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From genome to phenome: omics perspectives on fish reproduction

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Fish reproduction, a complex biological process, is regulated by diverse molecular, biochemical, and physiological mechanisms. Advances in omics technologies, including genomics, transcriptomics, metabolomics, and phenomics, have provided every possible way to understand the underlying pathways of reproductive development in fish. In contrast to conventional approaches, omics technologies give us a detailed, molecule-by-molecule view of how an organism's energy, hormones, and metabolism change during its most important reproductive phases. Metabolomics and lipidomic studies in fish have revealed the importance of lipid and amino acid metabolism during embryogenesis and ovarian development, while transcriptomics and proteomics helped to identify key genes and proteins involved in steroidogenic pathway and reproductive development. Nutritional omics on the other hand highlights the role of essential fatty acids, in enhancing overall reproductive performance, so the offspring quality. Moreover, omics is transforming genetic conservation by providing a new toolkit to optimize the freezing process and ensure the long-term survival of genetic resources, securing a future for endangered fish germplasm. Together, these strategies do more than optimize aquaculture like, fortify conservation efforts, build sustainable and resilient futures for fish populations worldwide.

KEYWORDS

fish, genomics, metabolomics, reproduction, transcriptomics

1 Introduction

Suboptimal reproductive performance in fish is a major economic limitation of aquaculture by restricting the production of quality seed and limiting population growth (Honji et al., 2025). Optimum reproductive success in fish is challenging and usually requires specific interventions. These treatments encompass the delivery of precise hormonal therapy, manipulation of environmental factors like photoperiod, temperature, and salinity, and the use of state-of-the-art reproductive drugs in order to drive processes

like gonadal development, ovulation, and gamete viability (Mylonas et al., 2010). Often, multiple hormonal and environmental approaches are used together, each necessitating a basis in scientific data. New research promotes reproductive technologies through the strategic application of hormone therapies in combination with proper brood stock nutrition to support the production of viable gametes and to establish favorable conditions for spawning or spermiation in many teleost species (Adatto et al., 2022; Fakriadis et al., 2020; Corriero et al., 2021; Hilsdorf et al., 2021; Hernandez de-Dios et al., 2022). These advances are essential to optimize both gamete production and quality and thus facilitate the propagation of species of economic value (Naylor et al., 2021; Bobe and Labbé, 2010; Bobe, 2015). Reproductive dysfunction is often seen in captive conditions, as reported by commercial producers. Female fish may not complete terminal oocyte maturation, ovulation, or spawning, and males usually produce low-quality and inadequate sperm, leading to decreased growth rates as well as overall production efficiency (Zohar and Mylonas, 2001; Mylonas et al., 2010; Zohar et al., 2010).

Aquaculture, defined as the cultivation of aquatic organisms and plants, represents a rapidly advancing discipline that contributes significantly to food security and livelihood enhancement. The sustainable development of this sector necessitates comprehensive assessments of population dynamics, genetic composition, species identification, and the functional characterization of genes. In this context, the application of genetics and biotechnology provides essential tools for advancing research and innovation (Tripathy et al., 2022). Omics technologies encompass a suite of high-throughput approaches designed to investigate the structure, function, and interactions of biomolecules, including genes, transcripts, proteins, lipids, and metabolites, within biological systems in an unbiased manner (Horgan and Kenny, 2011). Following the completion of the Human Genome Project, these approaches rapidly expanded to include genomics, transcriptomics, proteomics, metabolomics, and lipidomics, each providing complementary insights into cellular and molecular processes. In aquaculture, omics-based approaches are increasingly employed for diverse applications. These include deciphering the molecular basis of disease resistance and stress adaptation, developing disease diagnostics and vaccines, identifying and improving resistant strains, authenticating species for food safety and traceability, and improving post-harvest quality and value addition (Westerhoff and Palsson, 2004).

By integrating data across multiple molecular levels like DNA, RNA, proteins, lipids, and metabolites, omics enables a systems-level understanding of biological complexity. Its utility lies in characterizing global biomolecular states under specific physiological or pathological conditions, identifying key regulatory molecules, and clarifying the mechanisms underlying differential biomolecular responses. The versatility of omics further extends to both fundamental biology and applied research, particularly in disease etiology, biomarker discovery, diagnosis, and prognosis (Kell, 2006). Future research trajectories are expected to emphasize integrative omics and systems biology

approaches, which hold the potential to advance predictive, preventive, and personalized medicine (Evans and Relling, 2004).

Genomic sequences encode the fundamental blueprint of genetic information; however, the manifestation of performance and production traits is governed by complex regulatory interactions among the genotype, expressed phenotype, and environmental factors (Wang et al., 2009; Hill and Kirkpatrick, 2010). These regulatory hierarchies are examined through specialized scientific domains collectively referred to as omics. Within aquaculture systems, the principal omics disciplines encompass genomics, epigenomics, transcriptomics, proteomics, metabolomics, microbiomics, and metagenomics, each providing high-throughput datasets that elucidate specific molecular and cellular components (Mohanty et al., 2019). Genomics investigates the complete DNA repertoire of an organism, tissue, or cell, facilitating the study of genetic variation, structural organization, and heritability (Mushtaq et al., 2025). Epigenomics explores chemical and conformational modifications to DNA and RNA that modulate gene regulation, chromatin dynamics, and epigenetic inheritance without altering the nucleotide sequence (Russell, 2010). Transcriptomics focuses on the global expression profile of RNA transcripts, enabling the quantification of gene activity, alternative splicing patterns, and regulatory mechanisms involving both coding and non-coding RNAs. Proteomics interrogates the entire proteome to characterize protein structures, functions, post-translational modifications, and molecular interactions. Metabolomics assesses the complete spectrum of metabolites, thereby revealing biochemical pathways, cellular fluxes, and metabolic regulation (Davis, 2005). Microbiomics characterizes the composition, diversity, and functional dynamics of microbial consortia associated with the host and its surrounding environment, whereas metagenomics analyzes the collective genomic content of environmental samples, encompassing genetic material derived from host and non-host organisms alike (Kumar, 2021). Integration of two or more omics layers constitutes a multi-omics approach, which may also be described as poly-omics, pan-omics, trans-omics, integrative omics, vertical omics, or systems omics, and offers a comprehensive framework for dissecting complex biological processes in aquaculture organisms (Bashura et al., 2021).

