations that already possessed the effect (Figure 2c).

4 | Classifying Macro-Hybrid and Micro-Hybrid Lineages in Fish Breeding

Based on extensive studies of distant hybridization and gynogenetic development in fish, we systematically compared the similarities and differences between these two processes. It was found that both distant hybridization and gynogenetic development involve the fertilization of eggs by heterologous sperm and the initiation of embryonic development, thereby sharing the fundamental feature of "hybridization." The difference lies in the specific manipulations employed: gynogenetic development involves sperm inactivation and special treatment of fertilized

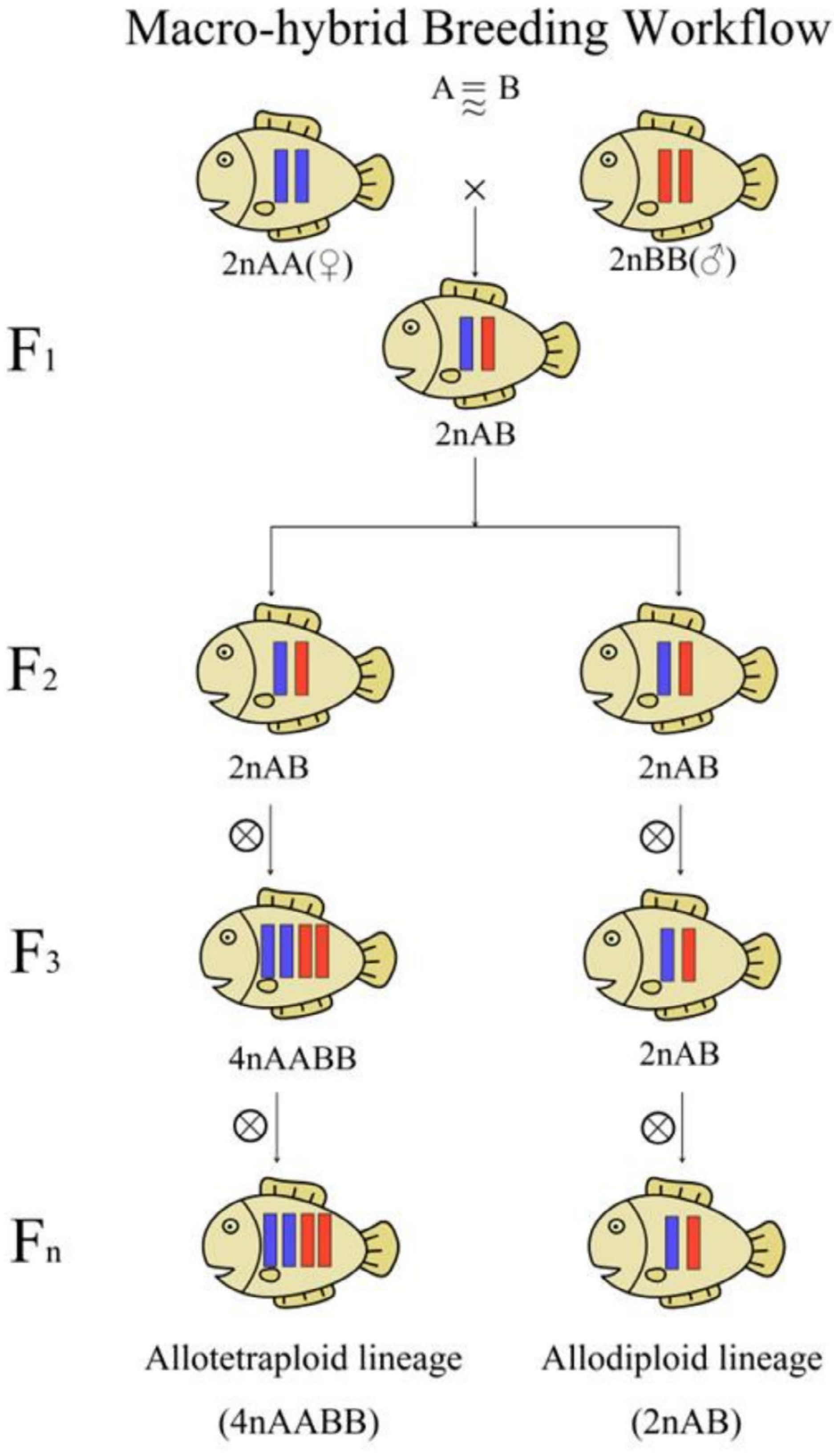

FIGURE 1 | Schematic diagram of macro-hybrid breeding technologies. The symbol "≈" indicates that the chromosome numbers of the two groups are numerically similar, differing by no more than two chromosome sets (2n), and are considered to have broadly compatible genomes for the purpose of hybridization.

