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REVIEW ARTICLE
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Fish Hybridization: Enhancing Genetic Potential, Ecological Implications and Ethical Perspectives

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ABSTRACT

Hybridization is an important tool in aquaculture to combine the desirable traits of parental fish stocks. This process produces offspring with disease resistance, improved feed conversion efficiency, accelerated growth, environmental resilience and superior flesh quality. All these traits are economically beneficial and can fulfill large demands in the industry without depleting wild stocks. Various techniques have been used to hybridize fish, including artificial insemination, selective mating and genetic manipulation. Molecular methods like gene editing and *in-vitro* fertilization can ensure speedy production of hybrid stocks with precise traits, but the processes should be supported by impact studies to provide a comprehensive understanding of hybridization outcomes. This review explores the diverse methods of fish hybridization in aquaculture, highlighting examples of their genetic and physiological impacts on wild fish populations, besides their ecological and evolutionary consequences. It also explores ethical considerations and public perception, particularly gene modification, along with an analysis of regulatory and policy frameworks. As global demand for food protein continues to rise, aquaculture is increasingly recognized as a sustainable solution to meet the demand. The increasing potential of hybrid species in enhancing aquaculture production underscores the importance of developing efficient and sustainable industry practices.

Keywords: Hybridization, Aquaculture, Genetic, Ecological, Ethical.

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INTRODUCTION

Fish hybridization has emerged as a pivotal strategy in aquaculture, enabling the production of new species and enhancing genetic diversity. By combining the desirable traits of parent species, hybridization creates offspring with higher commercial value and better chance of survival in controlled environments (Xu et al., 2015; Nguyen et al., 2022), aligning with the primary goal of aquaculture, that is to produce high-quality fish stocks in large quantities to meet market demand and maximize profits. The genetic diversity of fish has expanded alongside the growth of aquaculture, driven by both spontaneous occurrences and human intervention. Hybridization can be achieved through artificial insemination, selective mating and genetic modification in laboratory settings. The overarching goal is to leverage the genetic diversity of various fish species to address ecological and evolutionary questions, manage invasive species, conduct genetic research, conserve endangered species and enhance productivity (Hubbs, 1955; Bartley et al., 2001; Martsikalis et al., 2019).

Scope of Review

The detection and study of hybridization events in fish populations often utilize molecular techniques that yield rapid and accurate results. Hybridization events are often detected in fish populations through conservation efforts, and the ecosystem dynamics are investigated using a combination of morphological, genetic, behavioral and ecological approaches. Thus, the genetic and physiological repercussions of hybridization, as well as its ecological

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ramifications, role in species conservation and genetic introgression are reviewed and discussed. Additionally, the technological challenges, regulatory and policy considerations and ethical concerns are also discussed.

Objectives

Hybrid stocks, resulting from the cross-breeding of different fish species, play a crucial role in the global expansion of aquaculture production. With the objective of improving offspring quality, aqua culturists are increasingly encouraged to explore and generate fish hybrids. This review aims to provide a comprehensive analysis of the subject, focusing on its genetic, physiological and ecological implications. It seeks to examine the role of hybridization in species conservation, genetic introgression and ecosystem dynamics, besides addressing the challenges, regulatory frameworks and ethical concerns associated with hybridization.

Fish Hybridization Techniques

Artificial Hybridization

Artificial hybridization involves manipulating the breeding of fish within or between species through interventional methods. Parental fish with specific desirable traits are preselected, and their offspring are screened for culture in various environments (Bartley et al., 2001; Elaswad & Dunham, 2018).

Selective Breeding (Traditional)

Selective breeding aims to improve key traits in fish, such as feed conversion efficiency, disease resistance, environmental tolerance and growth rate. The traditional methods like population selection, pedigree selection, parental selection and integrated selection have been used to enhance these traits by producing natural offspring with better genes (Burdon & Klápště, 2019; Rutkoski et al., 2022; Seidy et al., 2023). The development of molecular markers has advanced breeding approaches, such as marker-assisted selection (MAS) and genomic selection, improving the efficiency of selecting specific traits. Successful examples of selective breeding include rainbow trout (*Onchorhyncus mykiss*) (Wiens et al., 2018), silver carp (*Hypophthalmichthys molitrix*) (Gheyas et al., 2009) and channel catfish (*Ictalurus punctutatus*) (Rezk et al., 2003; Minh et al., 2022) with molecular markers aiding in the identification of genes related to growth, disease resistance and other beneficial traits (Liu and Cordes, 2004). Although the identification of desirable offspring is often a tedious process, many aquaculture farmers are opting to use selectively bred fish stocks to maximize yield and profits (Ranjan et al., 2018; Szabóa et al., 2019).