2 Genomics in fish reproduction

Genomics deals with the large-scale study of genes and how they are organized within the genome. The genome serves as a long-term storage system for genetic information, but on its own, it does not fully explain how an organism functions. Unlike the proteome, which is dynamic and mirrors active biological processes, the genome remains relatively stable. The genetic information it contains influences an organism's traits by controlling essential cellular activities, mainly through protein synthesis. Genomic research is broadly divided into structural genomics, which examines genome structure, organization, and evolution, and

functional genomics, which focuses on patterns of gene expression (Mohanty et al., 2019). Over time, genomics has shifted from simply sequencing DNA toward understanding gene function. The field now explores how genes are expressed, how they interact in networks, and how these processes connect to biological functions. This expansion has also led to overlaps with proteomics, transcriptomics, and the study of protein–protein interactions. Such approaches have opened new opportunities in areas including clinical diagnostics, agricultural and environmental biotechnology, and pharmacogenomics (Misra et al., 2019). Functional genomics, in particular, aims to study the activity of all genes in a genome at once. This can be examined at the RNA level through transcriptomics or at the protein level through proteomics (Xu et al., 2014).

A crucial first step in genetic management is setting clear objectives, defining what to manage and how, by integrating ecological, evolutionary and population insights with agreed management priorities. Determining “what to manage” depends on several factors, including a species’ physical and behavioral traits, distribution, genetic diversity, ecological role, economic importance, cultural value, population size and structure, and overall extinction risk (Johnson and Koepfli, 2014). Reproductive technologies now play a vital role in managing both wild and captive populations. Techniques such as artificial insemination and *in vitro* fertilization are increasingly used to promote gene flow among isolated wild populations, between captive and wild groups, and across different conservation programs. These tools also help ensure that genes from individuals unable to breed naturally are still represented in future generations (Pukazhenthil and Wildt, 2004; Comizzoli et al., 2009; Wildt et al., 2010). Several captive-breeding programs have successfully supported or even re-established wild populations. Notable examples include the Puerto Rican parrot (Brock and White, 1992), California condor (Geyer et al., 1993), Micronesian kingfisher (Haig et al., 1995), whooping crane (Jones et al., 2002), primates such as lion-tailed macaques and bonobos (Morin and Ryder, 1991; Reinartz and Boese, 1997), black-footed ferret (Cain et al., 2011), and the Iberian lynx (Vargas et al., 2008; Gañán et al., 2010). The preservation of genetic diversity for future generations is further strengthened through the use of germplasm banks, cryopreserved gametes, and frozen cell lines, supported by ongoing advances in reproductive technologies. Cryo banking is already common in livestock species (Mazur et al., 2008) and is gradually gaining importance in wildlife conservation as well (Comizzoli et al., 2009; Swanson et al., 2007). However, wider application of these methods is often constrained by limited knowledge of the reproductive biology of many species (Andrabi and Maxwell, 2007).

In fishes, genomics plays an important role in understanding and improving fish reproduction by revealing the genetic basis of reproductive development, maturation, and fertility. Successful reproduction in fish hinges on the precise molecular programming of gonadal development, beginning with the differentiation of bipotential tissue into testes. This process is governed by a complex interaction of genetic cascades and environmental factors. Sex determination can be genotypic

(GSD), with master genes like *dmy* in medaka, *amhy* in pejerrey, or *sdY* in salmonids, or environmental (ESD), where factors like elevated temperature promote masculinization often by downregulating ovarian aromatase (*cyp19a1a*) and upregulating male genes like *amh* (Matsuda et al., 2002; Hattori et al., 2012; Navarro-Martín et al., 2011).

The differentiation of the testis itself is driven by key transcription factors. *Dmrt1* is a pivotal male determinant essential for Sertoli cell specification and spermatogenesis; its disruption leads to testicular dysgenesis and even sex reversal (Webster et al., 2017; Bhat et al., 2016). The *sox9* genes (duplicated into *sox9a* and *sox9b* in teleosts) contribute to Sertoli cell development and testis cord formation, with expression patterns varying between species but often influenced by androgens and temperature (Raghuveer and Senthilkumaran, 2010a). Anti-Müllerian hormone (*amh*), a member of the TGF- β superfamily, is crucial for testicular differentiation and acts as a negative regulator of spermatogenesis; its expression is upregulated by high temperature and cortisol but typically downregulated by androgens (Pfennig et al., 2015; Fernandez et al., 2013).

Steroidogenesis, the production of sex hormones, forms the functional core of the gonad. The pathway from cholesterol to androgens like 11-ketotestosterone (11-KT) involves coordinated expression of genes such as *star* (cholesterol transport), *cyp11a*, *cyp17*, *hsd3b*, and *hsd11b*. The final enzyme, aromatase (*cyp19a1a*), converts androgens to estrogens. This pathway is primarily regulated by the hypothalamic-pituitary-gonadal (HPG) axis. The hypothalamus releases gonadotropin-releasing hormone (GnRH), which stimulates the pituitary to secrete follicle-stimulating hormone (FSH) and luteinizing hormone (LH). These gonadotropins act on testicular somatic cells to drive steroidogenesis and gametogenesis. Kisspeptins (*kiss1/kiss2*) serve as upstream regulators of GnRH neurons, linking environmental cues like photoperiod to the onset of puberty (Schulz et al., 2010; Selvaraj et al., 2010).

Spermatogenesis, the transformation of primordial germ cells (PGCs) into spermatozoa, is the ultimate goal of testicular function. PGCs are marked by genes like *vasa* and *dnd*, which are essential for their migration, survival, and early development (Yoshizaki et al., 2002; Weidinger et al., 2003). The process is then orchestrated by FSH and locally produced 11-KT, which act through androgen receptors (*ar*) in Sertoli and germ cells to promote germ cell proliferation and differentiation. Other factors like insulin-like growth factors (*igf*), activin, and inhibin fine-tune this process by modulating germ cell proliferation and FSH feedback (Schulz et al., 2010; Miura et al., 1995).

Critically, the expression of all these genes—from sex determiners to steroidogenic enzymes—can be modulated by external factors. Hormonal manipulations (e.g., androgen or aromatase inhibitor treatments), environmental changes (temperature, pH), dietary components, and even plant-derived bioactives like eurycomanone can significantly alter transcriptional profiles to either enhance or impair reproductive outcomes (Bhat et al., 2018; Díaz and Piferrer, 2017). This molecular understanding provides a roadmap for aquaculture, offering strategies to overcome

reproductive dysfunction in captivity by selectively targeting these key genes and pathways to improve gonadal development, steroidogenesis, and ultimately, sustainable gamete production.

