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Review Article

Advances in Aquaculture Genomics, Genetics, and Breeding: Enhancing Sustainability and Efficiency Through Cutting-Edge Technologies

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Aquaculture genomics, genetics, and breeding are pivotal disciplines that enhance the efficiency and sustainability of fish farming. The advanced genomic technologies, including whole genome sequencing (WGS), genome-wide association studies (GWAS), and CRISPR/Cas9 gene editing, have revolutionized our understanding of the genetic foundations of economically important traits in aquaculture species. These technologies enable the identification of genetic markers linked to growth, disease resistance, and environmental adaptability, facilitating the development of improved breeding strategies. Marker-assisted selection (MAS) and genomic selection (GS) are now integral to breeding programs, allowing precise selection of desirable traits and accelerating genetic gain. Despite these advances, several challenges remain, including the need for extensive phenotypic and genomic databases, the complexity of polygenic traits, and ethical considerations surrounding genetic modifications. Furthermore, integrating these genomic tools into practical breeding programs necessitates bioinformatics infrastructure and expertise. This review provides a comprehensive overview of the present status of aquaculture genomics and genetics, highlighting key technological advancements and their applications in breeding programs. It also discusses the challenges faced by the industry and outlines future research priorities, such as enhancing genomic resources for under-researched species, improving phenotypic data collection accuracy, and developing sustainable breeding practices. By addressing these challenges and leveraging genomic insights, the aquaculture industry can significantly improve productivity, sustainability, and resilience, contributing to global food security and economic growth.

Keywords: aquaculture; breeding; genetics; genome; sequencing; transcriptome

1. Introduction

Aquaculture is essential for supplementing the world's food supply as wild fish stocks have become increasingly overexploited. The global demand for seafood has risen sharply due to population growth, increasing income levels, and shifting dietary preferences toward healthier protein sources. This sector has emerged as a vital sector encompassing cultivation of fish, shellfish, and seaweed to meet the growing demand. Aquaculture plays a crucial role in providing economic stability by ensuring global food security through a flourishing food production sector. Aquaculture production accounted for over 50% of the total harvest weight of aquatic animals for human consumption back in 2018 [1]. Rising food demand and nutrition security, in response to the world's growing population, drive the demand for intensive aquaculture to reinforce fish production. Wild-catch fishery activity has overexploited inland fishery resources, making aquaculture one of the fastest-growing industries employing sustainable practices for food supply [2]. Aquaculture intensification and diversification have resulted in the development of various cutting-edge technologies and approaches that could be used to boost fish production potential depending on the country's fish farmers and entrepreneurs' access to resources and willingness to invest.

Human genome project prompted to the emergence of genomics for comprehending genome structure, organization, expression, and functions by utilizing genetics and molecular biology techniques. Advances in numerous genome mapping technologies overcame the key constraint of contigs positioning and order to the genome that provides the framework for hierarchical sequencing. Aquaculture species genome projects necessitate comparable innovative approach to accurately assemble billions of DNA base pairs. The first Aquaculture Genomics Workshop, held in Dartmouth, Massachusetts, United States of America, in 1997, marked the beginning of aquaculture genomics focusing on shrimps, oysters, catfish, tilapia, striped bass, and salmonids [3]. Since then, the cost of sequencing a genome has decreased to a manageable level with the advancements of second and third generation sequencing technologies [4].

Transgenic technology in fish serves various purposes, including creating model systems for studying biological and cellular functions, identifying regulatory elements in gene expression, investigating gene roles in development, testing pharmaceuticals, developing human disease models, environmental monitoring, modifying phenotypes in ornamental fish for commercial purposes, producing therapeutic compounds, and breeding disease-resistant fish species [5–7]. Since the emergence of next-generation sequencing (NGS) technologies in 2005, biological research has significantly advanced due to reduced costs per base and increased data output. This technological leap has facilitated extensive genetic and genomic studies, leading to deeper insights into the genetic architecture of aquaculture species and enhancing breeding programs aimed at improving desirable traits.

While traditional breeding methods have achieved considerable success, they are limited by a lack of detailed knowledge about the genetic foundations of key traits. The incorporation of genomics and genetics into aquaculture breeding holds the promise of significantly enhancing productivity, sustainability, and resilience in the industry. These advancements enable a thorough understanding of the genetic architecture of complex traits, facilitate the identification of genetic markers associated with desirable attributes, and lead to the development of more effective breeding strategies. Cutting-edge genetic tools such as whole-genome sequencing (WGS), genome-wide association studies (GWAS), and CRISPR/Cas9 gene editing revolutionize aquaculture breeding practices [8]. Technologies like marker-assisted selection (MAS) and genomic selection (GS) have further refined breeding methodologies, allowing for precise and efficient selection decisions [9]. These advancements make it possible to target and propagate traits such as fast growth, disease resistance, and environmental adaptability more effectively, ultimately enhancing the overall productivity and sustainability of aquaculture operations.

Despite these advancements, the adoption of genetically improved farmed fish has remained relatively low, with only a small proportion of aquaculture production coming from managed breeding and improvement programs [10]. Technological and methodological hurdles, such as the complexity of aquatic genomes and the need for advanced bioinformatics tools, must be overcome. Environmental and ethical concerns, including the impact of genetically modified organisms (GMOs) on wild populations and the welfare of farmed fish, require careful consideration. Understanding the present state and future possibilities enables stakeholders in the aquaculture industry to make informed decisions that enhance the sustainability and productivity of aquaculture operations, thereby contributing to global food security and economic growth. This review examines various genomic advancements, technologies, and application-related discoveries to understand the genetic and molecular mechanisms underlying different traits, supporting the sustainable genetic improvement of aquaculture fish species.

2. Current Status: Advances in Genomics and Genetic Tools

2.1. Sequencing and Assembly of the Whole Genome. WGS has advanced aquaculture genomics by enabling researchers to map the complete DNA sequence of organisms. This comprehensive genetic information provides critical insights into the genetic basis of important traits, such as growth, disease resistance, and environmental adaptation. WGS facilitates the identification of single nucleotide polymorphisms (SNPs) and other genetic markers essential for GS and breeding programs. The initiative to sequence the genomes of aquaculture species began in the mid-2000s in the USA, Europe, and Asia. The Japanese pufferfish, *Fugu rubripes*, was the first fish to have its entire genome sequenced [11, 12], later utilized for commercial benefits in China and Japan. Since 2005, significant advances in NGS technologies have addressed numerous aquaculture challenges including biodiversity in environmental samples [13], identifying genetic markers [14], stress tolerance [15], recognizing probiotics and antimicrobial peptides [16], understanding molecular mechanisms of physiological processes [17], and studying the genes–genomes interaction and their impact of dietary components on metabolism [18]. Technological improvements have increased sequencing output from less than 1 Gb per run in 2007 to 1500 Gb per run in 2016, reducing costs by over 1000-fold and expediting genetic variation studies. A landmark achievement in aquaculture genomics was the sequencing of the Atlantic salmon, *Salmo salar* genome [19, 20]. This comprehensive reference genome has been instrumental in identifying genetic markers linked to growth rate and resistance to diseases such as Infectious Salmon Anemia (ISA) [21]. Vincent et al. [22] used WGS to study the genetic diversity of wild and farmed *S. salar* populations, highlighting the need for conservation strategies to maintain genetic diversity.