Spawn Induction

Spawn induction allows the synchronization and control of fish reproduction. This method involves hormonal stimulation to induce gamete maturation and ovulation, and its success depends on hormone dosage, fish maturity and environmental conditions (water temperature, current and rain). Both natural and synthetic hormones, such as gonadotropin-releasing hormone analogue (GnRHa) and pimozide (antidopaminergic medication) have been used successfully in various species, including the walking catfish (*Clarias batrachus*) (Basu et al., 2000; Sahoo et al., 2008), Asian stinging catfish (*Heteropneustes fossilis*) (Alok et al., 1993; Alok et al., 1994) and snakehead fish (*Chana spp.*) (Zohar & Mylonas, 2001).

Technological Advances in Gene Manipulation

Gene-editing technology has provided researchers with an opportunity to control hybridization up to the genetic level (Hallerman et al., 2023). When combined with advancements in in-vitro fertilization, the efficiency and success rates of producing genetically modified fish stocks could be increased. The integration of these technologies into fish breeding programs promises to accelerate the development of new, high-performance hybrids that can meet the demands of modern aquaculture (Chen et al., 2014; Wang et al., 2019a).

CRISPR-Cas9 is a precise genome-editing tool that has revolutionized genetic research by allowing targeted modifications in the organisms' genome. This technology allows the introduction of new genes to enhance desirable traits (Kim et al., 2024) or induce targeted mutations to knock out specific genes to establish their genotype-phenotype relationships (Sifuentes-Romero et al., 2023). Targeted genomes may be edited with high efficiency, as demonstrated in mutational experiments of zebrafish and medaka, achieving gene knockout rates of up to 94% without detectable off-target effects (Zheng et al., 2023; Dorner et al., 2024). When integrated with traditional breeding methods, CRISPR-Cas9 can enhance aquaculture traits like the successful modification of growth-associated genes in red sea bream and channel catfish (Aich et al., 2023). In addition to growth enhancement, CRISPR-Cas9 can also precisely insert genes related to disease resistance, allowing for the creation of hybrids that withstand various pathogens. For example, the alligator cathelicidin gene (which transcribes and translates a host defense peptide with antimicrobial activity) has been introduced in channel catfish stocks to enhance their survival against infections and reduce reliance on chemical antibiotics (Wang et al., 2023; Wang et al., 2024).

The CRISPR/Cas9 gene-editing technology has also been used in Nile tilapia (*Oreochromis niloticus*) to knock out selected genes to determine their functions *in vivo*. When genes like nanos2, nanos3, dmrt1 and foxl2 were knocked out, it has been observed that the tilapia would subsequently develop germ cell-deficient gonads and undergo masculinization (Li et al., 2014). These observations were validated using immunohistochemistry and hormonal assay, where the knocked-out gene proteins were not detected. Therefore, such functional genes would be important to produce hybrid fish that are fertile and easy to breed in quantity.

The development of tools like the Mongrail program, which assists in detecting and analyzing hybridization events (model linkage and recombination in genomic datasets) (Chakraborty & Rannala 2023), complements CRISPR-Cas9 by enabling researchers to better understand genetic variations and introgression patterns in hybrid fish populations, thereby facilitating more accurate studies on the consequences of hybridization.

Concurrently, next-generation sequencing (NGS) technologies have revolutionized the identification of molecular markers critical for phylogenetic studies. For instance, tools like GeneMiner leverage advanced assembly techniques to mine these markers from vast genomic data, even in the absence of comprehensive reference genomes for non-model organisms (Xie et al., 2024). The integration of CRISPR-Cas9 and NGS in hybrid fish studies also offers significant advantages over traditional methods, such as zinc-finger nucleases or TALENs, which often present complex designs and delivery challenges (Aich et al., 2023). Complementary NGS advancements can provide high-throughput analysis of genetic variations, streamlining the identification of hybridization markers, advancing the efficiency and accuracy of genetic analysis in fish hybrids, overcoming the limitations of labor-intensive genotyping, and significantly enhancing our understanding of genetic traits and evolutionary biology (Mattiello et al., 2022; Dorner et al., 2024).