Genomics forms the foundation of genome-wide association studies (GWAS) by enabling high-density, genome-wide scanning of single nucleotide polymorphisms (SNPs) to unravel the genetic basis of complex traits such as growth rate and age at sexual maturation in fishes. GWAS and high-resolution QTL mapping in Atlantic salmon (*Salmo salar*) have revealed a well-defined but largely polygenic genetic architecture underlying growth rate and age at sexual maturation. A landmark GWAS by Gutiérrez et al. (2015) identified a major locus on chromosome 25 harboring VGLL3, which explains a substantial proportion of variation in age at maturation, with alleles showing sex-dependent dominance effects on early and late maturation. Adjacent and supporting regions include genes such as SIX6, involved in hypothalamic-pituitary axis development, and HIP1, associated with reproductive investment and maturation timing. Growth-related QTLs identified through high-density linkage maps and GWAS overlap with components of the GH-IGF axis (*igf1*, *igf1r*, *ghr*), as well as metabolic and muscle development genes (*myod*, *stat5*), indicating tight genetic coupling between somatic growth and reproductive maturation. Similar polygenic patterns for fecundity-related traits have been reported in rainbow trout (*Oncorhynchus mykiss*), where GWAS detected numerous small-effect loci including FSHR, LHR, VIT, ESR1, and BMP15, reinforcing the complexity of female reproductive traits (D'Ambrosio et al., 2020). Collectively, these studies demonstrate that while VGLL3 represents a major-effect maturation gene in Atlantic salmon, most growth and reproductive traits are controlled by many loci of small effect, supporting the use of genomic selection rather than single-marker approaches in salmonid breeding programs (Gutiérrez et al., 2015; D'Ambrosio et al., 2020).

Teleost fishes show remarkable diversity and plasticity in sex determination, with genetic sex determination (GSD) and temperature-dependent sex determination (TSD) operating either independently or in combination across species. Rapid evolution of master sex-determining genes is a characteristic feature of teleosts; the first such gene, DMY, a Y-linked duplicate of DMRT1, was identified in medaka (*Oryzias latipes*) (Matsuda et al., 2002), whereas closely related species employ alternative regulators such as GsdY, indicating frequent turnover of sex-determining mechanisms (Myosho et al., 2012). In salmonids, including rainbow trout and Atlantic salmon, SdY, a duplicated immune-related gene, functions as the master sex-determining gene by interacting with FOXL2 to repress *cyp19a1a* (aromatase) expression and inhibit ovarian differentiation, thereby promoting testicular development (Yano et al., 2012, 2013; Bertho et al., 2018). Increasing evidence demonstrates that epigenetic regulation, particularly DNA methylation, plays a central role in sex determination, differentiation, and temperature-induced sex reversal, with sexually dimorphic methylation patterns often concentrated on sex chromosomes and key pathway genes such as *dmrt1* and *cyp19a1a* showing sex-specific methylation-expression relationships. Temperature-driven changes in DNA

methylation can bias sex ratios toward masculinization or feminization in a species-specific manner, highlighting the integrated effects of genetics, epigenetics, and environment in teleost sex determination (Metzger and Schulte, 2018; Yang et al., 2022).

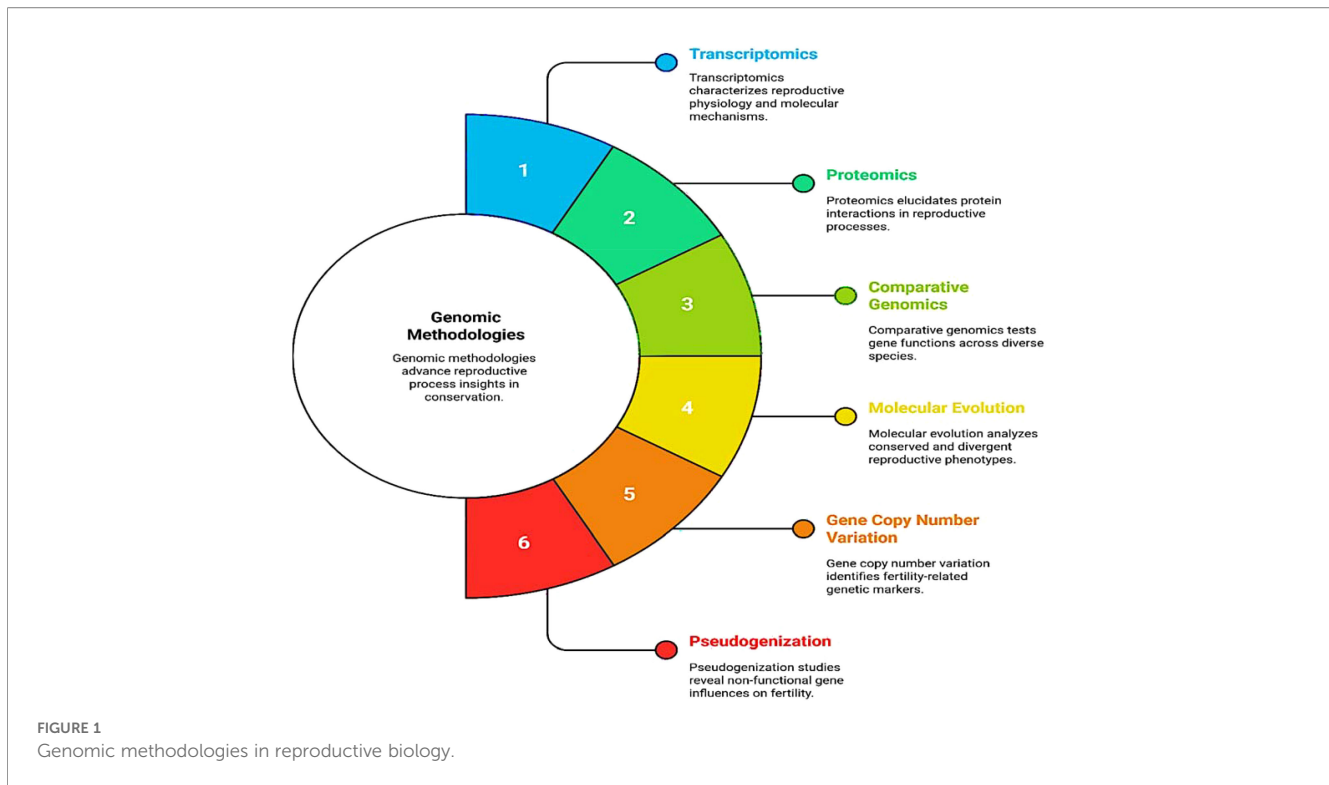
In recent years, genomics has become a powerful tool in conservation biology, helping to uncover the genetic basis of key life-history and adaptive traits. Although progress has been fastest in model and domestic species where genes related to growth, milk production, and disease resistance have been identified (Fan et al., 2010). These studies have revealed candidate genes linked to reproduction, development, and behavior (Li et al., 2011; Miller et al., 2011a; Sarropoulou and Fernandes, 2011; Nakamura et al., 2013). Expanding genomic resources for non-model species remains essential for deepening our understanding of the genetic foundations of key evolutionary traits (Ekblom and Galindo, 2011).