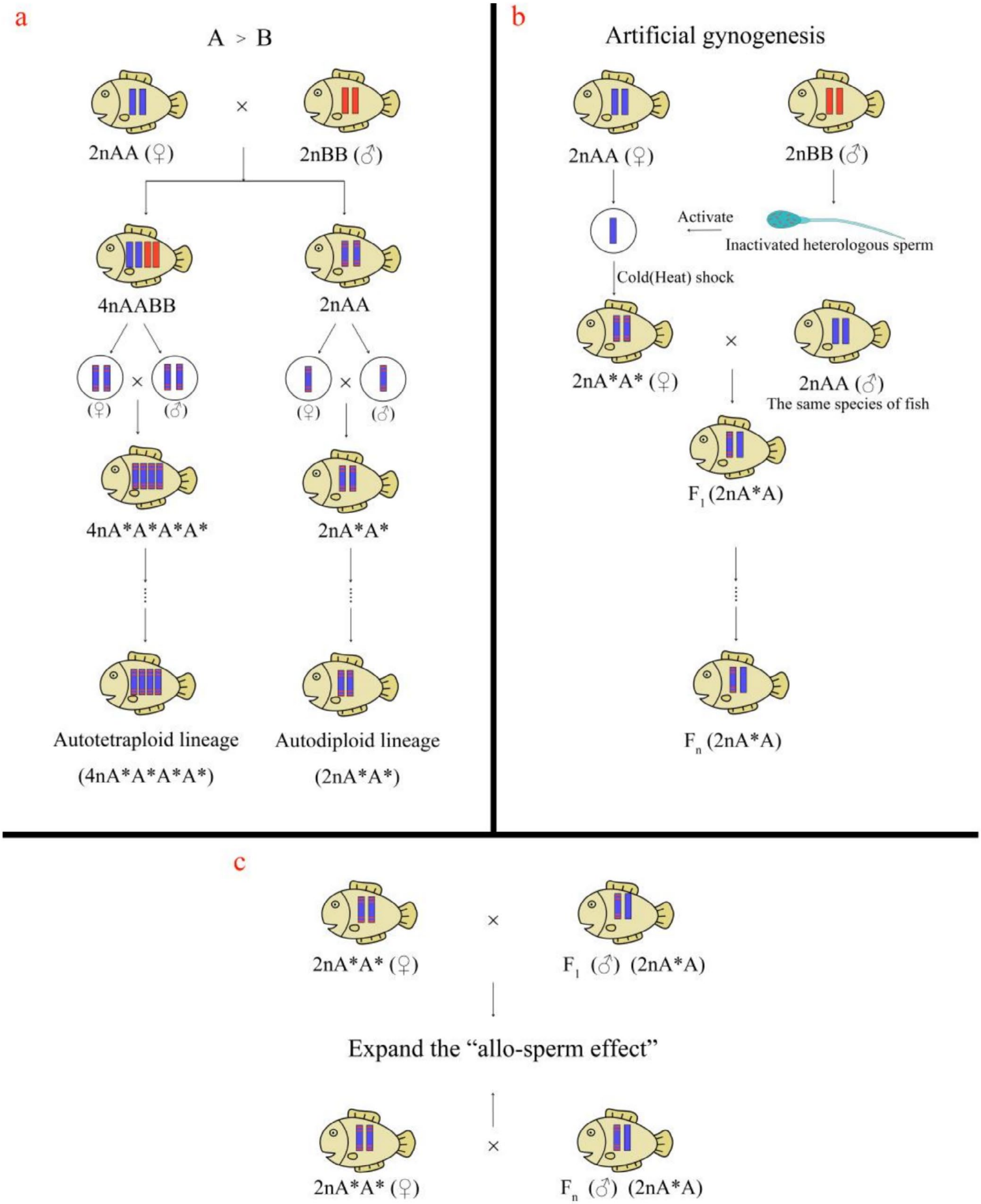

FIGURE 2 | Schematic diagram of micro-hybrid breeding technology (The self-fertilization of 4nAABB has been consistently demonstrated to produce exclusively 4nAAAA offspring in multiple experiments). (a) The auto-progenies derived from distant hybridization, which possess the genome from the maternal dominantly but contains DNA fragments originating from the paternal; (b) The auto-progenies derived from heterologous sperm-induced gynogenesis, which possess the genome from the maternal dominantly but contains DNA fragments originating from the paternal; (c) Amplification of the micro-hybrid effect was achieved through repeated crossings of multiple populations that already possessed the effect.

eggs (such as cold or heat shock to promote chromosome duplication), whereas distant hybridization does not involve such interventions (Figure 4) [155].

We proposed the theoretical framework of "macro-hybrid" and "micro-hybrid". Distant hybridization can yield both macro-hybrid and micro-hybrid lineages, whereas gynogenesis yields only micro-hybrid lineages.

We conducted systematic studies on the genetic patterns and mechanisms underlying trait formation in fish derived from distant hybridization and gynogenesis. Comparative analyzes at the gene, transcriptome, and genome levels were performed between various fish lineages, including allo-diploid BSB-culter hybrids, culter-BSB hybrids, and allo-tetraploid crucian-carp hybrids and their respective parents. These studies revealed the coexistence and stable inheritance of biparental subgenomes. For instance, both the allo-tetraploid AABB and the allo-diploid AB individuals maintain two coexisting subgenomes, which can be stably passed on. Furthermore, recombination between homologous sequences of different subgenomes was observed, and this recombination was found to accumulate over successive generations [242, 243]. The expression of recombinant genes between subgenomes significantly influences the genetic characteristics and trait development of hybrid fish [244, 245].

Moreover, analyzes of auto-tetraploid crucian and auto-tetraploid carp lineages (originating from distant hybridization) and their parental species revealed that the maternal genome predominates (e.g., tetraploid AAAA and diploid AA). Insertion of paternal DNA fragments was also observed in these genomes [246, 247]. Similar insertions were detected in various fish derived from artificial gynogenesis [155, 208, 217].

Macro-hybrids are typically associated with prominent morphological changes, whereas micro-hybrids tend to exhibit subtler morphological differences but significant improvements in growth rate, stress resistance, and other traits.

The components of heterologous sperm-induced gynogenesis, including homozygosity, heterologous sperm, and cold (heat) shock, are all associated with intense selective pressure. The "homozygosity effect" arises from the chromosomal doubling of the maternal genome, which purges deleterious recessive alleles through homozygous expression (e.g., lethality or disease), while retaining and accumulating beneficial mutations. The heterologous sperm effect constitutes a form of micro-hybrid variation that may also eliminate unfavorable traits and preserve advantageous ones. Thermal shock eliminates weaker individuals, contributing further to selection. The combination of these three factors including homozygosity, heterologous sperm, and thermal shock-creates intense selective pressure that identifies and enriches for superior individuals or populations. Earlier research suggested that the homozygosity effect of gynogenetic development was equivalent

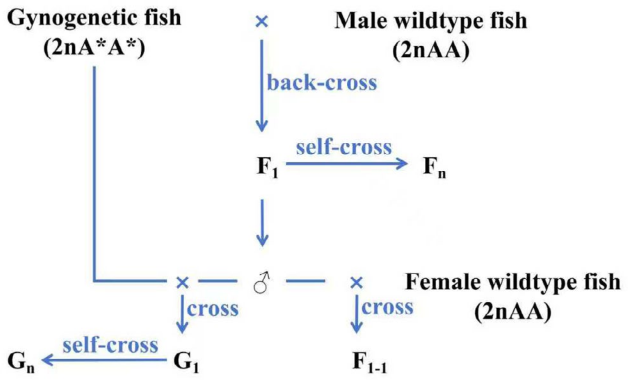

FIGURE 3 | Breeding strategies of micro-hybrid.

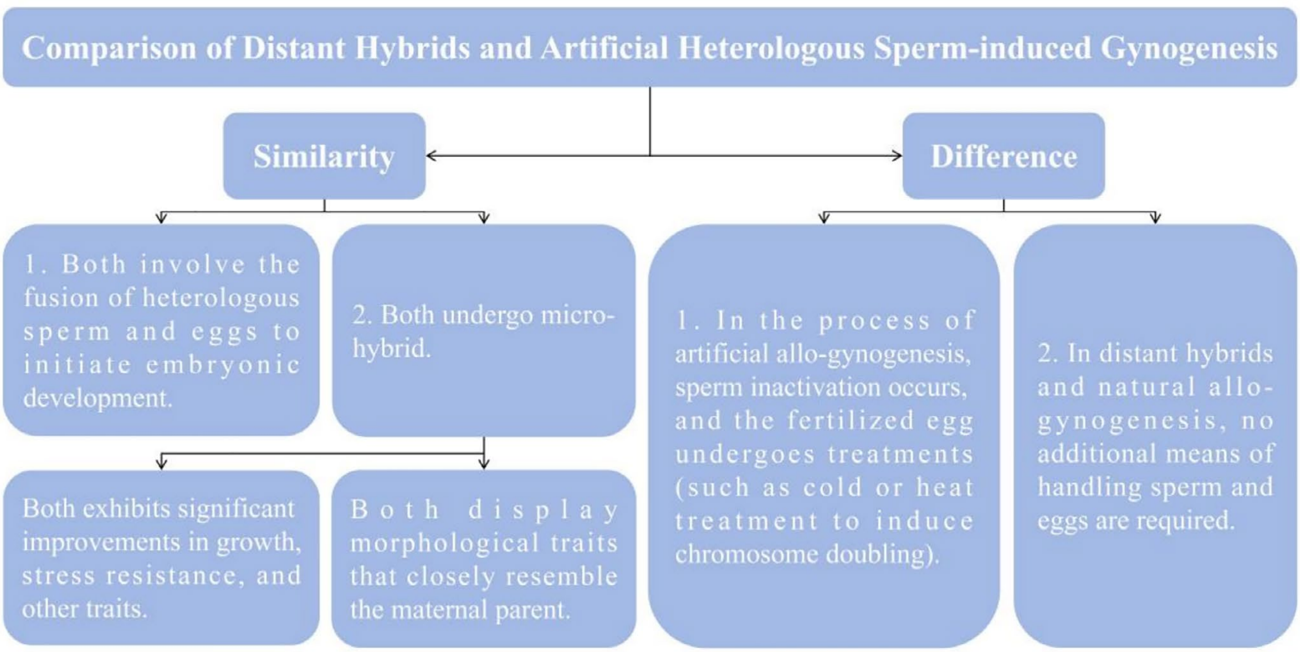

FIGURE 4 | Comparison of distant hybridization and artificial heterologous sperm-induced gynogenesis.

to 8–10 generations of inbreeding [248, 249]. We propose that the combined selective effects of homozygosity, heterologous sperm, and cold (heat) shock likewise approximate 8–10 generations of selection, establishing a new theoretical framework.