Researchers sequenced and published the rainbow trout, *Oncorhynchus mykiss*, genome in 2014, offering valuable insights into the species' evolutionary history and genetic diversity [23]. This reference genome has been utilized to identify quantitative trait loci (QTL) associated with growth [24], flesh quality [25], and disease resistance [26]. The genome sequencing of common carp, *Cyprinus carpio* revealed high levels of genetic diversity and complex evolutionary history [27]. Recent studies have identified SNPs linked to better growth rates and feed conversion ratios, which are now applied in MAS programs to breed more efficient carp strains. Shrimp, *Penaeus* spp. aquaculture has also benefitted from WGS, providing resources to study genetic markers associated with white spot syndrome virus (WSSV), a major economic threat to shrimp farming [28].

Studies leveraging this genome have improved selective breeding programs by enabling more precise selection of superior broodstock. Diverse genetic markers that are connected to the morphological characteristics, biology, physiology, stress tolerance, and nutritional requirements of aquaculture species were deduced by WGS [29]. Ye et al. [30] built different reference panels for genotype imputation of Nile tilapia utilizing 361 whole genome resequencing information from different projects. Various public genomic databases, including eFish, NCBI Genome database, Ensembl, UCSC, SalmoBase, Grass Carp Genome Database (GCGD), cBARBEL, FisOmics, and FishDB, have assembled genomes of over 200 fish species (Table 1). The application of whole genome sequencing in aquaculture is expanding at an ever-increasing rate as the costs of NGS decrease and bioinformatics analysis pipelines advance (Table 2).

2.1.1. First-Generation DNA Sequencing (FGS). FGS, often referred to as Sanger sequencing, has played a pivotal role in the development of aquaculture genomics and breeding programs. Developed by Frederick Sanger in 1977, this method relies on chain-terminating dideoxynucleotides to produce DNA fragments that can be used to read the genetic code. While newer technologies have emerged, Sanger sequencing remains a cornerstone in many genetic studies due to its accuracy and reliability. Sanger sequencing is instrumental in species identification through DNA barcoding [42]. By sequencing a standard region of the genome, such as the mitochondrial cytochrome c oxidase I (COI) gene, researchers can accurately identify and classify fish species [43]. This is essential for biodiversity conservation, monitoring fish stocks, and detecting mislabeled products in the market. Understanding species' evolutionary relationships is crucial for conservation and breeding programs [44]. Sanger sequencing of specific genetic markers helps construct phylogenetic trees, providing insights into the genetic diversity and evolutionary history of aquaculture species. This is critical for understanding genetic diversity and informing conservation strategies [45].

Researchers can evaluate genetic diversity, population structure, and gene flow by sequencing targeted genetic loci across various populations. The technique has been used to identify and validate markers linked to desirable traits. For examples, marker associated with growth rate, disease resistance, and flesh quality can be used in MAS to select broodstock with superior genetics, thereby accelerating genetic improvement in breeding programs [46]. Sanger sequencing helps track genetic variation within and between breeding populations, allowing breeders to make informed decisions to avoid inbreeding depression. For endangered or threatened species, Sanger sequencing provides essential genetic data for developing conservation breeding programs. Moen et al. [47] have used Sanger sequencing to identify genetic markers associated the resistance to infectious pancreatic necrosis (IPN). These markers are now used in MAS programs to breed IPN-resistance salmon, significantly reducing disease outbreaks and improving aquaculture productivity. Well-established protocols and widespread availability of Sanger sequencing facilities make it accessible for many researchers and breeding programs. Compared with NGS, this kind has a lower throughput, limiting its use for large-scale genomic studies. Sequencing large genomes or extensive marker panels using Sanger sequencing can be time-consuming and expensive.

2.1.2. Second-Generation Sequencing (SGS). SGS often referred to as NGS, has revolutionized genomics and breeding in aquaculture. Technologies such as Illumina sequencing, 454 pyrosequencing, and Ion Torrent sequencing enable high-throughput, cost-effective, and comprehensive genetic analysis [48]. Aquaculture researchers extensively employ SGS technologies in various research areas including general breeding programs, disease and health management, sex determination and reproductive biology, environmental stress response, nutrigenomics, morphological traits, and meat quality/texture [29]. These technologies are vital for selective breeding programs and population genomics because they generate diverse and valuable data. Wong et al. [29] reviewed aquaculture species research, noting a shift from gene-based to genome-wide studies due to high-throughput sequencing technologies. The application of advanced sequencing technologies has enabled the identification of QTL and novel genes associated with commercially valuable traits. These discoveries are crucial for selective breeding programs, including population genomics evaluation, MAS, and GS. Additionally, genomic approaches serve as genetic traceability tools to assess seafood fraud and track farm escapees, aiding in the conservation of wild stocks. Research on the grass carp, *Ctenopharyngodon idellus* genome has led to the creation of the GCGD and Grass Carp Genomic Visualization Database (GCGVD), focusing on breeding, nutrigenomics, and disease prevention [49]. Sequencing platforms have generated the genomes of numerous high-value marine and freshwater fish, including Asian sea bass, *Lates calcarifer* [50], Atlantic salmon, *S. salar* [31], common carp, *C. carpio* [27], European sea bass, *Dicentrarchus labrax* [51], large yellow croaker, *Larimichthys crocea* [52], pufferfish, *Takifugu flavidus* [53], rainbow trout, *O. mykiss* [23], tongue sole, *Cynoglossus semilaevis* [54], and turbot, *Scophthalmus maximus* [55].

Table 1: Genomics databases for fishes.

Database	Species	Genome with gene sets	URL
cBARBEL	1	1	https://catfishgenome.org
EFish	3	2	https://efishgenomics.integrativebiology.msu.edu/
Ensembl	48	48	https://asia.ensembl.org/index.html
FishDB	303	91	https://fishdb.ihb.ac.cn
FishExp	44	—	https://bioinfo.njau.edu.cn/fishExp/
FisOmics	—	—	https://mail.nbfgr.res.in/FisOmics/
GCGD	1	1	https://bioinfo.ihb.ac.cn/gcgd/php/index.php
MitoFish	3762	—	https://mitofish.aori.u-tokyo.ac.jp
NCBI (Genome)	294	74	https://www.ncbi.nlm.nih.gov/genome/
SalmoBase	2	2	https://salmobase.org/
UCSC	10	10	https://genome.ucsc.edu/
ZFIN	1	—	https://zfin.org
Fish T1K	1000	—	https://db.cngb.org/fisht1k/ (ongoing)
FishGET	8	—	—
FishBase	35,400	—	https://www.fishbase.se/search.php

The complete genomes of Atlantic salmon, *S. salar*, and Pacific oyster, *C. gigas* have been sequenced using NGS platforms [32, 56]. These genome assemblies provide a foundational resource for studying genetic variations and trait association. High-quality reference genomes are essential for genomic studies and breeding programs. SGS facilitated the generation of reference genomes for numerous species, enabling more precise genetic mapping and functional genomics research [57]. RNA sequencing (RNA-seq) leveraging SGS technologies enables thorough analysis of gene expression across various tissues and developmental stages. This method enhances our understanding of the molecular foundations of traits like growth, immunity, and stress response. Additionally, SGS has facilitated the study of DNA methylation, which is critical for gene expression regulation and influences traits that are significant in aquaculture. Studies on methylation patterns in fish and shellfish have revealed their impact on growth and development [28]. The use of SGS in metagenomics allows for the characterization of microbial communities associated with aquaculture species including the gut microbiome, which influences nutrition, immunity, and overall health [59].