2.1 Genomics and reproductive biology at the cellular level

At the cellular level, reproductive success and, consequently, the fitness and long-term survival of animal populations including fish depend largely on the production of healthy gametes and their ability to create viable offspring (Kime, 1999). Genomic tools are poised to make some of their most significant contributions to conservation biology by deepening our understanding of the molecular mechanisms underlying reproduction across a wide range of species. Modern high-throughput techniques such as transcriptomics and proteomics are increasingly being used to explore reproductive physiology and uncover the molecular basis of phenomena like reproductive isolation, gamete incompatibility, and related disorders (as illustrated in Figure 1). Comparative genomics, which is inherently iterative, allows researchers to identify candidate genes in one species and then test their functions across evolutionarily distant taxa. For instance, Li et al. (2012) identified variable markers in 14 candidate genes that are conserved across species ranging from insects to mammals, linking them to male and female fertility outcomes. By integrating data on conserved and divergent traits with genomic features, such as rates of molecular evolution, gene copy number variation, and pseudogenization, scientists can generate testable hypotheses about reproductive mechanisms. When these insights are combined with proteomic datasets, they further help clarify protein-protein interactions, including those critical for sperm, egg recognition and fertilization.

2.2 Comparative genomics and adaptive potential

Comparative genomic approaches shed light on the many ways organisms preserve their adaptive potential across different evolutionary contexts. Among vertebrates, the degree of reproductive isolation varies widely: some species diverge rapidly,



forming strong postzygotic barriers such as hybrid sterility, while others, like parthenogenetic lizards, maintain hybridization as a recurring mechanism to preserve genetic diversity and reduce inbreeding (Fujita and Moritz, 2009). Comparative studies of normal and diseased tissues also provide valuable insights, particularly in understanding and managing heritable disorders through improved diagnostic and therapeutic tools. For example, genomic investigations into equine genetic disorders have contributed to better disease management and breeding practices (Brosnahan et al., 2010). In addition, metagenomic and large-scale ecosystem studies such as the NIH Human Microbiome Project are revealing how microbial communities influence reproductive health, homeostasis, and pathology (Aagaard et al., 2012). Despite a common vertebrate framework, the embryonic gonad retains dual potential to form either testes or ovaries via distinct pathways, with many non-mammalian vertebrates exhibiting remarkable flexibility beyond chromosomal sex determination. In such species, sex determination is often shaped by environmental and hormonal cues such as temperature, endocrine factors, and chemical exposure reflecting an adaptive response to ecological conditions (Parma and Radi, 2012; Ungewitter and Yao, 2013). This plasticity carries important evolutionary consequences. In fishes, for instance, sex ratios are influenced by the combined effects of genetic, environmental, and biochemical factors, resulting in variations in selection pressures and population dynamics across time and space (Piferrer et al., 2012). Recent genomic technologies are offering unprecedented insights into gametogenic pathways during both embryonic and postnatal development. Transcriptomic analyses of reproductive tissues, when paired with population-level genomic data, have revealed that genes expressed specifically in gonads tend to evolve faster than

ovary-biased genes and that reproductive genes in general evolve more rapidly than non-reproductive ones. Interestingly, despite these accelerated evolutionary rates, functional orthologs of reproductive genes maintain broadly similar divergence patterns across vertebrate groups (Grassa and Kulathinal, 2011). These observations highlight both the dynamic evolutionary nature of reproductive systems and the conserved molecular architecture that supports vertebrate reproduction. Genomic research is also transforming our understanding of epigenetics, the study of how gene activity is regulated without changes to the underlying DNA sequence. Epigenetic modifications involve chemical processes that activate or silence specific genomic regions in a cell- and time-dependent manner. Core mechanisms such as DNA methylation, RNA interference, and histone modification play vital roles in controlling the inheritance and expression of traits with both biological and economic importance (Hong et al., 2011). Within reproductive genetics, epigenetic regulation is especially important for understanding cellular reprogramming events, including the formation of pluripotent embryonic stem cells and induced pluripotent stem cells, which regain the ability to differentiate into multiple specialized cell types.

3 Transcriptomics in fish reproduction

The transcriptome represents the complete set of RNA molecules expressed in a cell at a given time, providing a real-time snapshot of gene activity. Transcriptomic approaches especially RNA sequencing (RNA-seq) have become indispensable for studying non-model fish species that lack reference genomes

(Garg et al., 2011). These techniques enable researchers to reconstruct coding regions, detect alternative splicing and post-transcriptional modifications, and quantify gene expression under varying developmental or environmental conditions (Liu et al., 2013). Unlike earlier microarray-based methods, which required prior genomic information and were limited by hybridization biases and restricted dynamic range (Clark et al., 2002; Reinartz et al., 2002; Bertone, 2004; Harbers and Carninci, 2005; Qian et al., 2014), RNA-seq provides far greater accuracy, sensitivity, and resolution for transcriptome profiling (Wang et al., 2009).

In aquaculture research, transcriptomics is increasingly being used to identify genes associated with key biological processes such as reproduction, growth, stress adaptation, and disease resistance. These insights are accelerating selective breeding programs and contributing to more sustainable production practices. Transcriptome profiling has proven particularly valuable for identifying gene expression patterns and discovering novel molecular markers useful for genetic improvement (Chandhini and Rejish Kumar, 2019). A notable example comes from research on zebrafish, a well-established model organism in genetics and biotechnology. Extensive transcriptomic analyses in zebrafish have uncovered numerous genes, molecular markers, and expression signatures relevant to developmental and reproductive biology (Vesterlund et al., 2011). Similarly, transcriptome sequencing of the common caridean shrimp *Crangon crangon* across five developmental stages revealed that nuclear receptors, key biological markers for sex determination, were expressed exclusively in females, alongside RNA interference (RNAi)-related genes. The nuclear receptor superfamily encompasses transcription factors that regulate vital processes such as growth, molting, cell differentiation, and reproduction, while RNAi genes are increasingly being explored as potential antiviral therapeutic targets (Christiaens et al., 2015). *De novo* transcriptome assemblies are now available for several economically important aquaculture species, including *Lates calcarifer* (Xia and Yue, 2010), *Oreochromis niloticus* (Zhang et al., 2013), *Epinephelus coioides* (Huang et al., 2011), *Ctenopharyngodon idella* (Chen et al., 2012), *Macrobrachium rosenbergii* (Jung et al., 2011), *Fenneropenaeus chinensis* (Li et al., 2013a), *Eriocheir sinensis* (Li et al., 2013b), and *Crassostrea virginica* (Zhang et al., 2014) as shown in Table 1. Collectively, these studies demonstrate that transcriptome sequencing is a powerful strategy for identifying genes and regulatory pathways associated with desirable traits in aquaculture species particularly those related to immunity, growth, and reproduction. By offering comprehensive insights into gene expression, transcriptomics continues to strengthen the molecular foundation for selective breeding and species improvement programs across aquatic organisms.