Both the homozygosity effect and the heterologous sperm effect are potent sources of genetic variation in fish breeding. These findings underscore the principle that macro-hybrids result in notable phenotypic changes, while micro-hybrids lead to subtler phenotypic shifts [155, 217]. Our team provides substantial evidence supporting the heritability of micro-hybrid effects in gynogenetic fish through back-cross and self-cross [250], thereby laying a theoretical foundation for developing gynogenetic breeding strategies based on micro-hybridization.

Traditionally, gynogenesis has been regarded primarily as a method for producing highly homozygous populations. Few have recognized that homozygosity itself represents a form of genetic variation. Our team argues that the essence of breeding lies in identifying variation and seeking useful individuals or populations within diverse genetic backgrounds. Thus, increased homozygosity is a form of beneficial variation. Moreover, we highlight that sperm inactivation and cold (heat) shock during gynogenesis are critical drivers of variation. Coupled with the theory of micro-hybrid, these insights provide a more comprehensive understanding of the principles underlying gynogenetic breeding and support the development and broader application of relevant breeding techniques.

Based on survival rates (from fertilized egg to fry) in experiments using cohorts of 2000 eggs, the rates in increasing order were [208–211, 214, 217]: mandarin fish: 0.01%–0.02%; Mrigal carp: 0.5%; northern snakehead: 1%–5%; goldfish, *Hemibarbus maculatus*: 2%–8%; blunt snout bream: 1%–3%; tetraploid lineages: 2%–5%; common carp and koi: 3%–8%; red crucian carp and white crucian carp: 5%–9%; largemouth bass: 6%; grass carp and large yellow croaker (collaborating with Professor Xinhua Chen's team at Fujian Agriculture and Forestry University): 10%. These rates, ranging from 0.01% to 10%, demonstrate the low survival rates and intense selection pressures associated with heterologous sperm-induced gynogenesis. The few surviving individuals typically exhibit enhanced resistance to stress and disease, as well as accelerated growth.

In the field of gynogenesis, our team made significant theoretical and technological innovations by emphasizing the mutational effects of both homozygosity and heterologous sperm. The integration of distant hybridization and gynogenesis led to the proposal of the macro-hybrid and micro-hybrid framework, which forms a solid foundation for the establishment and application of corresponding breeding technologies. Given the strong selective effects inherent in heterologous sperm-induced gynogenesis, this micro-hybrid breeding approach can be applied not only to natural fish and fertile distant hybrids but also to their descendants. We have recently documented the successful induction of gynogenesis in marine bivalves. This suggests the potential for broad adaptability of these technologies across diverse species. While numerous global cases of gynogenesis and hybrid fish exist, few have yielded established breeding lines. Our macro- and micro-hybridization approaches provide a methodological framework to guide subsequent research in this domain.

5 | Applications of Macro-Hybrid and Micro-Hybrid

Based on extensive and systematic practical and theoretical studies of fish distant hybridization and gynogenetic development, our team proposed the theories of macro-hybrid and micro-hybrid and subsequently designed and established corresponding breeding technologies. These approaches build upon previously established "one-step" and "multi-step" breeding methods [188, 246, 251], further refining them and expanding their application scope. The contents of the breeding technologies are detailed below:

Macro-Hybrid Breeding (Figure 2) involves designing crosses between fish species with equal chromosome numbers. Their offspring may form fertile allo-tetraploid or allo-diploid fish, which can then self-cross to establish respective allo-tetraploid or allo-diploid lines, each containing both parental subgenomes. This method effectively addresses survival issues (via chromosomal compatibility) and reproductive challenges (by enabling both meiotic and ameiotic gamete formation). Using this strategy, multiple tetraploid and diploid fish lines have been developed [149, 151, 156, 159, 164, 220, 245, 252, 253], creating new germplasm resources.

Micro-Hybrid Breeding (Figure 2) is designed using specific parental combinations and breeding strategies based on both distant hybridization and gynogenesis. In distant hybridization, the parents are chosen such that the maternal species has significantly more chromosomes than the paternal species. This enables the formation of fertile auto-tetraploid and auto-diploid offspring dominated by the maternal genome but containing inserted paternal DNA fragments. These offspring can self-cross to form stable auto-tetraploid and auto-diploid lines. This strategy effectively addresses survival and reproductive barriers, yielding valuable germplasm resources [153, 161, 192, 218, 219, 221, 227, 254, 255].

In heterologous sperm-induced gynogenesis, parental species from different taxa are selected. The primary generation produced is typically a fertile diploid female (if the sex-determination system is homogametic XX), dominated by the maternal genome and with inserted paternal DNA fragments. These individuals are then crossed with ordinary males to generate the first filial generation, which is subsequently self-crossed to produce the second generation. Male individuals from either generation can be back-crossed with original gynogenetic females to further enhance the micro-hybrid effect (Figure 2). This method overcomes the lack of males and the limited original population size in gynogenetic offspring.

In natural gynogenetic offspring resulting from distant hybridization, both sexes may be present, and the micro-hybrid effect is observable in both. This effect can be inherited through self-crossing. In addition to self-cross, back-cross with normal males or females is also proposed as a breeding strategy to propagate the micro-hybrid effect. During gynogenesis, paternal DNA segments may integrate via special mechanisms resembling distant hybridization, generating sexually dimorphic populations. These male and female individuals can then be used in a self- or back-cross to expand the population. This represents a novel fusion of gynogenetic and distant hybridization processes. Notably, reducing sperm vitality may enhance offspring survival in certain cases. Partial inactivation, non-inactivation, or complete inactivation of sperm during gynogenesis can lead to diverse outcomes, a novel concept not explored in prior studies.

Given the high selection intensity, low retention rates, and small initial populations in heterologous sperm-induced gynogenesis, the establishment of the micro-hybrid theory and breeding technologies effectively overcomes these limitations, enabling rapid expansion of effective populations. The core of this system lies in clearly distinguishing high-quality germplasm types: first, by obtaining primary populations through gynogenesis; then expanding these using self- or back-cross. Although the micro-hybrid effect may be diluted in later generations, experimental evidence demonstrates that advantageous traits in the original gynogenetic fish can be stably inherited and expressed through these means [250], greatly enhancing breeding efficiency [155].

Macro-hybrid and micro-hybrid provide a strong theoretical and technical foundation for the previously established one-step and multi-step breeding methods [155, 188], while enhancing the precision of the multi-step breeding method. For instance, one-step breeding emphasizes the use of F_1 distant hybrids with equal parental chromosome numbers, while macro-hybrid breeding highlights the biparental subgenome composition of these F_1 hybrids. Multi-step breeding emphasizes the fertility of distant hybrid offspring and their role as new breeding parents; macro-hybrid and micro-hybrid further elucidate the genomic compositions of the derived allo- and auto-tetraploid and diploid lines. Moreover, the breeding technologies organically integrate distant hybridization and gynogenesis, significantly broadening the application scope of these approaches.