2.1.3. Third-Generation Sequencing (TGS). TGS technologies, developed by Pacific Biosciences (PacBio) and Oxford Nanopore Technologies (ONT), have significantly advanced aquaculture genetics, genomics, and breeding. TGS offers real-time, long-read sequencing that surpasses many limitations of SGS by providing more comprehensive and accurate genomic data [29]. TGS is being used to complement or validate genomes generated by previous technologies, requiring fewer DNA fragments or lower coverage depth, thus enhancing the detection of complete structural variants such as insertions, inversions, and duplications that SGS often misses [60]. PacBio SMRT sequencing produces High Fidelity (HiFi) long reads, an improvement over earlier long-read technologies, allowing for efficient, rapid, error-free, and highly accurate genome assemblies [57]. Similarly, ONT provides real-time monitoring and performance capabilities comparable to PacBio, with data outputs up to 9.6 TB per run, enabling both small- and large-scale experiments at reasonable costs [61]. High-quality long reads have been crucial for assembling complex genomes to understand genes related to vision and locomotion in benthic adaptation, reproductive traits of Anguillid eels for eel farming [62, 63], genome duplication events and highly repetitive regions of the genomes of Atlantic salmon, *S. salar* [64] and rainbow trout, *O. mykiss* [65], and the precise sequencing of the Y chromosome of channel catfish, *I. punctatus*, important for sex selection in breeding programs [66]. Additionally, the genomes of yellow catfish, *Pelteobagrus fulvidraco* [67] and pikeperch, *Sander lucioperca* [68] have been sequenced to study the immune system, sex determination, glycosphingolipid biosynthesis, and fatty acid biosynthesis using PacBio SMRT. Recently, a combination of Hi-C scaffolding, Illumina short reads, and ONT long reads has been used in hybrid assembly methods to identify the genomes of various aquatic animals.

TGS technologies have greatly enhanced the quality of genome assemblies by producing longer reads up to several metabases. This assists in resolving complex genomic regions, including those with high GC content, repetitive sequences, and structural variations, which are often challenging for SGS. The application of PacBio sequencing has notably enhanced the assembly of the Atlantic salmon genome, offering deeper insights into its genetic structure [32]. TGS can accurately detect structural variants such as insertions, deletions, inversions, and translocations that play crucial roles in phenotypic diversity and adaptation. Recent studies have leveraged TGS to uncover structural variations in aquaculture species, providing new avenues for genetic improvement [69]. PacBio's Iso-Seq technology allows for the sequencing of full-length transcripts without the need for assembly, capturing complete isoform diversity. This is particularly valuable for studying gene expression and alternative splicing in aquaculture species. Research on fish, such as common carp, has utilized Iso-Seq to better understand the transcriptome complexity and functional genomics [70]. ONT's direct RNA sequencing technology

Table 2: Description of whole genome sequencing (WGS) in aquaculture genetics, genomics, and breeding.

Applications	Fish species	Description	Key findings	References
Reference genome assembly	Atlantic salmon	Sequencing the genome to create a comprehensive reference genome that serves as a foundation for genetic studies and breeding programs	Provides a complete genomic map, enabling better identification of genetic variants and markers for selection	[31, 32]
	Rainbow trout	Assembly of a high-quality reference genome to aid in the study of genetic variation and trait mapping	Facilitates the understanding of complex traits and supports genome-wide association studies	[33]
Trait mapping and QTL identification	Nile tilapia	Using whole genome sequencing to identify QTL associated with important traits such as growth and disease resistance	Identifies key genetic regions influencing growth and disease resistance, aiding in marker-assisted selection	[34]
	Yellowtail	Sequencing to map QTL related to disease resistance and environmental adaptability	Enhances the selection process for disease-resistant and environmentally adaptable strains	[35]
Genetic variation and diversity analysis	Common carp	Analyzing genomic data to assess genetic diversity and structure within and between populations	Provides insights into genetic diversity, population structure, and potential for breeding program design	[36]
	Sea bass	Evaluating genetic variation to understand population dynamics and enhance breeding strategies	Helps in managing genetic resources and developing strategies to maintain genetic diversity	[37]
Gene function and functional genomics	Atlantic salmon	Integrating WGS with transcriptomics to study gene expression and function related to growth and stress responses	Provides a comprehensive understanding of gene function and regulation under various conditions	[38]
Breeding program design	Tilapia	Utilizing WGS data to develop genomic selection models for improving traits such as growth rate and disease resistance	Improves the accuracy of selection and accelerates genetic gains in breeding programs	[39]
Population genomics and evolutionary studies	Cod	Analyzing WGS data to understand evolutionary processes and adaptation to changing environments	Provides insights into adaptive evolution and informs strategies for managing populations in changing environments	[40]
	Pangasius	Studying population genomics to support conservation and sustainable management practices	Enhances the management of wild and farmed populations by understanding genetic adaptation and diversity	[41]

enables real-time sequencing of native RNA molecules, providing insights into RNA modifications and expression levels. This has been used to study stress responses and developmental processes in aquaculture species [71]. TGS technologies provide a more accurate and comprehensive understanding of epigenetic modifications by directly detecting DNA methylation without bisulfite conversion. Recent studies have used TGS to explore methylation patterns in aquaculture species, linking them to traits such as growth, development, and disease resistance [29].

TGS enables high-resolution genotyping by providing detailed genetic information, including rare variants and structural variants. This enhances the accuracy of genomics selection models, improving the prediction of breeding values. Studies on species like Atlantic salmon have demonstrated the benefits of TGS in enhancing GS strategies [72]. Long reads from TGS facilitate accurate haplotype phasing, which is crucial for understanding the inheritance of complex traits and improving GS accuracy, that has been applied in aquaculture breeding programs to enhance genetic gain and efficiency [73]. The comprehensive genomic coverage provided by TGS improves the resolution of GWAS, allowing identification of causal variants associated with important traits. This technique has been used to fine-map QTLs identified through GWAS, leading to the identification of candidate genes and casual variants. This information is critical for developing MAS strategies and improving breeding programs. TGS provides a detailed view of genetic diversity within and between populations, making it essential for managing breeding programs and conserving genetic resources. Studies on endangered species and wild populations have utilized TGS to inform conservation strategies and minimize inbreeding [74]. This enables the detection of hybridization events and the extent of genetic introgression between domesticated and wild populations.