3.1 Unraveling reproductive mechanisms through transcriptomics

Reproduction is a fundamental aspect of aquaculture and selective breeding programs, directly determining the success and

sustainability of commercial production systems. In controlled hatchery environments, artificial reproduction techniques are routinely applied to enhance spawning efficiency and ensure predictable seed supply. In contrast, in wild populations, accurate species identification becomes critical to prevent unintended hybridization and maintain genetic integrity (Pereiro, 2022). Many marine species possess wide geographic distributions and complex population structures, which must be carefully considered in both conservation and aquaculture management (Uengwetwanit et al., 2018). Although artificial reproduction is now commonplace, concerns persist regarding its potential long-term effects on progeny fitness and genetic diversity, particularly under conditions of intensive artificial selection (Yang et al., 2022). In this context, transcriptomic approaches have emerged as powerful tools to evaluate reproductive performance and elucidate the molecular mechanisms that regulate reproductive physiology and success.

A comprehensive understanding of the genetic loci involved in sex determination is vital for both fisheries management and aquaculture. Fish exhibit remarkable diversity in sex determination systems, ranging from monogenic to polygenic mechanisms located on autosomes or sex chromosomes, often influenced by environmental cues such as temperature, hormones, and other abiotic factors (Devlin and Nagahama, 2002). Comparative transcriptomic studies between sexes have facilitated the identification of key loci and regulatory pathways associated with sexual differentiation (Chen et al., 2015; Sun et al., 2013; Lin et al., 2017). Analyses of reproductive tissue transcriptomes have also deepened understanding of sex-specific gene expression patterns and the molecular basis of gonadal differentiation (Zhang et al., 2019; Tao et al., 2018). Several candidate genes have been consistently identified across fish species (discussed in genomics section) all of which play pivotal roles in sex determination, gametogenesis, and gonadal maturation (Matsuda et al., 2002; Yokoi et al., 2002; Yano et al., 2012; Takehana et al., 2014; Bhat et al., 2016, 2021). In the Amur sturgeon (*Acipenser schrenckii*), an economically valuable caviar-producing species, transcriptomic investigations have revealed that long non-coding RNAs (lncRNAs) may modulate gene expression linked to sex-specific traits (Zhang et al., 2019). Nonetheless, broader transcriptomic analyses across diverse taxa are required to refine our understanding of sex determination and to develop more precise and sustainable breeding strategies. In both wild and cultured fish populations, egg quality remains a decisive factor influencing reproductive success. Considerable variability in egg viability and developmental competence has been documented among species (Chapman et al., 2014). During early embryogenesis, rapid and synchronized cell divisions occur, relying heavily on maternal mRNA transcripts accumulated during oocyte maturation. These transcripts regulate crucial cellular processes, including cell cycle progression (e.g., cyclins, nucleoplasmin), growth and apoptosis (e.g., insulin-like growth factors, prohibitin), and cytoskeletal organization (e.g., tubulin beta, keratins 8 and 18) (Aegerter et al., 2005; Bonnet et al., 2007a, 2007b). In several aquaculture species, such as striped bass, poor egg quality remains a major constraint to production (Chapman et al., 2014). Comparative transcriptomic

TABLE 1 Molecular insights from *de novo* transcriptome research in aquaculture.

Species	Purpose of transcriptome study	Reference
<i>Lates calcarifer</i>	Construction of a <i>de novo</i> transcriptome for gene discovery and molecular marker development	(Xia and Yue, 2010)
<i>Oreochromis niloticus</i>	Gene expression profiling for aquaculture traits and adaptation to environmental stress	(Zhang et al., 2013)
<i>Epinephelus coioides</i>	Understanding reproductive biology and immune-related gene expression	(Huang et al., 2011)
<i>Ctenopharyngodon Idella</i>	Study of immune and stress response pathways	(Chen et al., 2012)
<i>Macrobrachium rosenbergii</i>	First large-scale transcriptome for growth and reproduction studies	(Jung et al., 2011)
<i>Fenneropenaeus chinensis</i>	Analysis of immune response and viral defense mechanisms	(Li et al., 2013a)
<i>Eriocheir sinensis</i>	Investigation of developmental and reproductive gene networks	(Li et al., 2013b)
<i>Crassostrea virginica</i>	Study of gene expression under environmental stress and disease challenge	(Zhang et al., 2014)

studies using model organisms like zebrafish (*Danio rerio*) and medaka (*Oryzias latipes*) have been instrumental in revealing the molecular and developmental pathways governing early reproduction and embryogenesis (Vesterlund et al., 2011; Qiao et al., 2016). For instance, gene ontology (GO)-based gene set enrichment analyses (GSEA) using zebrafish annotations have been applied to European glass eels, offering new insights into developmental dimorphism and morphological differentiation (De Meyer et al., 2017). As genomic and transcriptomic datasets continue to expand, the ability to make robust inferences about fertilization, sex determination, and reproductive physiology in fish will strengthen significantly. These advances will directly support the optimization of spawning management and the enhancement of reproductive efficiency, contributing to more sustainable and productive aquaculture systems worldwide.