Gynogenetic breeding techniques reflect both genetic variation and selection mechanisms at the chromosomal (genomic) and DNA levels. These processes include genomic homozygosity, micro-hybrid effects, and cold (heat) shock-induced selection. Together, they improve growth rate, disease resistance, cold tolerance, and hypoxia tolerance in gynogenetic offspring (Figure 5).

TABLE 1 | Micro-level auxiliary breeding techniques.

Micro-level auxiliary breeding techniques	
1	Genome sequencing is used for overall subgenomic identification
2	Molecular marker screening, employed for partial subgenome recognition
3	PCR, used for identifying paternal DNA fragments
4	SNP site detection and related genotyping tools

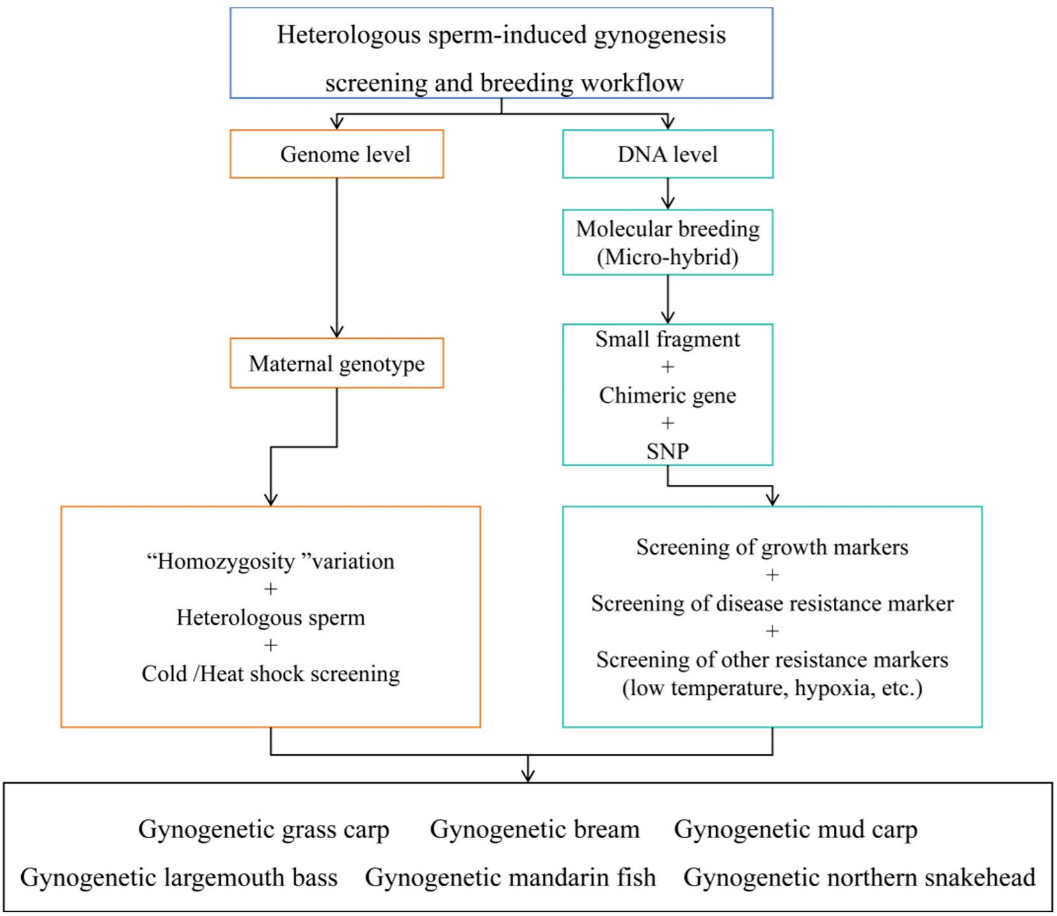

FIGURE 5 | Combination of heterologous sperm-induced gynogenesis and molecular screening.

Compared with distant hybridization, gynogenesis is less restricted by parent compatibility and thus can be more widely applied across fish species. However, it is generally more difficult to obtain fertile tetraploids through gynogenesis alone, something that distant hybridization can achieve more effectively.

In terms of breeding guidance, a macro-level design perspective can be adopted based on the fact that distant hybridization may result in two types of effects: macro-hybrid and micro-hybrid.

TABLE 2 | Macro-level auxiliary breeding techniques.

	Macro-level auxiliary breeding techniques
1	Compatibility between sperm head size and egg micropyle [256]
2	Genetic relationship and trait complementarity between parental species, ensuring the survivability and trait contribution of the paternal genome
3	Cryopreservation of sperm
4	Optimization of the duration of sperm inactivation
5	Prolonging the growth period of hybrid fish to ensure sexual maturity
6	Pooling sperm from low-fertility males to ensure fertilization success, designing parental crosses based on chromosomal inheritance
7	Supporting techniques such as flow cytometry, chromosome analysis, FISH, and gamete assessment
8	Drip incubation and temperature-controlled hatching

Additionally, heterologous-sperm-induced gynogenesis can generate micro-hybrid effects. Macro-hybrids are typically characterized by substantial changes in both phenotype and genetic composition, whereas micro-hybrids exhibit relatively minor alterations in these aspects. These distinctions provide a theoretical framework for the purposeful and precise design and implementation of breeding strategies.

6 | Auxiliary Breeding Techniques

Centering on macro-hybrid and micro-hybrid, we developed a comprehensive breeding system by incorporating various auxiliary techniques. These include both micro-level and macro-level auxiliary breeding approaches (Tables 1 and 2).

These techniques have been applied to identify subgenomic structures in allo-tetraploid crucian carp hybrids, Hefang crucian carp lines, bluntnose black bream-culter hybrids, gynogenetic largemouth bass, gynogenetic mandarin fish, and their respective parents [257–260].

Combining the established micro-hybrid gynogenetic breeding system with these auxiliary methods, we successfully bred multiple gynogenetic fish lines, including grass carp, blunt snout bream, largemouth bass, mandarin fish, northern snakehead, and marine species such as large yellow croaker. These tools significantly enhanced the success rate and efficiency of gynogenesis.

A patented hatching apparatus for adhesive fish eggs was developed (Figure 6), offering high efficiency, safety, and ease of operation. It effectively mitigates water quality effects, allows