Aquatic organisms often have large and complex genomes with high levels of polymorphism and repetitive elements. This complexity poses challenges for sequencing, assembly, and annotation. Many aquaculture breeding programs suffer from limited genetic diversity, which can lead to inbreeding depression and reduced resilience to environmental changes [75]. Maintaining genetic diversity while achieving selective breeding goals is a significant challenge. Effectively integrating genomic data into practical breeding programs requires advanced bioinformatics tool expertise [76]. The sheer volume of data generated by modern sequencing technologies necessitates sophisticated data management and analysis solutions. The escape of genetically modified or selectively bred fish into the wild can have ecological consequences, including competition with wild population and genetic introgression. Ensuring the containment and biosecurity of aquaculture operations is crucial. Ethical concerns regarding the welfare of genetically modified fish need to be addressed as rapid growth rates induced by genetic modifications can lead to physiological and health issues in farmed fish [77]. The high cost of genomic technologies, including sequencing and bioinformatics, remains a barrier for widespread adoption, particularly in developing countries. Reducing these costs is essential for broader implementation. Scaling up the breeding programs to meet global demand while maintaining genetic diversity and biosecurity is complex logistical challenge. Developing efficient and scalable breeding strategies is crucial for industry's growth.

2.2. Genome-Wide Association Studies (GWAS). GWAS have become a crucial tool for unraveling complex traits' genetic basis in aquaculture species. It facilitates identifying genetic markers useful for selective breeding by finding associations between genetic variants and phenotypic traits, thus enhancing productivity and sustainability [78]. This process involves scanning the entire genome of a population to identify genetic variants, typically SNPs, that are statistically associated with specific traits. Unlike approaches that require prior knowledge of candidate genes, GWAS can uncover novel genes and pathways involved in trait variation. In aquaculture, GWAS has been applied to various species to improve traits such as growth rate, disease resistance, stress tolerance, and product quality [14, 72, 78]. These discoveries enable breeders to select broodstock with the most favorable genetic profiles, expediting the improvement of aquaculture stocks. The typical GWAS workflow in aquaculture includes the population selection, phenotyping, genotyping, statistical analysis, and validation to confirm their reliability and utility (Figure 1).

One of the most extensively studied species in aquaculture GWAS is Atlantic salmon, where this technique has identified SNPs associated with resistance to IPN, a viral disease causing significant economic losses. Houston et al. [21] discovered several loci on different chromosomes linked to IPN resistance, providing markers integrated into selective breeding programs. Xu et al. [27] conducted a GWAS to identify SNPs associated with growth rate and body weight, revealing several significant loci now used in MAS to enhance growth performance in breeding programs. Zhang et al. [79] identified several SNPs associated with WSSV resistance in Pacific white shrimp, offering potential targets for genetic improvement. GWAS in rainbow trout has uncovered SNPs linked to traits like growth rate, fillet yield, and disease resistance. Vallejo et al. [80] identified SNPs associated with resistance to bacterial cold-water disease, providing insights that are now being applied to enhance disease resistance in breeding programs.

Genetic diversity and population structure pose significant challenges for conducting GWAS in aquaculture species. Aquaculture species often have complex population structures due to domestication, selective breeding, and hybridization [72]. This can lead to spurious associations if not properly accounted for in the analysis. Accurate phenotyping is crucial for the success of GWAS. Ensuring consistent and accurate phenotyping across large populations is a significant challenge as traits like disease resistance and growth rate can be influenced by a variety of environmental factors. The statistical power of GWAS depends on the sample size and the effect size of the genetic variants. Increasing the sample size and improving statistical methods to detect small-effect variants are ongoing areas of

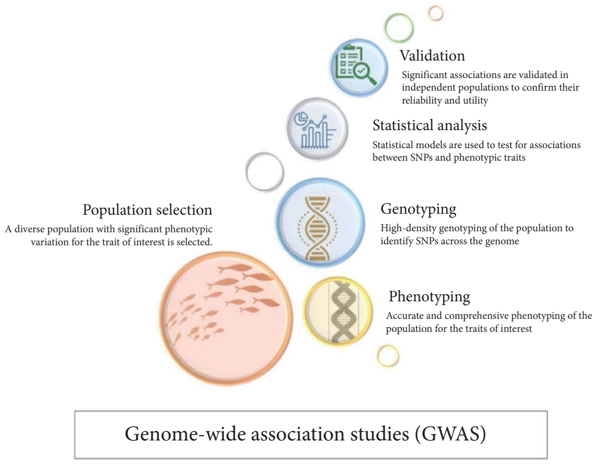


Figure 1: GWAS workflow.

research. Traits in aquaculture species are often influence by environmental and epigenetic factors, which can complicate the interpretation of GWAS results. Understanding the interaction between genetics, environment, and epigenetics is crucial for fully leveraging GWAS findings.

2.3. Genome Editing Technologies to Enhance Aquaculture Production. Fish utilization has consistently expanded with increasing consumer demand. There is a requisite to enhance to deliver additional fish from less water and space to stay up with the rising interest of fish. The growing population has compelled the aquaculturists to look for additional ways to increase productivity even though progress in all these areas has increased productivity overall. To secure food supplies in the coming decades, aquaculture must address several challenges, including adapting to climate change, reducing reliance on traditional animal feed, and combating infectious and parasitic diseases. Various technologies can help meet the increasing demand for fish while maintaining water quality and balanced nutrition. These technologies include genomic ploidy manipulation, hybridization, sex reversal, transgenesis, gene editing, and micro-RNA. Since the early 1980s, transgenic methods have been used with certain fish species, showing improvements in growth rates, health, and environmental stress tolerance, which can boost productivity [81]. Recent research on transgenic growth factor genes, like growth hormone (GH), offers promising solutions for enhancing aquaculture species such as fish, molluscs, crustaceans, and aquatic plants [82].

Polygenic variation helps organisms adapt to human-induced changes or develop desirable traits over time, facilitating domestication. From a genetic and evolutionary standpoint, it is helpful to know how wild-type organisms have been changed into domesticated organisms [83]. This knowledge also provides fundamental information that can be used to improve agricultural strains in the future through traditional breeding and transgenic methods. Leveraging genetic variants identified from imputed resequencing data and GWAS has enhanced the precision of GS for chronic thermal stress tolerance in rainbow trout [84]. Combining advanced computational methods with parallel sequencing, high-throughput genotyping, genome selection, and gene editing allows genomic technologies to significantly speed up genetic advancements in animal breeding [85]. Although the relatively recent domestication of fish species and the scarcity of genomic resources such as molecular markers, genetic maps, DNA sequences, and reference genomes have limited the scale of selection signature research, ongoing genomic innovations are expected to broaden our understanding of genomic regions. According to Yáñez et al. [86], a major challenge for the widespread use of GS in low-input smallholder animal production systems is the high cost of genotyping. Genotyping several thousand animals per generation is typically necessary to reap the benefits of assembling genomic information into breeding programs. Small-scale aquaculture producers may not be able to afford the additional costs associated with producing genomic data. Genomic approaches have yet to be integrated into breeding programs for many small-scale production systems, despite their extensive use in advanced and industrialized animal production sectors [87]. Although new techniques have not been widely adopted in aquaculture, there is growing interest in incorporating high-resolution genomic data into these applications. More studies examining the potential of genomic technologies for their applications in farmed fish and shellfish are anticipated are long.