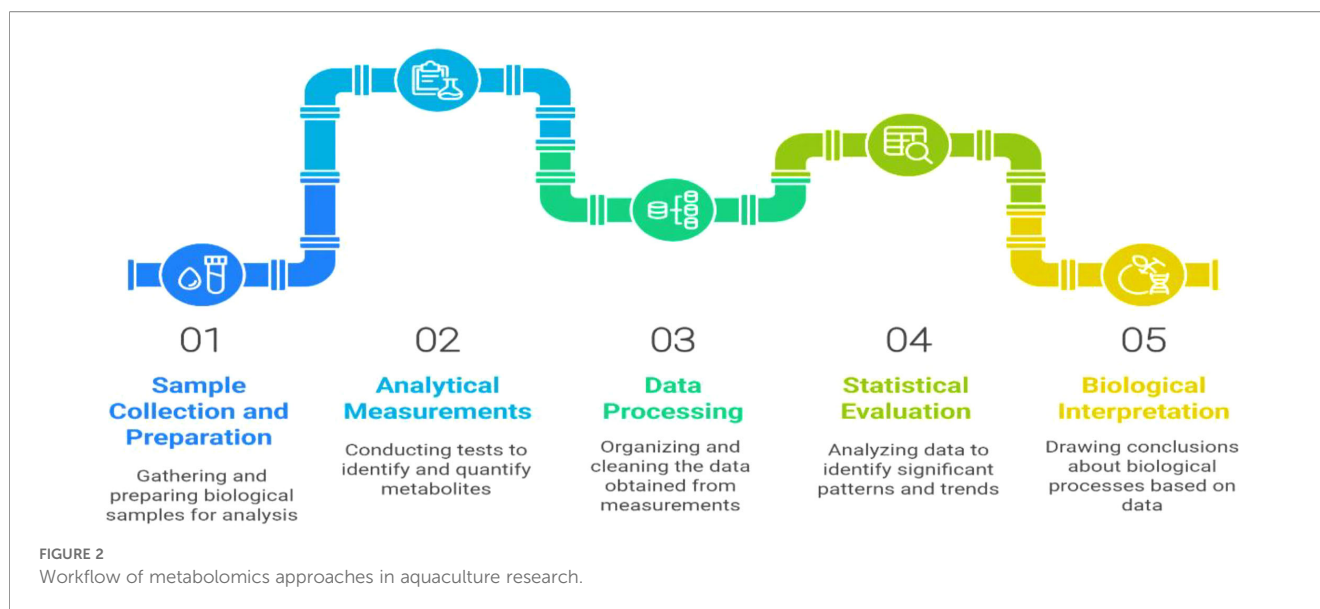
4 Metabolomics in fish reproduction

Metabolomics is the comprehensive study of metabolites, the small molecular substrates, intermediates, and end products of cellular metabolism (Daviss, 2005). In essence, it captures the unique chemical fingerprints that reflect the physiological state of a cell or organism (Wang et al., 2019). The metabolome represents the complete set of metabolites within a biological system (cell, tissue, organ, or organism), serving as the final output of diverse biochemical pathways. In aquaculture research, Nuclear Magnetic Resonance (NMR) and Mass Spectrometry (MS) are the two principal analytical platforms used to characterize metabolite profiles. Within this field, two major methodological approaches

have gained prominence. The first, metabolic fingerprinting, employs high-throughput analysis across multiple species or experimental conditions to generate predictive models from the full spectrum of detected metabolites. This approach has proven valuable not only in improving aquaculture practices, such as fish health monitoring and farm management, but also in the authentication of fish and feed products (Alfaro and Young, 2018). The second, metabolic profiling, focuses on the identification and quantification of metabolites through non-targeted analyses of biological systems, thereby revealing global metabolic changes associated with physiological or environmental variations (Roques et al., 2020). Accurate metabolite identification is critical for elucidating metabolic pathways and understanding how they respond to intrinsic physiological factors (such as growth, reproduction, and stress) or extrinsic environmental stimuli (including diet composition, temperature, and water quality). In aquaculture, metabolomic studies have advanced our knowledge in several key areas, including fish health and welfare, environmental adaptation, and nutritional physiology. In particular, environmental metabolomics has emerged as a powerful subdiscipline, providing insights into how physical, chemical, and biological stressors affect the metabolic homeostasis of aquatic organisms (Bundy et al., 2009). Furthermore, metabolomics has become instrumental in deciphering pathogen-induced metabolic alterations, contributing to improved understanding and management of disease resistance in cultured fish populations. Among the diverse applications of metabolomics, fish nutrition research remains a primary focus. By profiling metabolite changes in response to diet composition and feeding strategies, metabolomics enables a more detailed understanding of nutrient utilization, metabolic efficiency, and the biochemical basis of feed optimization (Tripathy et al., 2022).

A typical metabolomics workflow involves several sequential stages: sample collection and preparation, analytical measurement, data processing, statistical analysis, and biological interpretation (as illustrated in Figure 2). Muscle and liver tissues are commonly analyzed due to their pivotal roles in metabolic regulation and energy storage. However, alternative biological matrices including plasma, serum, gut contents, feces, mucus, and skin are increasingly employed to investigate pathway-specific responses. To ensure the reliability of metabolomic data, it is crucial to control for potential sources of environmental and biological variability, such as seasonality, tank effects, fish sex, reproductive stage, and water quality parameters, during both experimental design and sampling. Careful standardization at these stages enhances reproducibility and ensures that metabolomic datasets accurately reflect true physiological and environmental effects rather than confounding noise.

Unlike genes, transcripts, and proteins, metabolites are not directly encoded by the genome. Instead, they encompass a chemically diverse collection of small molecules, such as carbohydrates, amino acids, lipids, nucleotides, and other compound classes, that collectively constitute the metabolome. The metabolome represents the final downstream outcome of gene expression and protein activity, effectively linking molecular



processes to cellular function. Because the metabolome integrates inputs from both genetic and environmental factors, its composition tends to fluctuate more rapidly and dramatically than that of the transcriptome or proteome. These variations provide a magnified and highly sensitive snapshot of an organism's physiological state, making metabolomic analysis a powerful approach for detecting subtle biological responses to internal regulation and external stressors (Horgan and Kenny, 2011).

4.1 Metabolomic perspectives on reproductive processes in fish

Metabolomics is fundamentally connected to the phenotypic expression of organisms, offering a powerful framework to understand how they adapt and respond to environmental cues. By examining metabolite composition, this approach provides a precise and dynamic reflection of an organism's physiological state (Fiehn, 2002). Even subtle variations in genomic or proteomic activity can lead to measurable shifts in metabolite levels, which are often easier to detect and quantify. Compared to genomics and transcriptomics which depend on high-throughput sequencing and extensive reference databases, metabolomics presents a distinct yet complementary methodology. It is at once broader in biological scope and more straightforward in terms of analytical application. Because metabolites are small, chemically diverse molecules that are not constrained by species-specific genetic codes, they serve as versatile and sensitive indicators of biological function (Taylor et al., 2002). The value of metabolomics becomes especially evident when integrated with other "omics" approaches. For example, Zhou et al. (2023) explored energy utilization during embryonic development in Chinese sturgeon (*Acipenser sinensis*) by combining biochemical analyses of embryos at various developmental stages with transcriptomic data. Their results revealed that proteins and lipids act as key energy sources throughout development, with marked

variations in amino acid and fatty acid profiles across stages. Notably, lipids were identified as the primary energy substrates during early embryogenesis, highlighting their essential role in fueling rapid cell division and growth. Similarly, studies on ovarian development in Chinese sturgeon have shown that lipid and amino acid metabolism are central to energy supply during reproductive maturation. Analyses of serum metabolomes and ovarian gene expression demonstrated that metabolic activity peaks during stages II and III, when dietary lipids are absorbed and oxidized for energy. Concentrations of histidine, alanine, sarcosine, and multiple fatty acid derivatives reach their highest levels at stage IV, suggesting an increased demand for energy as oocyte maturation progresses. These findings emphasize that lipid and amino acid pathways are fundamental to ovarian development in sturgeons (Zhu et al., 2020).