Natural Hybridization

Natural hybridization involves the cross-breeding of genetically distinct groups or individuals within or between species, often occurring in environments where multiple fish species coexist.

Natural hybridization is more prevalent in fish than other vertebrates, with significant occurrences documented in both marine and freshwater environments (Hubbs, 1955; Campton, 1987). This process plays a critical role in evolutionary innovation, allowing the transfer of genetic material between species through backcrossing and genetic introgression (Arnold & Martin, 2009; Meier et al., 2017; Bradbury et al., 2022).

Environmental Factors Influencing Natural Hybridization

Environmental factors, such as external fertilization, species abundance, competition for spawning habitats and habitat complexity can influence natural hybridization. Fish often respond to environmental cues like photoperiod, water temperature and lunar cycles (Sims et al., 2004; Katselis et al., 2007; Forsythe et al., 2012; Perkin et al., 2015; Tibblin et al., 2016; Šmejkal et al., 2018; de Magalhães Lopes et al., 2018) during their reproductive migrations, with changes in these factors potentially leading to hybridization events. The presence of hybrids can also alter species interactions, affecting growth, survival and reproductive success. This can be seen in certain fish species recognized for their distinct population biology, where individuals migrate to specific marine spawning areas and engage in panmictic reproduction (Jacobsen et al., 2014). An illustration of this phenomenon is observed in the Atlantic herring (*Clupea harengus*) (Ruzzante et al., 2006; Mueller et al., 2023) and anchovies (*Engraulidae* family) (Catanese et al., 2017; Catanese et al., 2020). Consequently, variations in habitat accessibility, water flow patterns and environmental influences can also affect the extent of species habitat overlapping.

Case Studies of Successful Projects

There are many cases of successful fish hybridization in aquaculture. The projects have demonstrated significant advancements in enhancing food security and productivity. For example, the hybridization of silver carp and channel catfish has led to the development of progenies that exhibit rapid growth, improved feed conversion, and enhanced disease resistance (Rezk et al., 2003; Gheyas et al., 2009; Minh et al., 2022). Another project is the development of hybrid groupers (*Epinephelus fuscoguttatus* × Giant Grouper *E. lanceolatus*), which combined the fast growth rates of one species with superior flesh quality of another (Ch'ng & Senoo, 2008), showcasing the benefits of hybrid vigor. These case studies demonstrated the practical benefits of hybridization in achieving specific aquaculture goals, providing valuable insights into the potential of hybrid species to meet commercial and environmental objectives.

Other notable examples include the production of hybrid tilapia in Malawi, Africa, where the small-scale aquaculture project has thrived through locally adapted practices (Munthali et al., 2022). This project also highlights the importance of integrating social and biophysical research to optimize aquaculture systems. Meanwhile, in the United States (US), the hybridization of white bass (*Morone chrysops*) and striped bass (*Morone saxatilis*) has led to the creation of hybrid striped bass, a species that is valued for its rapid growth, hardiness and adaptability to different environmental conditions (Andersen et al., 2021). This hybrid has become a cornerstone of the aquaculture industry in the southern US, particularly in states like North Carolina and Mississippi, where it is farmed extensively for food and recreational fishing.

In Scandinavia, particularly Norway and Sweden, the hybridization of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) has been explored. Although hybrid viability can vary, some have shown promising traits, such as enhanced resistance to disease and better adaptation to fluctuating water temperatures (Adams et al., 2023). These hybrids are being studied for their potential to improve the sustainability and productivity of salmonid aquaculture, which is a significant industry in this region. The research on salmon-trout hybrids may be seen as a solution to the challenges posed by climate change in cold-water aquaculture as they are more robust to temperature change.

Other examples of commercially important aquaculture hybrids include the channel x blue hybrid catfish (Arias et al., 2012; Torrans and Ott, 2018) and various sturgeon crosses like the Bester (*Huso huso* x *Acipenser ruthenus*) (Bronzi et al., 2011). In China, the aquaculture industry is mostly focused on tilapia and carp hybrids (mainly between subspecies of *Cyprinus carpio* and *Carassius carassiusare)*, which suit the local palate (Zhou and Gui, 2018).

These case studies from various regions around the world highlight the versatility and global applicability of fish hybridization techniques (Table 1). By tailoring hybridization programs to the specific environmental and economic demand of each region, these techniques can play a crucial role to enhance aquaculture production, support food security and promote sustainable practices in the face of global challenges.