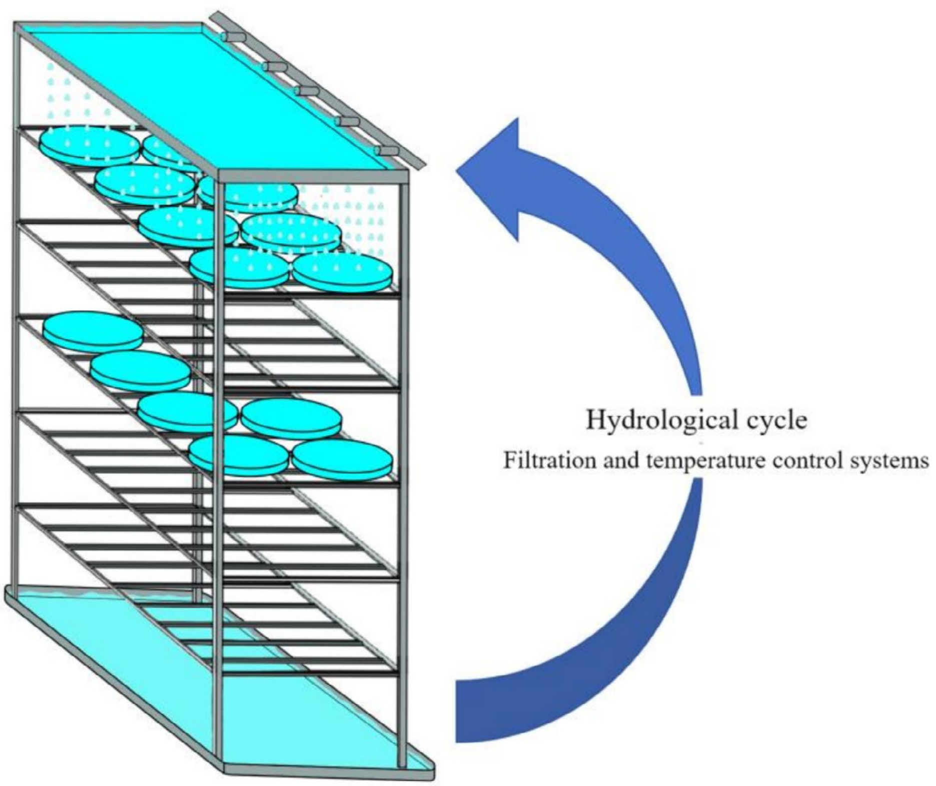

FIGURE 6 | Drip incubation and temperature-controlled hatching support system.

precise control of incubation temperature, and significantly increases hatch rates. In alignment with ecological principles of “simulating nature and minimizing human intervention,” the team designed an eco-spawning pond that supports natural fertilization, reduces hormone usage, and facilitates the collection and transport of eggs with netting panels [251].

To date, there is no integrated device for gynogenetic (or androgenetic) procedures. Our team has initiated the design and patent process for such equipment, a gynogenesis/androgenesis experimental apparatus. This device offers user-friendly operation, a compact structure, and uniform UV exposure for samples, minimizing external interference and reducing UV harm to operators. Its availability will provide convenient and precise support for researchers and breeders.

Through the application of macro-hybridization and micro-hybridization technologies, empowered by these auxiliary breeding techniques, we have successfully developed a series of novel fish strains and premium varieties. This has enriched germplasm resources and enhanced fish population quality. The integrated application of these methods has addressed three key challenges in distant hybridization: (1) low survival, (2) reproductive difficulty, and (3) difficulty in identification. They also solve the two key issues in gynogenesis: (1) low survival and (2) difficulty in population expansion.

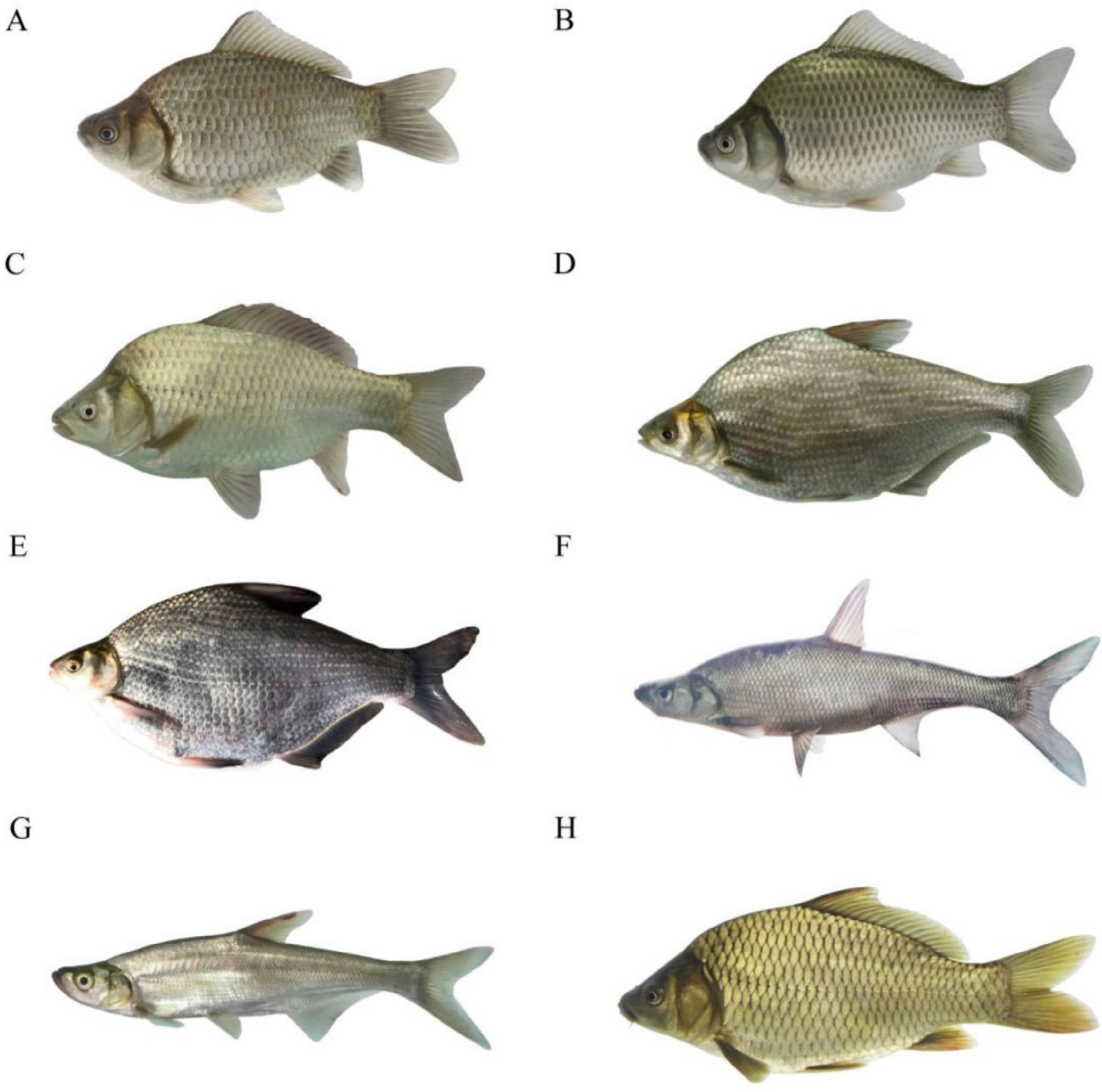

FIGURE 7 | Representative high-quality fish breeds developed via macro-hybrid breeding. (A) Hefang crucian carp; (B) Hefang crucian carp No. 2; (C) Hefang crucian carp No. 3; (D) Hefang Bream; (E) Hefang Bream No. 2; (F) XiangJun culter; (G) XiangJun culter No. 2; (H) Allotriploid carp.