Complementary evidence from Leng et al. (2019) further supports this conclusion, showing that dietary lipid levels significantly influence ovarian development in Chinese sturgeons. Using combined serum metabolomic and gonadal transcriptomic analyses, their study demonstrated that appropriate lipid supplementation enhances reproductive performance and energy metabolism. In another application, Rahimi et al. (2019) utilized ¹H NMR-based metabolomic profiling to examine changes in sperm metabolites of Persian sturgeon following cryopreservation with 2-hydroxypropyl- β -cyclodextrin (H₂CD) as a cryoprotectant. The inclusion of 10 mM H₂CD helped preserve several key metabolites such as glucose, guanidinoacetate, O-phosphocholine, and N, N-dimethylglycine while others including lactate, carnitine, and betaine, were less effectively maintained. Although H₂CD demonstrated partial success in protecting sperm metabolites, its limited efficacy for compounds like creatine phosphate and creatine, which are vital energy substrates, underscores the challenges of maintaining metabolic integrity during cryopreservation. Further integration of lipidomics and metabolomics has provided insights into steroid hormone biosynthesis in sturgeons. Wu et al. (2022) investigated the role of

dietary arachidonic acid [20:4(ω-6)] in promoting steroidogenesis in female Chinese sturgeon. Through combined transcriptomic and lipidomic analyses, they identified differentially expressed genes and metabolites across diets containing 0%, 0.5%, 1%, and 2% arachidonic acid. The results revealed that arachidonic acid enhances steroid hormone synthesis by stimulating cholesteryl ester metabolism and upregulating genes involved in steroidogenic pathways. This regulation supports gonadal development and cholesterol metabolism, ultimately improving ovarian maturation and reproductive potential. However, since cholesteryl ester synthesis and hydrolysis are tightly controlled by specific enzymes, the authors emphasized the need for further quantitative analysis of cholesterol esterase and cholesteryl ester hydrolase to validate these mechanisms. *Fei et al. (2024)* conducted a study on blotched snakehead (*Channa maculata*) brood stock after fed with a high-protein diet (48%) which significantly enhanced maternal fecundity, egg size, antioxidant capacity, and larval health without affecting fertilization or hatching rates. Integrated metabolomics and transcriptomics revealed that enhanced reproductive performance and egg quality were driven by altered energy and lipid metabolism, particularly arachidonic acid metabolism, steroidogenesis, and TGF-β signaling. Collectively, these findings demonstrate the versatility of

metabolomic and lipidomic tools in elucidating the molecular and biochemical foundations of reproduction in aquaculture species. By integrating metabolomic data with transcriptomic and genomic analyses, researchers can better understand how nutritional inputs, environmental stressors, and physiological states shape reproductive performance, providing a strong foundation for optimizing aquaculture management and breeding strategies.

5 Potential utilization of omics approaches in sustainable aquaculture

The integration of omics technologies into fisheries and aquaculture offers significant benefits for both commercial and conservation-oriented operations, improving product quality, sustainability, and overall competitiveness (Figure 3).

Omics approaches not only enhance production efficiency but also support the development of farming practices that promote the health and welfare of aquatic organisms, while maintaining environmental sustainability and economic viability. Aquatic species are susceptible to a wide array of pathogens including viruses, bacteria, and parasites many of which remain difficult to detect in the absence of overt clinical signs (*Altinok and Kurt,*

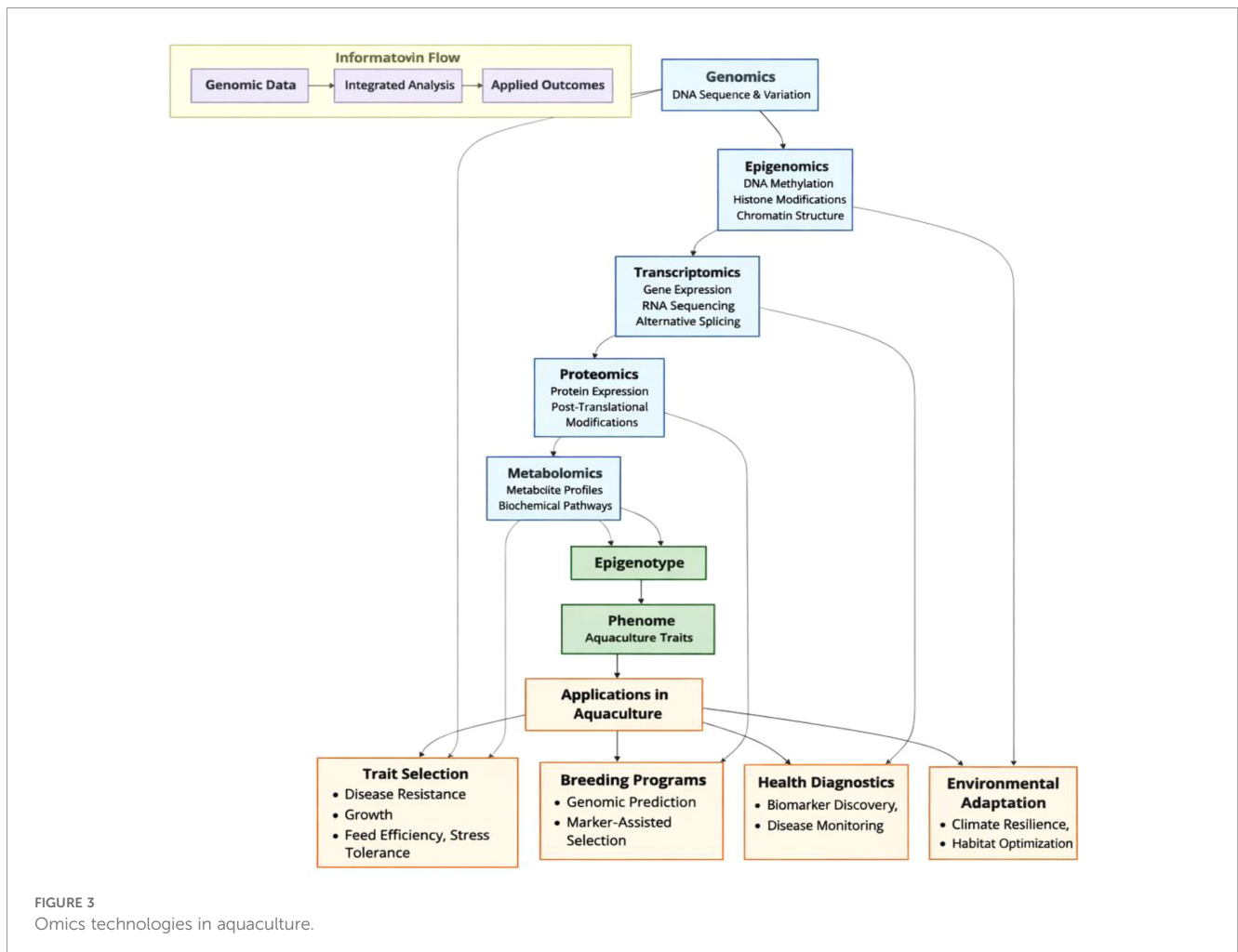


FIGURE 3
Omics technologies in aquaculture.