Table 1: Summary of Some Successful Fish Hybridization in Aquaculture

Hybrid Species	Region	Advantages	References
Silver Carp & Channel Catfish	Global (Alabama, USA, Parbatipur, Bangladesh, Mekong Delta, Vietnam)	Rapid growth, improved feed conversion, enhanced resistance disease	Rezk et al. (2003); Gheyas et al. (2009); Minh et al. (2022)
Hybrid Groupers (*E. fuscoguttatus* × *E. lanceolatus*)	Southeast Asia	Fast growth, superior flesh quality	Ch'ng & Senoo (2008)
Hybrid Tilapia	Malawi, Africa	Adapted to local practices, highlights integration of social and biophysical research	Munthali et al. (2022)
Hybrid Striped Bass (White Bass × Striped Bass)	United States (US)	Rapid growth, hardiness, adaptability to diverse environments; cornerstone for food and recreational fishing	Andersen et al. (2021)
Atlantic Salmon × Brown Trout	Scandinavia (Norway, Sweden)	Enhanced disease resistance, adaptability to temperature fluctuations; potential for sustainable salmonid aquaculture under climate change	Adams et al. (2023)
Channel × Blue Catfish	United States (US)	Increased production efficiency	Arias et al. (2012); Torrans & Ott (2018)
Bester (*Huso huso* × *Acipenser ruthenus*)	Europe	High-value sturgeon hybrid used in caviar production	Bronzi et al. (2011)
Tilapia and Carp Hybrids	China	Suited to local palate and market demand	Zhou & Gui (2018)

Consequences of Hybridization

Genetic Introgression

Genetic introgression refers to the exchange of genes between species or populations and their subsequent backcrossing (Arnold, 1997). While this process can introduce gene novelty and provide ecological and evolutionary advantages, it can also negatively impact parental populations, potentially leading to a loss of unique genetic diversity and complicating conservation efforts (Shechonge et al., 2018; Ottenburghs, 2020; Tesfaye et al., 2021).

Hata et al. (2019) recently reported the threat of genetic introgression to native species of bitterling fish (*Tanakia (T.) lanceolata*) in Matsuyama, Japan, which gave rise to invasive hybrids. This was a result of the introduction of another bitterling species (*Tanakia limbate*) from West Kyushu into local streams. Most of the samples that the authors obtained were hybrids that covered the entire range of *T. lanceolata* habitats, causing them to conclude that was the result of niche replacement in local streams.

Depending on the degree of hybridization and subsequent gene flow, introgression can blur boundaries between species, promote gene mixing or create hybrid zones, where genetically distinct populations meet. Genes that interact extensively with other genes, or involved in the "evolutionary arms race", are particularly prone to causing hybrid incompatibilities, as seen in the three-spine stickleback fish (Thompson et al., 2022). Dobzhansky (1937) and Muller (1942) suggested that hybrid incompatibility involved multiple genetic changes. They developed a model indicating that unviability could arise from hybrids being heterozygous for different alleles at a single locus (underdominance). An example is the platyfish hybrid (*Xiphophorus maculatus*) and green swordtail (*Xiphophorus helleri*) (Coyne & Orr, 2004). Platyfish with spots have an X-linked gene for spots and an autosomal repressor that regulates the gene, while green swordtails lacked both gene and repressor. In some backcross hybrids of these species, those receiving the spot-producing gene without the repressor will develop enlarged spots that turn into malignant tumors. The spot-producing gene is a duplicated copy of the *Xiphophorus* melanoma receptor kinase (Xmrk), specifically Xmrk-2, while the Xmrk-1 gene, present in both species, does not cause spots.

Hybrid Vigor (Heterosis)

Hybrid vigor, or heterosis, can enhance genetic diversity and lead to superior performance and fitness in hybrid offspring. This phenomenon is particularly beneficial in aquaculture. However, the extent of heterosis varies, with some hybrids showing less pronounced benefits, particularly in unpredictable or changing environments (Ellison & Burton, 2008a; Chen et al., 2018; Liu, 2022; Wang et al., 2023).