2.3.1. CRISPR/Cas9. The introduction of CRISPR/Cas9 technology has transformed genetic engineering by offering precise, efficient, and user-friendly genome editing tools [88]. This technology holds significant promise for enhancing traits like growth rate, disease resistance, stress tolerance, and reproductive efficiency. CRISPR/Cas9, derived from the adaptive immune system of bacteria, uses guide RNA (gRNA) to direct the Cas9 nuclease to a specific DNA sequence, where it creates double-strand breaks. These breaks are repaired by the cell's natural mechanisms either through nonhomologous end joining (NHEJ), which can lead to insertions or deletions, or through homology-directed repair (HDR) if a repair template is supplied.

In aquaculture, infectious diseases represent a major challenge, leading to high mortality rates and significant economic losses. One key application of CRISPR/Cas9 in this field is in improving disease resistance [89]. This technology holds promise for creating GMOs with enhanced performance and resilience. Improving growth rates and feed efficiency are critical for enhancing the productivity, viability, and sustainability of aquaculture. This can be used to edit genes involved in growth hormone pathways, metabolism, and nutrient uptake. The technique has been applied to knock out myostatin (MSTN), a gene that negatively regulates muscle growth in Nile tilapia [90]. The resulting fish exhibited increases muscle mass and improved growth rates, demonstrating the potential of CRISPR/Cas9 for enhancing aquaculture production. Genes involved in nutrient uptake and metabolism can be edited to improve feed efficiency such as targeting the insulin-like growth factor for enhancing growth and feed conversion ratios.

Reproductive control is essential for managing breeding programs and preventing the spread of farmed fish into wild populations. CRISPR/Cas9 can be used to knockout gene essential for fertility, creating sterile fish that are unable to reproduce if they escape into the wild such as tilapia [91]. Controlling sex ratios can improve production efficiency, especially in species where one sex grows faster or is more marketable. Knocking out the amh gene in tilapia results in all-male populations, preferred in aquaculture due to their faster growth rates.

Environmental stressors such as temperature fluctuations, salinity changes, and hypoxia can negatively impact fish health and growth. Genes involves in osmoregulation can be targeted to improve the ability of fish to adapt to varying salinity levels. This is particularly important for species like salmon that transition between freshwater and seawater during their life cycle. Sea lice infestations are a major problem in salmon farming. Edited salmon showed increased resistance to infestations, reducing the need for chemical treatments [92]. CRISPR/Cas9 has been employed to knock-out susceptibility genes, leading to shrimp strains with increased resistance to WSSV and other pathogens [93]. The technique is utilized to edit genes involved in growth and development, aiming to produce shrimp that grow faster and reach market size more quickly.

A key concern with CRISPR/Cas9 is the risk of off-target effects, where the Cas9 enzyme may inadvertently cut DNA at unintended locations, resulting in unwanted mutations. Advanced bioinformatics tools are used to design highly specific guide RNAs that minimize off-target binding [94]. Modified versions of the Cas9 enzyme with higher specificity are being developed and tested to reduce off-target activity. The use of CRISPR/Cas9 in food production raises significant regulatory and ethical concerns. Regulations regarding the use of GMOs in aquaculture vary widely across countries. Ensuring compliance with local and international regulations is a critical challenge. Public acceptance of genetically edited fish is crucial for the technology's success. Transparent communication about the benefits, risk, and safety of CRISPR/Cas9-edited fish is essential to gain public trust. Edited genes could potentially spread to wild populations, affecting their genetic diversity and fitness. Containment strategies, such as including sterility, are necessary to mitigate this risk. The introduction of genetically modified fish could disrupt local ecosystem. Comprehensive environmental impact assessments are required to evaluate and mitigate potential risk.

2.3.2. Marker-Assisted Selection (MAS). MAS is a valuable tool in contemporary aquaculture breeding programs. It uses molecular markers associated with desirable traits to identify and select the most suitable candidates for breeding, thereby improving the efficiency and precision of genetic advancements [9]. This involves using molecular marker segments of DNA closely associated with a trait of interest to guide breeding decisions. These markers can be identified through various genomic approaches, such as GWAS and QTL mapping (Figure 2). GWAS involves scanning the entire genome to identify markers associated with traits. QTL mapping involves identifying genome regions linked with variation in quantitative traits. Once researchers identify markers linked to desirable traits, they can use them to select individuals carrying these markers for breeding, thus accelerating genetic improvement. In Atlantic salmon, MAS has been used to select for resistance to sea lice, *Lepeophtheirus salmonis*, a major parasitic threat to salmon farms [95]. By using markers linked to sea lice resistance, breeders can produce offspring with increased resilience to these parasites. Markers linked to genes that influence growth rates and feed conversion ratios can help select fast-growing, efficient fish [96]. Identifying markers associated with resistance to diseases can help breed fish that are less susceptible to infections, reducing mortality and the need of antibiotics [97, 98]. Markers linked to tolerance of environmental stressors such as temperature and salinity can be used to breed more resilient fish. Markers associated with fertility, sex determination, and spawning success can improve breeding efficiency and output. Selecting markers linked to desirable flesh characteristics can enhance product quality. Validation of the selected markers for their reliable association with the trait in different populations and environments ensures their robustness and applicability across breeding programs. Validated markers are used to screen breeding candidates carrying favorable alleles for breeding, thus enhancing the desired traits in the offspring. Integration of traditional techniques with MAS maximizes the genetic gain using phenotypic data to make more informed breeding decisions.

MAS provides several benefits compared with traditional breeding methods. Utilizing molecular markers enables breeders to make more precise selection choices, particularly for traits that are challenging to measure directly [96]. Additionally, MAS can speed up the breeding process by allowing for early selection of desirable traits, thereby shortening the generation interval. Combination of MAS with traditional technologies can lead to cumulative genetic gains over successive generations. Furthermore, the reduction of incidence of diseases lowering the mortality rates and the need for antibiotics can be managed by selecting disease-resistant markers. Selecting for the markers linked to flesh quality and other consumer-preferred traits can improve the marketability of aquaculture products [98]. In Atlantic salmon, MAS has been used to improve resistance to diseases like IPN. Palaiokostas et al. [97] identified markers linked to IPN resistance through QTL mapping and validated these markers in commercial breeding populations. The use of these markers has significantly reduced mortality rates from IPN in farmed salmon populations. The technique has been employed to enhance growth rates and feed efficiency in Nile tilapia. QTL mapping identified markers linked to growth traits, and these markers were used to select fast-growing individuals. This approach has led to substantial improvements in growth rates and feed conversion ratios in commercial tilapia farming. In Pacific white shrimp, MAS has been used to improve resistance to WSSV. You et al. [99] identified markers linked to WSSV resistance through GWAS and validated these markers in breeding