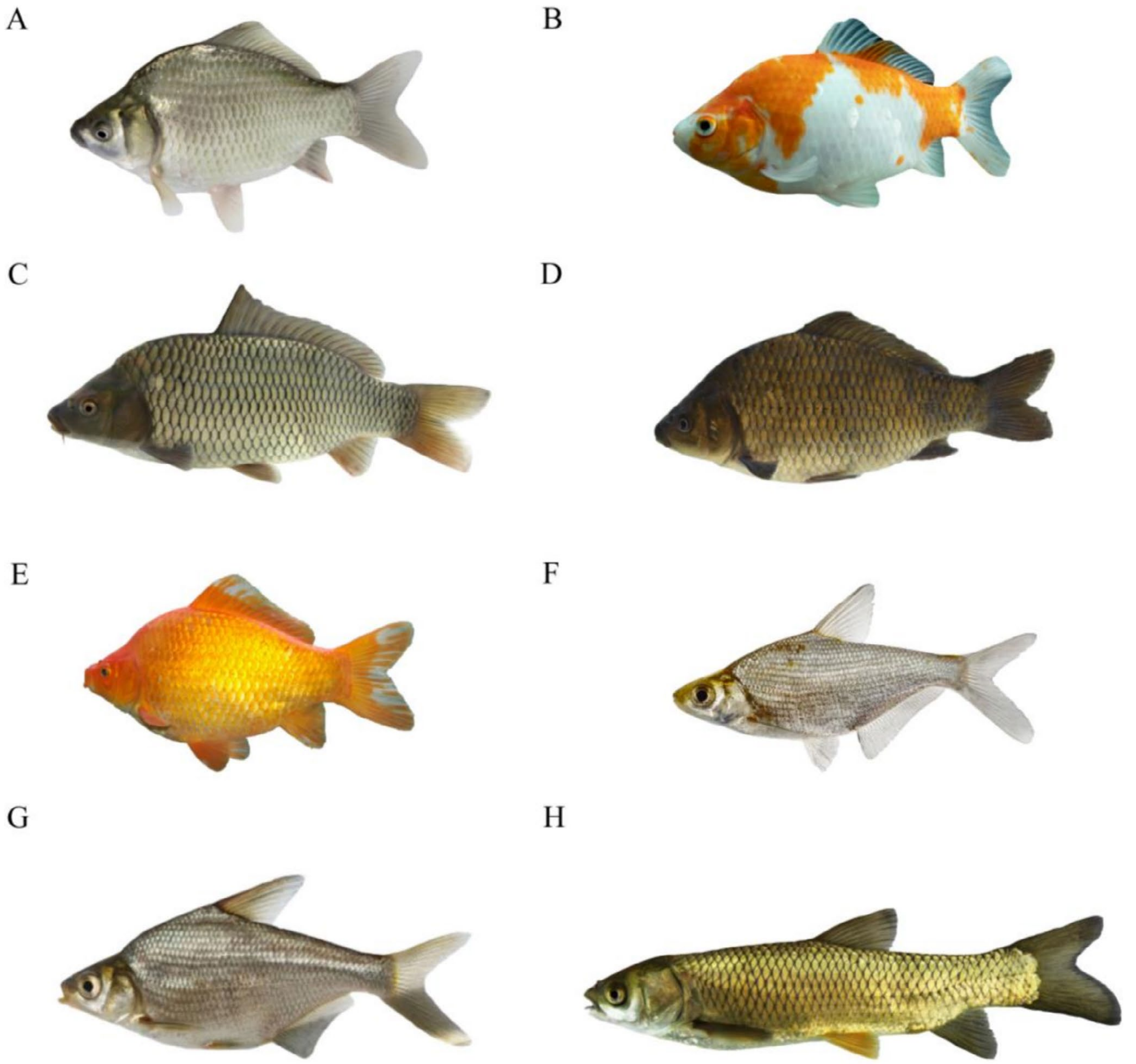

FIGURE 8 | Representative natural gynogenetic high-quality fish breeds. (A) XiangJun Crucian; (B) XiangJun Flower Crucian; (C) XiangJun Carp; (D) Homotetraploid Crucian (micro-hybrid effect); (E) Red Crucian; (F) Natural gynogenetic bluntnose black bream (bluntnose black bream × *Xenocypris davidi* Bleeker); (G) Natural gynogenetic bluntnose black bream (bluntnose black bream × mandarin fish); (H) Natural gynogenetic grass carp.

7 | Application Cases of Macro-Hybrid and Micro-Hybrid

Over the years, our team has employed macro-hybrid breeding technologies to successfully cultivate a variety of high-quality fish species including Hefang crucian carp (Figure 7A) [261], Hefang crucian carp No. 2 (Figure 7B) [262], Hefang crucian carp No. 3 (Figure 7C) [263], Hefang bream (Figure 7D) [164], Hefang bream No. 2 (Figure 7E) [245], Xiangjun culter (Figure 7F), Xiangjun culter No. 2 (Figure 7G) [253], triploid common carp (Figure 7H) [246]. These diploid and triploid fish exemplify the effectiveness and great potential of macro-hybrid technologies in aquaculture:

Macro-Hybrid Case: The Hefang crucian carp Series: This is a typical example of combining one-step and multi-step breeding technologies through the application of macro-hybrid methods. By crossing the Japanese white crucian (female) with the red crucian (male), the F_1 generation was obtained and named Hefang crucian carp. Subsequent self-cross (from F_1 to F_5) led to the establishment of a stable line containing both parental subgenomes, classifying it as a macro-hybrid. Hefang crucian carp exhibits a favorable body shape, rapid growth, superior flesh quality, and strong stress resistance [264, 265]. Based on this, Hefang crucian carp was back-crossed with male Japanese white crucian to breed Hefang crucian carp No. 2, which also qualifies as a macro-hybrid, and received national certification