A number of studies reported smaller heterosis effects, which mostly did not exceed the best parent; for example, the hybrid catfish cultured in Thailand is a cross between the African catfish (*Clarias (C.) gariepinus*) and the Thai catfish (*C. macrocephalus*) (Nwadukwe, 1995). This hybrid combined the fast growth rate of the African catfish with the desirable flesh characteristics of the Thai catfish. The resulting product is a fast-growing offspring with acceptable flesh taste to Thai consumers, even though it does not grow as quickly as the pure African catfish. It is reasonably common for reciprocal hybrids to have different performance (Deng et al., 2010) and it is generally accepted that heterosis shows genetic correlations between pure species and hybrid results that are favorable in all traits (Kube et al., 2024).

Loss of Genetic Diversity (Genetic Swamping)

Hybridization can lead to loss of genetic diversity, particularly when one population contributes more genetic material to another, resulting in genetic swamping (Sundqvist et al., 2016). This process can erode unique genes that contain traits for local adaptation, potentially reducing the adaptive capacity of hybrid populations (Roberts et al., 2010; Waples et al., 2012; Parvez et al., 2022). The numerically dominating or asymmetrical introgression may cause unique alleles or genetic variations that are previously present in one group to be diluted or eliminated due to hybridization and gene flow (Roberts et al. 2010). Genetic introgression can result in the swamping of the gene pool of one population with another population or species when hybrid individuals outperform purebreds in terms of fitness or reproductive success (Crozier, 2000). This may also lead to the loss of alleles that are locally adapted or the introduction of alleles through hybridization that replace native genetic diversity.

Aside from that, genetic introgression may disproportionately affect rare alleles or low-frequency variants in the receiving group (Gompert, 2012). Rare allele's specific to the recipient population may be lost because of genetic drift or selection against introgressed alleles, particularly between small or isolated populations, if hybridization occurred with preferential transmission of alleles from one parental group over others. Thus, over time, genetic diversity will decrease as a consequence of the introduced alleles being fixed or disappearing as a result of chance events. According to some research, the adaptive capacity and stress-resilience of hybrid populations may be lowered by a reduction in genetic diversity. (Owens and Samuk, 2019).

Integrating Fish Hybridization with Conservation Efforts

Fish hybridization can be integrated with conservation strategies that assist in the recovery of endangered species. Hybridization may be employed to introduce new genetic material into small or isolated populations, enhancing their resilience to environmental changes and reducing the risk of inbreeding (Ralls et al., 2018; Feuerstein et al., 2024).

For example, hybridization can introduce adaptive alleles, enhancing resilience to environmental changes, as seen in rockfish species' population structure and genetic diversity (Wray et al., 2024). Genetic analysis of hybridized fish populations can also guide conservation by assessing hybridization levels, identifying management effectiveness and informing proactive measures for recovery in large river ecosystems. This has been applied on the Yellowstone Cutthroat Trout, where the management actions successfully reduced hybridization in the fish, demonstrating the importance of monitoring hybridization trends to formulate conservation strategies (Hargrove et al., 2024). Moreover, genetic monitoring of hybridized fish populations can provide insights into population viability and extinction risk, as evidenced by the endangered Lahontan Cutthroat Trout study in the US, which highlighted the need for immediate management interventions to address its hybridization (Hemstrom et al., 2022). Additionally, the genetic analysis of hybridized fish populations can also improve conservation efforts through assisted gene flow, which aided in species recovery of the Coho Salmon population in California, USA, without causing outbreeding depression (Pregler et al., 2022). Careful management is necessary to ensure that hybridization does not compromise the genetic integrity of native species or lead to unintended ecological consequences (Nevado et al., 2011; Shechonge et al., 2018; Hata et al., 2019).

Genomic Imprinting

Genomic imprinting, an epigenetic mechanism that results in parent-specific gene expression, plays a significant role in shaping the genetic and phenotypic characteristics of hybrid offspring. It is characterized by allele-specific expression of genes within chromosomal domains. This process can influence traits, such as growth rate, disease resistance and reproductive performance in fish hybrids (McGowan & Martin, 1997; Yang et al., 2022; Wang et al., 2022). Genomic imprinting has been widely reported in mammals (Bartolomei et al., 1991; Babak et al., 2008), plants (Kermicle et al., 1970; Raissig et al., 2011) and insects (Lloyd 2000).