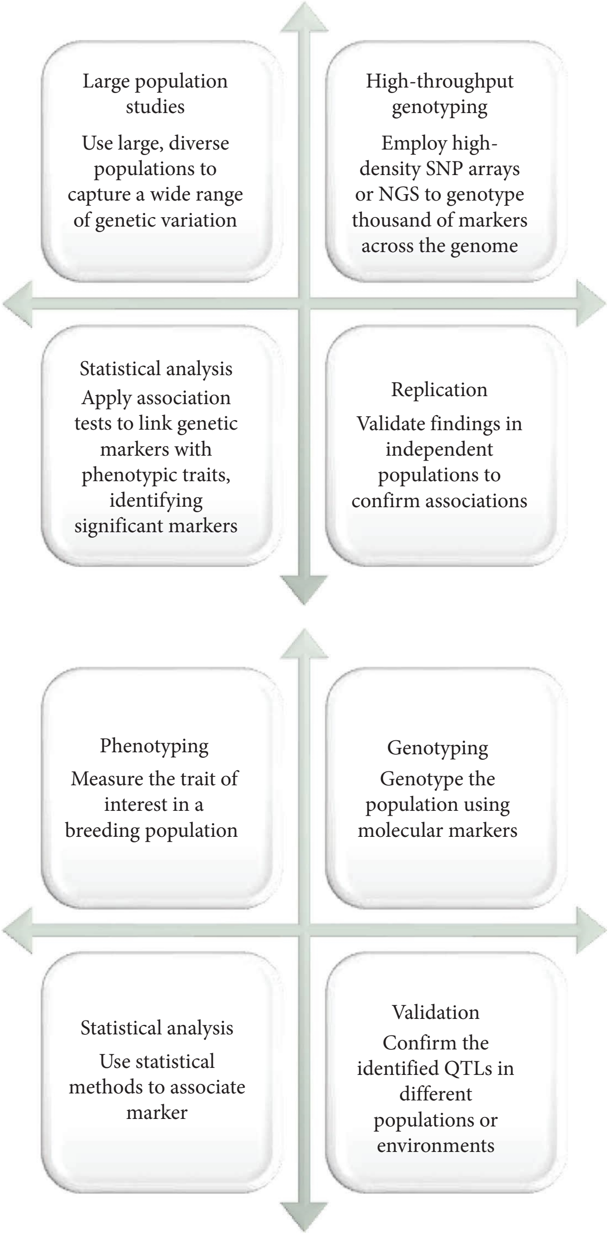


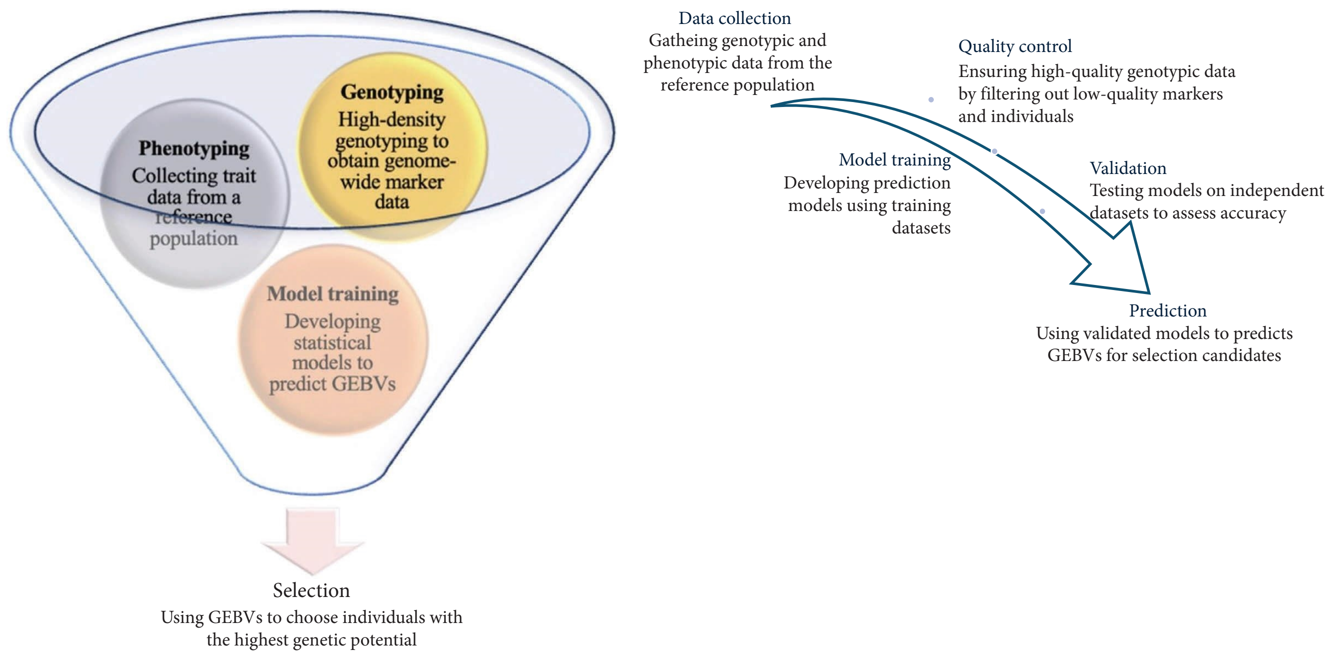
Figure 2: Techniques used to identify and utilize molecular markers in Marker-assisted Selection: Genome-wide association studies (GWAS) involve large population studies, high-throughput genotyping, statistical analysis, and replication; Quantitative trait loci (QTL) mapping involves phenotyping, genotyping, statistical analysis, and validation.

programs. The use of these markers has helped produce shrimp strains with enhanced disease resistance, reducing mortality and improving productivity.

Despite its advantages, MAS faces several challenges. Ensuring that the markers are consistently associated with the traits across different populations and environments is crucial but can be resource intensive. Implementation of MAS requires significant investment in genotyping infrastructure and expertise in bioinformatics and statistical genetics. Many traits of interest in aquaculture are controlled by numerous genes and environmental factors, making it challenging to identify and use markers effectively. Maintaining genetic diversity while selecting for specific markers is important to avoid inbreeding and ensure long-term sustainability.

2.3.3. Genomic Selection (GS). GS is a groundbreaking technique in aquaculture breeding that employs genome-wide marker data to predict the breeding values of individuals (Figure 3). This method offers notable advantages over traditional selection techniques by improving accuracy and speeding up genetic advancements for complex traits [100]. GS uses high-density genetic markers across the genome to assess the genetic potential of breeding candidates. Unlike traditional methods, which rely on phenotypic selection or a limited number of markers (MAS), GS utilizes extensive genetic information to estimate genomic breeding values (GEBVs) with high precision. This approach has been effectively applied in the breeding programs for rainbow trout, *O. mykiss*, leading to more accurate selection of broodstock and quicker genetic improvements in traits such as growth rate, fillet yield, and disease resistance [80]. GS has also been used successfully in various aquaculture species to enhance traits like growth, disease resistance, and environmental tolerance. Improving growth rates and feed efficiency is crucial for profitability of aquaculture operations. GS enhances these traits by using GEBVs to select individuals with superior growth rates and selecting fish with favorable genomic profiles for feed efficiency, thereby reducing feed costs. Disease resistance against the outbreaks is improved using GEBVs to identify resistant individuals and thus reducing mortality and treatment costs. GS can breed more resilient fish by selecting individuals with genomic profiles that confer greater tolerance to environmental stressors and by developing strains that withstand varying climatic conditions, ensuring sustainable production [39].