2003). Advances in molecular diagnostics, particularly DNA-based tools, now allow for the early detection of pathogens at low concentrations, before disease symptoms manifest.

Current molecular diagnostic strategies in aquaculture primarily include:

1. Direct sequencing of pathogen DNA, such as ribosomal RNA gene subunits (16S and 23S) for bacterial identification.
2. Polymerase chain reaction (PCR), including endpoint PCR (visualized via gel electrophoresis) and real-time PCR using fluorescence-based detection.

Nucleic acid microarrays, which enable simultaneous detection of multiple DNA targets or assessment of pathogen gene expression. In parallel, metabolite profiling the measurement of low-molecular-weight compounds and their intermediates provides insight into the physiological responses of organisms to genetic, environmental, and pathological influences. For aquaculture applications, metabolomics must be efficient, reliable, sensitive, and comprehensive. One prominent use is in nutritional studies, where metabolomic and mineral profiling of edible tissues informs dietary value. For instance, Mohanty et al. (2016) analyzed 35 Indian food fishes and highlighted small indigenous species (SIFs) as rich sources of essential minerals: *Xenentodon cancila* and *Gudusia chapra* for calcium, *Stolephorus waitei* and *X. cancila* for zinc, and *G. chapra* and *Penaeus monodon* for iron. Such findings underscore the potential of these species to contribute to meeting recommended dietary allowances. The availability of genomic resources for fish has expanded rapidly since the Human Genome Project. In 2014, draft genome sequencing for two key indigenous species, Rohu (*Labeo rohita*) and Magur (*Clarias batrachus*), was initiated by the Rohu and Magur Genome Sequencing Consortium. These reference genomes facilitate whole-genome selection, enabling the identification of genes associated with production traits and supporting selective breeding programs. Additionally, complete mitochondrial genome sequences have been reported for several economically important species, including *Catla catla* (Sahoo et al., 2017), *Clarias batrachus*, *Pangasius pangasius* (Mohindra et al., 2015), and *Rita rita* (Lashari et al., 2015). These genomic resources enhance the available genetic database for aquaculture, providing essential tools for conservation, genetic improvement, and selective breeding. DNA-based molecular techniques have also become crucial for identifying viral pathogens that threaten aquaculture industries, particularly in cultured finfish and penaeid shrimp. For finfish, diagnostic assays have been developed for pathogens such as infectious hematopoietic necrosis virus, viral hemorrhagic septicemia virus, viral nervous necrosis virus (VNNV), and *Renibacterium salmoninarum*. In Japan, PCR screening of striped jack (*Pseudocaranx dentex*) brood stock for VNNV has allowed for the selection of virus-free individuals, reducing the risk of vertical transmission to larvae (Muroga et al., 1998). Despite these advances, DNA-based approaches have limitations and require careful

validation and implementation in aquaculture health management. Beyond genomics, phenomics has emerged as a novel discipline, shifting the focus from single genotype-phenotype relationships to large-scale genome-phenome analyses. This perspective provides a more comprehensive understanding of disease mechanisms and informs strategies for combination therapies (Han et al., 2015). Traditionally, genotype-phenotype interactions were studied via forward genetics (starting from phenotype to gene) or reverse genetics (starting from genotype to phenotype). However, multi-omics approaches have revealed that the complexity of many biological traits and disease phenotypes cannot be fully captured by classical frameworks alone. Instead, integrated genomic, proteomic, and metabolomic datasets are necessary to account for the full spectrum of biological variation, providing a holistic understanding of organismal health, nutrition, and reproductive performance.

6 Future perspectives

Future research on fish reproduction should emphasize the integration of multi-omics approaches, including transcriptomics, proteomics, metabolomics, and phenomics, to unravel the intricate molecular and physiological mechanisms underlying gonadal development, gametogenesis, and spawning. The application of advanced molecular diagnostics and metabolite profiling can offer early insights into reproductive health, facilitating precise monitoring of brood stock and timely detection of reproductive disorders. Nutritional omics will be pivotal in designing species-specific diets that optimize reproductive performance and offspring quality, while phenomic approaches can elucidate the complex relationships between genotype, phenotype, and reproductive traits such as fecundity and hormone regulation. Moreover, the integration of omics into cryopreservation and germplasm conservation will support the long-term maintenance of genetic diversity in threatened or commercially valuable species. Together, these strategies promise to advance precision aquaculture, enhancing reproductive efficiency, ensuring genetic sustainability, and supporting the effective conservation and management of fish populations.

7 Conclusion

Omics technologies have emerged as transformative tools for investigating fish reproduction, providing multi-layered insights into the genetic, molecular, and metabolic processes that govern reproductive development. The integrated application of genomics, transcriptomics, proteomics, and metabolomics has enhanced our understanding of how energy substrates, metabolic pathways, and hormonal signals drive embryogenesis, ovarian maturation, and overall reproductive performance. Complementary approaches,

such as nutritional and metabolic profiling, have underscored the pivotal role of diet in supporting reproductive efficiency, while cryopreservation and germplasm conservation offer strategies for maintaining genetic diversity. These advances not only improve aquaculture productivity and brood stock management but also support the conservation of endangered fish species. Looking ahead, the continued integration of omics with reproductive biology will be essential for developing sustainable aquaculture strategies that maximize efficiency while safeguarding the long-term resilience of fish populations.

Author contributions

MM: Data curation, Formal Analysis, Conceptualization, Writing – original draft. MR: Visualization, Writing – review & editing, Methodology. IK: Writing – review & editing, Supervision. HB: Writing – review & editing, Resources, Data curation. IM: Resources, Data curation, Writing – review & editing, Methodology. RB: Writing – review & editing, Supervision, Formal Analysis, Visualization, Resources. IB: Methodology, Writing – review & editing, Supervision, Conceptualization, Visualization, Validation.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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