Studies have investigated genomic imprinting in fish and other aquaculture animals to elucidate its potential impact on important traits, such as growth disease resistance and reproductive performance (Zhou et al., 2019; Yang et al., 2022; Wang et al., 2022). Imprints from both parental species may be present in the genomes of hybrid fish created by crossing two distinct fish species. These imprints can alter the expression of certain genes in the hybrid offspring, resulting in distinct features or phenotypes not seen in either parent. Imprinting is a critical sensitive period in fish development (Gómez-Laplaza & Gil-Carnicero 2008) and it has been discovered that early separation of eggs from the mother has a substantial adverse effect on filial social bonding of fish fry later in life (Russock, 1999).

Hybrid Breakdown

Hybrid breakdown is characterized by reduced fitness in post-F1 generations and it is a common phenomenon in hybrid populations. Genetic incompatibility between parental species can lead to maladaptive traits and reduced survival in hybrid offspring (Ellison & Burton, 2008a; Renaut & Bernatchez 2011; Burton et al., 2013; Stelkens et al., 2015). This has been recorded in post-F1 generations, with backcross and F2 generations being the most often studied. For example, *Tigriopus californicus*, a copepod that lives in tidal pools, has been the subject of extensive research on hybrid breakdown (Burton 1990; Edmands 1999; Edmands et al., 2009). In this copepod, heterosis was seen in F1 interpopulation hybrids, but post-F1 generations showed a reduction in fitness even though they were viable and fertile (Edmands, 1999; Edmands et al., 2009; Barreto et al., 2014). In another study of African haplochromine cichlid fish by Stelkens et al. (2015), F2 hybrids consistently showed lower viability (survival) with loss of fitness of up to 43 per cent when compared with non-hybrid crossings, and up to 21 per cent when compared with F1 hybrids. In addition, Renaut et al. (2009) found that backcross hybrids had higher levels of gene misexpression during the embryonic and juvenile phases of development in normal and dwarf whitefish when compared with F1 hybrids.

Hybrid breakdown that occurs in the subsequent generations arise from molecular incompatibilities within cells. These incompatibilities occur at both the structural level (protein-protein interactions) and the regulatory level (gene-gene interactions) (Ellison and Burton, 2008b; Burton, 2022). In fish hybridization studies, such incompatibility has been linked to intermediate or novel phenotypes in hybrids, which are sometimes maladaptive, due to disrupted gene interactions affecting development (Davies et al., 2012; Lu et al., 2020). These incompatibilities can be caused by the organelle genome's (mainly uniparental) and nuclear genome's (biparental) inheritance patterns (Rand et al., 2004; Burton et al., 2013; Han and Barreto, 2021). Paternal (inter-mitotype) backcrosses, in contrast to maternal (intra-mitotype) backcrosses, tend to result in mismatched mitochondrial and nuclear genomes. Ellison and Burton (2008b) showed that disruptions in nuclear-mitochondrial gene interactions can contribute to reduced fitness in *T. californicus* interpopulation hybrids, also noting that maternal backcross hybrids could recover mitochondrial electron transport system (ETS) function and improve fitness and survival.

Physiological Consequences

Fish hybridization can have complex physiological consequences, with hybrid offspring exhibiting a range of traits that differ from their parental species. These traits can be influenced by environmental conditions, with hybrids potentially being more vulnerable to changes in water temperature and pH (Deutsch et al., 2008; Sunday et al., 2012; Peng et al., 2014; Morgan et al., 2019; Thalib et al., 2020).

Several studies have shown that changes in environmental quality beyond certain thresholds can detrimentally affect biochemical and physiological processes in fish (Šimková et al., 2015; Thalib et al., 2020). Evidence indicates that hybrid offspring are more vulnerable to fluctuations in water temperature and pH changes. For example, the growth of juvenile hybrid groupers (*Epinephelus fuscoguttatus* ♀ × *Epinephelus lanceolatus* ♂) were significantly impacted by warm water (32°C) and low pH (pH 6) conditions in 25 days (Thalib et al., 2020). Surprisingly, it was observed that the interactive effects of acidic and warm conditions (usually brought on by climate change) had a positive effect on the hybrid groupers' growth. However, the authors stated that such conditions also increased the living cost by decreasing the hepatosomatic index 2.3-fold compared with the optimal environment. They believed that such conditions had caused the hybrid fish to mobilize their protein for energy to support metabolic needs. Similarly, tropical fish species such as zebrafish living at the upper limits of their temperature tolerance range were also severely impacted by further environmental changes (Deutsch et al., 2008; Sunday et al., 2012; Ehrlén and Morris, 2015; Morgan et al., 2019).