High-density genotyping arrays and NGS are essential for obtaining comprehensive genetic information. SNP array provides high-resolution genotyping by covering thousands of SNP markers across the genome. WGS offers the most comprehensive genetic information, capturing all genetic variants within an individual's genome. Various statistical models are used to predict GEBVs from genotype data such as base linear unbiased prediction (BLUP) extended to incorporate genome-wide marker data (GBLUP). Bayesian methods incorporate prior information and are effective for complex traits with many small-effect loci and advanced techniques (random forests and support vector machines) that can capture complex interactions between the markers [78]. Vallejo et al. [101] reported that genomic predictions for these traits resulted in substantial genetics gains compared with traditional selection methods. High-density SNP arrays and machine learning models have refined selection accuracy further. Wang et al. [102] showed the enhance resistance to WSSV in Pacific white shrimp with reduced mortality rates and improved overall production efficiency with GS. Implementing GS requires significant investment in genotyping infrastructure and expertise in bioinformatics and statistical genetics. Ensuring markers are consistently



(a) (b)

FIGURE 3: (a) The process of genomic selection for breeding in aquaculture; (b) Genomic prediction pipeline.

associated with traits across different populations and environments is crucial but resource intensive. Many traits of interest are controlled by multiple genes and environmental factors, complicating the identification and utilization of markers. Balancing selective intensity with maintaining genetic diversity is essential to avoid inbreeding and ensure long-term sustainability.

2.3.4. Hybridization and Polyploidy. Hybridization and polyploidy are valuable techniques in aquaculture breeding used to create fish with enhanced traits, boost genetic diversity, improve growth rates, increase disease resistance, and help fish adapt to environmental stress. Hybridization involves crossing individuals from different species, strains, or populations to produce offspring that inherit desirable traits from both parents. This often results in hybrid vigor, where the hybrids demonstrate superior performance compared with their parent species. Intraspecific hybridization involves crossing individuals within the same species, usually between different strains or populations, to introduce genetic diversity and improve traits such as growth, fecundity, and disease resistance. In contrast, interspecific hybridization involves crossing individuals from different species. This can result in hybrids with unique combinations of traits that neither parent species possesses. Hybridization in tilapia, *Oreochromis* spp., has produced hybrids like the Nile tilapia, *O. niloticus*, x blue tilapia, *O. aureus*, which exhibits enhanced growth rates, better stress tolerance, and improved disease resistance [103]. These hybrids are also more adaptable to different environmental conditions, making them suitable for diverse aquaculture systems. For instance, hybrid catfish (*Ictalurus punctatus* x *I. furctaus*) are known for their fast growth rates from channel catfish, *I. punctatus*, with disease resistance and hardiness from blue catfish, *I. furcatus*, resulting in production of robust hybrid that performs well in commercial aquaculture operations [104]. Similarly, Guo et al. [105] demonstrated triploid oysters (*Crassostrea gigas*) to be favored in aquaculture due to sterility and superior growth compared with diploid counterparts. In salmonids, hybridization between different species, rainbow trout, *O. mykiss*, x brook trout, *Salvelinus fontinalis*, has been explored to combine desirable traits such as growth rates, flesh quality, and environmental tolerance. Artificial hybridization is controlled breeding programs where selected individuals from different species or strains are crossed. Natural hybridization occurs in the wild or in extensive aquaculture systems where different species coexist and interbreed naturally. Molecular markers are used to confirm hybrid status and assess the genetic contribution of each parent species.

Polyploidy involves having more than two complete sets of chromosomes. In aquaculture, polyploidy can be artificially induced to create triploids (with three sets of chromosomes) or tetraploids (with four sets of chromosomes). This condition can lead to benefits such as sterility, faster growth, and improved survival rates. Triploidy is achieved by subjecting fertilized eggs to physical or chemical shocks such as heat, cold, pressure, or chemicals like colchicine that prevent the expulsion of the second polar body during meiosis, resulting in an additional set of chromosomes. Tetraploidy is induced by applying treatments to developing embryos to halt the first cell division, which results in four sets of chromosomes [106]. Tetraploids can then be crossed with diploids to produce triploid offspring. Methods for

Table 3: Summary of the applications of genetic genomics in aquaculture, including specific fish species.

Applications	Fish species	Description	References
Genomic selection	Atlantic salmon	Utilizes genome-wide marker data to predict breeding values, enhancing traits like growth rate, disease resistance, and fillet yield. This approach accelerates genetic improvement and has been implemented in breeding programs with significant success	[5, 109]
	Rainbow trout	Applying genomic selection to improve growth rates and stress tolerance by predicting genetic potential using high-density genetic markers	[84, 110]
Disease resistance	Rainbow trout	Using GWAS to identify genetic variants linked to resistance against diseases such as infectious pancreatic necrosis (IPN), and against *Piscirickettsia salmonis*	[111]
	Tilapia	Employing CRISPR/Cas9 to create knockout lines to study and enhance resistance to diseases such as tilapia lake virus (TiLV)	[39, 93]
Growth rate improvement	Rainbow trout	Utilizing high-throughput sequencing and genomic selection to enhance growth traits and feed efficiency	[78, 112]
Stress tolerance	Atlantic salmon	Identifying genetic markers for stress resilience using GWAS, helping to select fish that can better withstand environmental stressors such as temperature fluctuations	[7, 113]
	Zebrafish	Employing functional genomics and gene editing tools to explore genetic bases of stress tolerance and related phenotypes	[114, 115]
Polyploidy induction	Triploid trout	Creating triploid individuals by applying physical or chemical shocks to fertilized eggs, resulting in sterility and improved growth rates	[108]
	Tetraploid tilapia	Inducing tetraploidy by treating embryos to prevent the first cell division, followed by crossing with diploids to produce triploid offspring with enhanced traits	[36, 116];
Hybridization	Hybrid tilapia	Crossbreeding different strains or species to produce hybrids with superior traits such as growth rate and disease resistance	[118, 119]
Functional genomics	Atlantic salmon	Applying gene overexpression and knockout techniques to validate the role of specific genes in growth and disease resistance	[89, 120]
Marker-assisted selection (MAS)	Tilapia	Utilizing molecular markers linked to desirable traits such as disease resistance for more precise selection in breeding programs	[14, 121]
	Catfish	Employing MAS to select for traits like feed efficiency and resistance to environmental stressors	[14, 122]
Whole genome sequencing	Rainbow trout	Providing draft genome sequences to facilitate the study of genetic diversity and trait mapping, aiding in the development of improved breeding strategies	[36, 124]
	Atlantic salmon	Generating and utilizing reference genomes to support research on genetic improvement and adaptation in aquaculture	[32, 72]

Table 4: Future perspectives in aquaculture genetics, genomics, and breeding.