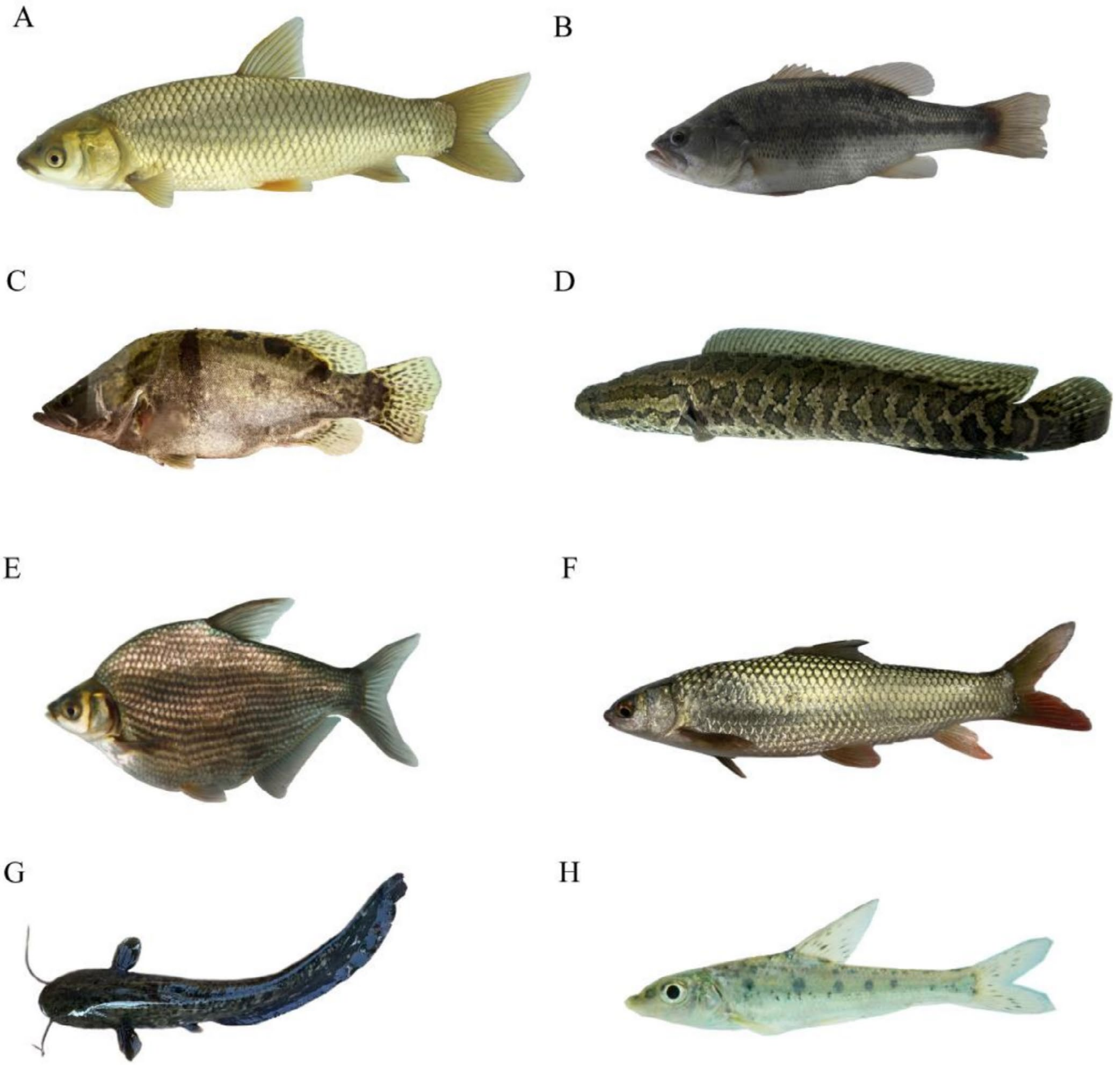

FIGURE 9 | Representative high-quality fish breeds developed via artificial gynogenesis (micro-hybrid). (A) Disease-resistant gynogenetic grass carp; (B) Gynogenetic largemouth bass; (C) Gynogenetic mandarin fish; (D) Gynogenetic northern snakehead; (E) Gynogenetic bluntnose black bream (koi sperm); (F) Gynogenetic mrigal carp (common carp sperm); (G) Gynogenetic catfish; (H) Gynogenetic *Hemibarbus maculatus*.

in 2022 [266]. Hefang crucian carp No. 2 features a small head, tall back, fast growth, and excellent resilience, making it suitable for various rearing environments (lakes, ponds, paddy fields, lotus fields). With a high content of umami amino acids, it is ideal for soup production. The team developed frozen Hefang crucian carp No. 2 fish soup and commercialized it as a culinary product. A complete supply chain from quality seed to healthy farming and culinary commercialization was established, delivering notable economic, social, and ecological benefits [267]. Hefang crucian carp No. 2 was also crossed with male auto-tetraploid crucian to produce Hefang crucian carp No. 3, a high-quality triploid fish with features including a tall back, barbelless mouth, fast growth, stress resistance, tender flesh, and high amino acid content.

Macro-Hybrid Case: The Hefang Bream Series: This represents another successful application of macro-hybrid breeding through the multi-step approach. By hybridizing bluntnose black bream and topmouth culter, the F_1 generation was obtained and then back-crossed with bluntnose black bream to produce a hybrid of topmouth bream. Further back-crossing with female bluntnose black bream yielded Hefang Bream, characterized by a tall back and small head. All these hybrids contained biparental subgenomes, thus qualifying as macro-hybrids. Hefang Bream is well-suited for lakes, ponds, and paddy-lotus fields. Subsequently, a hybrid of topmouth bream was back-crossed with bluntnose black bream to produce Hefang Bream No. 2 (high-back bream), which exhibits rapid growth, low-oxygen tolerance, herbivorous feeding habits,

TABLE 3 | Natural gynogenetic fish.

Number	Name	Description
1	XiangJun Crucian (Figure 8A)	This novel fish variety, obtained through hybridization between Xiangjiang wild carp and bluntnose black bream, exhibits high survival rates, rapid growth, strong stress resistance, and high nutritional value [161]
2	XiangJun Flower Crucian (Figure 8B)	This stable F_6-generation ornamental crucian hybrid, obtained by crossing ornamental koi carp with bluntnose black bream, demonstrates rapid growth, robust stress tolerance, high fecundity, and superior ornamental quality [153]
3	XiangJun Carp (Figure 8C)	Derived from hybridization between Xiangjiang wild carp and bluntnose black bream, this hybrid variety exhibits good survival rates, rapid growth, a docile temperament, and adaptable feeding behavior, making it well-suited for paddy field culture systems [268]
4	Auto-tetraploid Crucian (Figure 8D)	Developed through hybridization of red crucian carp and bluntnose black bream, this hybrid lineage exhibits stable diploid gamete formation, enhanced stress tolerance, and favorable morphological traits [260]
5	Natural gynogenetic red crucian (Figure 8E)	Originating from hybridization between red crucian carp and bluntnose black bream, this hybrid exhibits rapid growth, superior morphological traits, and stable reproductive performance [260]
6	Natural gynogenetic bluntnose black bream (Figure 8F)	Developed through hybridization of bluntnose black bream and *Xenocypris davidi*, this hybrid exhibits increased dorsal body depth, high fecundity, and has been stably maintained through self-crossing to the F_3 generation [269]
7	Natural gynogenetic bluntnose black bream No. 2 (Figure 8G)	Developed through distant hybridization of bluntnose black bream and mandarin fish, this hybrid exhibits fast growth, high flesh quality, and fertility in both sexes [192]
8	Natural gynogenetic grass carp (Figure 8H)	Developed through distant hybridization of grass carp and topmouth culter, exhibits accelerated somatic growth rates and an enhanced nutritional profile characterized by high protein content and beneficial fatty acid composition [191]

excellent flesh quality, and high protein levels. This strain is ideal for lake and pond culture [164]. Additionally, the hybrid of topmouth bream was back-crossed with topmouth culter to produce XiangJun culter, a macro-hybrid with fast growth, tall body, tender flesh, high meat yield, and strong disease resistance, with 5.7% fewer intermuscular bones than its parent. A further back-cross between XiangJun Blicca and white bream yielded XiangJun culter No. 2, which inherited superior growth and flesh quality traits [253].

In collaboration with Luo Yongju's team from the Guangxi Academy of Fishery Sciences, the author's team also completed the southern breeding of gynogenetic largemouth bass, performing self-cross of back-crossed offspring, laying a solid foundation for large-scale commercial application.

Macro- and micro-hybridization technologies have yielded numerous elite aquatic varieties (Tables 3 and 4). Future advancements require deeper integration with cutting-edge biotechnologies, including the implementation of GS to accelerate trait fixation in hybrid progeny, the application of gene editing to accurately modify disease- and stress-resistance loci in micro-hybrid lines, and the development of AI-driven predictive models for parental matching. Integrating classical heterosis with molecular design and intelligent prediction tools is crucial for addressing the multifaceted challenges of germplasm innovation efficiency, food safety, and ecological sustainability.

8 | Conclusion

Based on our long-term research in fish distant hybridization and gynogenesis, we have for the first time integrated the theories and technologies of these two fields, establishing the conceptual and technical framework of macro-hybrid and micro-hybrid breeding. By synergizing this framework with our previously developed one-step and multi-step breeding strategies, we have successfully generated a series of novel, high-quality fish strains and germplasm resources. This study systematically introduces these innovative theories, technologies, and their practical applications, which we believe will significantly advance the theoretical foundations and technical capabilities of genetic breeding in aquaculture.

TABLE 4 | Artificial heterologous sperm-induced gynogenetic fish.