Genomic technologies		
Whole genome sequencing (WGS)	**CRISPR/Cas9 and gene editing**	**Epigenetics**
1. High-quality reference genomes for diverse species 2. Enhanced resolution for trait mapping and genetic studies	1. Development of disease-resistant and faster-growing strains 2. Precise genetic modifications to enhance desirable traits	1. Integration of epigenetic data into breeding programs 2. Understanding epigenetic modifications affecting growth and stress responses
Breeding strategies		
Genomic selection	**Marker-assisted selection (MAS)**	**Hybridization and polyploidy**
1. Improved accuracy of breeding value predictions 2. Faster genetic gains in complex traits	1. Continued application for traits difficult to measure phenotypically 2. Integration with high-throughput genotyping technologies	1. Development of new hybrid strains with superior traits 2. Application of polyploidy for sterility and growth improvements
Omics integration		
Transcriptomics	**Proteomics**	**Metabolomics**
1. Analysis of gene expression patterns under different conditions 2. Identification of regulatory networks for important traits	1. Profiling of protein expression and modifications 2. Correlation of proteomic data with phenotypic traits	1. Comprehensive analysis of metabolites 2. Understanding metabolic pathways related to growth and health
Data integration and bioinformatics		
Big data analytics	**Machine learning and AI**	
1. Integration of multiomics data for holistic insights 2. Advanced computational tools for data analysis and interpretation	1. Predictive modeling for trait selection 2. Optimization of breeding strategies through AI-driven approaches	
Sustainability and ethical considerations		
Conservation genomics	**Ethical issues**	
1. Strategies to preserve genetic diversity in wild and farmed populations 2. Applications of genomics for sustainable aquaculture practices	1. Addressing concerns related to genetic modifications 2. Development of regulatory frameworks for responsible use of technologies	

inducing polyploidy include heat shock, cold shock, hydrostatic pressure, and various chemical agents. Flow cytometry, karyotyping, and molecular markers are used to confirm the polyploid status of individuals. Selective breeding programs incorporate polyploid individuals to establish and maintain polyploid lines. Triploid oysters, *C. gigas*, are widely cultured due to their superior growth rates and market advantages [107]. Triploids are sterile, which means they do not divert energy into reproduction, resulting in faster growth and better meat quality throughout the year. Triploid salmonids, such as rainbow trout and Atlantic salmon, are produced to reduce the risk of genetic contamination of wild populations and to improve growth rates [108]. These exhibits reduced aggression and improved welfare in aquaculture systems. Polyploidy in common carp. *C. carpio* has been explored to enhance growth rates and disease resistance. Triploids carp are particularly valued for their improved performance and sterility, which prevents uncontrolled breeding in farming environments. The applications of aquaculture genetics, genomics, and breeding are summarized in Table 3.

3. Priorities for Future Research

Developing cost-effective and high-throughput sequencing technologies is a priority. Innovations such as nanopore sequencing and improvements in long-read sequencing can facilitate genomic research in a wider range of species. Understanding the functional roles of genes and genetic pathways is essential for predicting and enhancing desirable traits. Functional genomics approaches, including transcriptomics and proteomics, can provide insights into gene function and regulation [30]. Implementing strategies to preserve genetic diversity in breeding programs is crucial. Techniques such as rotational mating and the use of genetically diverse broodstock can help maintain diversity. Its applications in species identification, genetic characterization, and MAS have significantly contributed to the advancement of aquaculture practices. Enhancing bioinformatics tools and training is necessary for the effective integration of genomic data into breeding programs. This includes developing user-friendly software and providing training for breeders and researchers.

Integrating Omics technologies such as transcriptomics, proteomics, and metabolomics can offer a more comprehensive view of the genetic basis of complex traits [125]. Multiomics approaches can aid in identifying functional variants and clarifying the biological pathways involved in trait variations. Functional genomics techniques, like gene knockout and overexpression studies, can confirm the causal links between specific SNPs and phenotypic traits. Tools like CRISPR/Cas9 and other gene-editing technologies are valuable for functional validation in aquaculture species [88]. Markers identified through GWAS can be used directly in GS programs, which predict the breeding values of individuals based on their genomic profiles and can accelerate genetic improvement. This method is already being applied successfully in species such as Atlantic salmon and tilapia. To ensure long-term sustainability, it is crucial to maintain and enhance diversity within breeding programs. GWAS can help pinpoint genetic variants that contribute to diversity and resilience, enabling breeders to design programs that achieve genetic advancement while preserving genetic diversity.

Multitrait improvement by targeting genes involved in growth, disease resistance, and stress tolerance, researchers can develop robust strains that perform well under various conditions. Integrating genomic prediction models with CRISPR/Cas9 editing can enhance the accuracy and efficiency of trait improvement. Systematic knockout of genes can reveal their functions and interactions, providing insights into the genetic architecture of complex traits. Editing genes within specific pathways can elucidate their roles in regulating traits, guiding targeted breeding and genetic improvement efforts. Analyzing gene expression changes following CRISPR/Cas9 editing can identify downstream effects and regulatory networks. Studying protein and metabolite profiles in edited fish can reveal biochemical impacts of genetic modifications, guiding further optimization. Advancements in genomic technologies and analytical methods continue to enhance the potential of GS in aquaculture [76, 126]. Combining genomic data with transcriptomic, proteomics, and metabolomic data can provide a more comprehensive understanding of trait biology. Developing more sophisticated computational tools and machine learning algorithms can improve the accuracy of genomic predictions. Collaborative efforts across countries and institutions can facilitate the sharing of genomic resources and breeding strategies, accelerating genetic improvement (Table 4).

4. Conclusion

Technologies such as WGS, GWAS, and CRISPR/Cas9 gene editing have fundamentally changed our understanding of the genetic basis of economically important traits in aquaculture species. These tools allow for the identification of genetic markers linked to traits like growth, disease resistance, and environmental adaptability, which are essential for developing improved breeding strategies. MAS and GS have become integral to breeding programs. MAS uses molecular markers associated with desirable traits for precise selection of breeding candidates. GS predicts breeding values based on an individual's genomic profile, accelerating genetic improvement. Despite these advancements, the manuscript acknowledges ongoing challenges, including the need for extensive phenotypic and genomic databases, the complexity of polygenic traits, ethical considerations regarding genetic modifications, and the necessity for robust bioinformatics infrastructure and expertise. The conclusion emphasizes that future research should focus on enhancing genomic resources for under-researched species, improving phenotypic data accuracy, and developing sustainable breeding practices. The future of aquaculture productivity and sustainability is strongly linked to the integration of current genomic technologies with other "omics" technologies and functional genomics. This multiomics approach provides a more comprehensive view of complex traits, aiding in the identification of functional variants and clarifying biological pathways. Functional genomics techniques like gene knockout and overexpression studies, often utilizing CRISPR/Cas9, can confirm causal links between genetic variations and phenotypic outcomes.

Data Availability Statement

The data supporting the findings of this study are available within the article and from the corresponding author upon reasonable request.

Conflicts of Interest

The authors declare no conflicts of interest.

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