Number	Name	Description
1	Gynogenetic grass carp induced by inactivated koi sperm (Figure 9A)	The new variety was back-crossed to wild-type males, resulting in disease-resistant strains characterized by rapid growth, high protein content, low-oxygen tolerance, and herbivorous traits [216, 270]
2	Gynogenetic largemouth bass induced by inactivated mandarin fish sperm (Figure 9B)	The new variety was subjected to iterative back-crossing and self-crossing, resulting in a stable population that preserved the micro-hybrid traits [211]
3	Gynogenetic mandarin fish induced by inactivated largemouth bass sperm (Figure 9C)	The new variety was subjected to successive generations of back-crossing and self-crossing to fix and preserve the favorable traits [208]
4	Gynogenetic northern snakehead induced using inactivated mandarin fish sperm (Figure 9D)	This new variety demonstrated favorable traits, including accelerated growth and improved resilience to abiotic stress [217]
5	Two gynogenetic bluntnose black breamlines induced by inactivated koi and topmouth culter, sperm (Figure 9E)	The new variety demonstrates strong hypoxia tolerance, rapid growth, and enhanced disease resistance [214]
6	Gynogenetic black scraper induced by inactivated common carp sperm (Figure 9F)	The new variety exhibited a 1.4°C reduction in its minimum tolerance temperature, effectively addressing the overwintering challenge in the Hunan region [210]
7	Gynogenetic catfish induced by inactivated spotted channel catfish sperm (Figure 9G)	We observed that the new variety displays micro-hybrid characteristics, accelerated growth, and considerable resilience (data not shown)
8	Gynogenetic *Hemibarbus maculatus* induced by inactivated koi sperm (Figure 9H)	This new variety is characterized by a combination of advantageous traits, including remarkable tolerance to hypoxic conditions, a high growth rate, desirable flesh characteristics, and robust resistance to common pathogens [209]
9	Gynogenetic white crucian induced by inactivated mirror carp or bluntnose black bream sperm	The new variety is characterized by rapid growth and disease-resistant properties [212]

Looking forward, the breeding system presented here holds substantial potential for broader application. To advance this field, future research should prioritize several key directions: systematic evaluation of macro-hybrid lines for growth performance, flesh quality, and environmental adaptability; enhancement of micro-hybrid breeding efficiency through AI-driven parental matching algorithms integrated with GS; and establishment of comprehensive ecological risk assessment frameworks encompassing long-term monitoring and predictive modeling of genetic introgression. Achieving this vision will demand interdisciplinary collaboration across genetics, bioinformatics, ecology, and policy science, thereby positioning this integrated system as a transformative driver of sustainable innovation in the aquatic seed industry.

Author Contributions

Qizhi Liu: conceptualization, writing – original draft, writing – review and editing, visualization. **Anmin Liao:** conceptualization, writing–original draft, writing – review and editing, visualization. **Min Tao:** writing – review and editing. **Qinbo Qin:** writing – review and editing. **Kaikun Luo:** writing – review and editing. **Chun Zhang:** writing – review and editing. **Shi Wang:** writing – review and editing. **Yi Zhou:** writing – review and editing. **Fangzhou Hu:** writing – review and editing. **Yude Wang:** writing – review and editing. **Chang Wu:** writing – review and editing. **Wuhui Li:** writing – review and editing. **Qingfeng Liu:** writing – review and editing. **Chenchen Tang:** writing – review and editing. **Jing Wang:** writing – review and editing. **Rurong Zhao:** writing – review and editing. **Shaojun Liu:** conceptualization, investigation, supervision, funding acquisition, visualization, project administration, resources, writing – original draft, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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Biographies

Qizhi Liu focuses on distant hybridization and gynogenesis of *Siniperca chuatsi*, innate immunity of Hefang crucian carp, and splicing coupling transcription in human and fish cells. He has published 19 SCI paper.

Anmin Liao mainly engages in research on fish genetics and breeding, focusing on distant hybridization of fish and gynogenesis in fish. He has achieved innovative research results in the creation of gynogenetic fish strains.

Min Tao is the Young Scholars of the Cheung Kong Scholars Award Program, Leading talents in science and technology innovation in Hunan Province. Research interest is fish genetics and breeding research. She has presided over a number of national, provincial projects. More than 30 papers were published in SCI.

Qinbo Qin mainly engaged in the research of fish genetic breeding and healthy breeding. Many kinds of fish with excellent traits, such as autotetraploid fish and its all-female autodiploid gynogenetic offspring, have been prepared by distant hybridization, gynogenesis and androgenesis.

Kaikun Luo has been working on distant hybridization of fish for more than 30 years. He created fish lineages including Hefan No. 2 crucian carp, Hefan crucian carp, and *Culter alburnus*. He has won second prizes of the China National Science and Technology Progress Award twice.

Chun Zhang, a researcher (Professor) at Hunan Normal University in China. She is a project leader of the National Key R&D Program of China and has been a visiting scholar at Stockholm University in Sweden, mainly engaging in fish genetics and breeding.

Shi Wang is mainly engaged in the research of fish genetics and breeding, focusing on the phenomenon of genome collision between homoploid and polyploid offspring of distant hybridization in fish, and has made innovative research achievements in the creation of autodiploid and autotetraploid fish lineages derived from distant hybridization of fish.

Yi Zhou is an expert in the field of fish genetics and breeding. With over 20 years of experience in the field, he has dedicated his career to advancing fish germplasm by hybridization. His work focuses on enhancing genetic diversity, growth rate, and meat quality in farmed fish populations.

Fangzhou Hu have accumulated extensive research experience in the fields of fish genetic breeding and related fields. The current research focuses on the improvement of freshwater fish germplasm by using traditional breeding methods (hybridization and gynogenesis), and explore of genes involved in superiority traits in hybrids or gynogenetic fish.

Yude Wang, male, Doctor, Associate professor, master mentor. He mainly engaged in fish genetic breeding and seed industry research. he has two national key research and development projects, more than 20 invention papers, 10 patents approved, and participated in the development of high-quality fish in a number of provinces and cities for large-scale farming.

Chang Wu has been engaged in fish genetics and breeding for more than 10 years, focoused on the genetic improvement of culter and the research of hybrid lineages of blunt black bream and topmouth culter, and created a series of new hybrid lineages and gynogenetic population by distant hybridization and gynogenesis technology.

Wuhui Li primarily focuses on fish genetic breeding and ecological health aquaculture research. As the first author, he has published 14 papers in journals such as Genome Research and Aquaculture.

Qingfeng Liu is working on fish genetics and breeding. His major research interest is the genetic mechanisms analysis of hybrid fish dominant traits. He has published over 30 articles.

Chenchen Tang is working as a research technician focusing on the genetic breeding of fish and secretary of Hunan Fisheries Society. He won the Science and Technology Innovation Team Award of Hunan Province in 2021.

Jing Wang is using distant hybridization to provide further insight into the mechanism of sterility and the formation of unreduced gametes. The study provides a framework for the further exploitation and application of hybrid germplasms.

Rurong Zhao has led a project funded by the National Natural Science Foundation of China's Youth Science Fund, focusing on the identification of the Kisspeptin/GPR54 signaling system in infertile female triploid fish and its role in regulating the HPG axis. She has also led a key research and development project in Hunan Province on the health enhancement, aquaculture technology, genetic improvement, and industrialization of Topmouth Culter

Shaojun Liu leads a team that has been engaged in fish genetic breeding research for a long time. He has overcome the challenge of reproductive barriers and explored the main genetic and reproductive rules of distant hybridization in fish. He established key breeding techniques for fish hybridization using both one-step and multi-step methods.