Some fish must adjust their behavior and physiological needs by either increasing their feed intake to meet new high energy demands (Liew et al., 2013) or conserving energy for essential metabolic functions. Such responses have been observed in Chinese breams (*Parabramis pekinensis*) (Peng et al., 2014), common carps (Pang et al., 2016) and cobias (*Rachycentron canadum*) (Yúfera et al., 2019), where higher water temperatures led to increased feed intake. The increased feeding activity also resulted in higher endogenous ammonia excretion due to protein catabolism (Bucking, 2017).

Ecological Implications and Evolutionary Consequences

Hybrid species may exhibit several evolutionary adaptations in response to climate change, enhancing ecosystem resilience through mechanisms like transgressive gene expression, seasonal resilience and reduced vulnerability, which are crucial for survival in changing environments. For instance, hybrid fish can display transgressive phenotypes, where they have greater fitness than parent species. This is particularly relevant under thermal stress, as hybrids may show unique gene expression patterns that allow them to adapt to changing temperatures (Schwartz et al., 2024).

Zhang et al. (2024) reported that temperate estuarine fish populations demonstrated seasonal adaptations to climate change, with habitat suitability shifting in response to environmental fluctuations. This seasonal resilience can help maintain functional assemblages and biodiversity, which are crucial for ecosystem stability (Zhang et al., 2024). Hybrid populations often possess greater genetic variation, which can lead to adaptive introgression, reducing vulnerability to climate change and introducing novel genetic variations for adaptation and evolutionary rescue (Brauer et al., 2023). The study of rainbowfish (*Melanotaenia spp*.) across an elevation gradient in the Australian wet tropics also supported this theory, suggesting that adaptive introgression can provide essential genetic variation for survival in fluctuating environments (Brauer et al., 2023).

Although these adaptations offer a promising perspective for hybrid fish survival, it is crucial to recognize that not all hybrids will necessarily succeed under the pressures of climate change. Many may still encounter substantial challenges in rapidly shifting environments. Moreover, the introduction of hybrid species has the potential to destabilize ecological balances and drive unforeseen evolutionary consequences, particularly in the face of ongoing climate change (Brennan et al., 2014; Chunco, 2014; Taylor et al., 2015).

Environmental Impact Assessment

Assessing the environmental impact of fish hybridization is crucial to understanding its long-term effects. Hybrid species may outcompete native species, leading to changes in community structure and biodiversity loss. Additionally, the introduction of hybrids into wild populations may result in genetic pollution, where the genetic integrity of native species is compromised (Hamilton et al., 2017; Saba and Balwan, 2023). In some cases, genetic pollution may inadvertently provide beneficial genetic variability, as seen in killifish adapting to polluted environments due to the introduction of a non-native congener (Vignieri, 2019). Therefore, thorough environmental impact assessments should be conducted before introducing hybrid species into new habitats, with strategies in place to mitigate potential negative consequences.

Assessing the ecological impacts of fish hybrid species involves various methodologies, including risk assessment models and case studies. One effective approach is the Hybridization Risk Model (HRM), which combines habitat modeling with spatial data to evaluate the risk of hybridization between native and introduced species, as demonstrated in a study of bull and brook trout (Manning et al., 2022). This model identifies areas of extreme to low hybridization risk based on habitat suitability and species presence. Additionally, comparative functional response analyses (CFR) can be employed to assess the ecological consequences of hybrid species, as shown in studies of invasive carp and goldfish hybrids, which revealed that hybridization did not produce novel phenotypes with enhanced ecological performance (Tarkan et al., 2024). Furthermore, ecological outcomes of hybridization can vary geographically, affecting biotic interactions and resource use, as evidenced by research on Catostomus fishes (Elizabeth et al., 2022). Integrating these methodologies can provide a comprehensive understanding of the ecological risks associated with fish hybridization (Ram and Fegade, 2024; Liwszyc and Larramendy, 2024).

One case of fish hybridization that resulted in adverse environmental consequences is reported by Hohenlohe et al. (2013) in the western US. The hybridization between native cutthroat trout (*Oncorhynchus (O.) clarkii*) and introduced rainbow trout (*O. mykiss*) had posed a significant threat to biodiversity in the local ecosystem. The introduction of rainbow trout for recreational fishing had resulted in widespread hybridization with local cutthroat trout, producing hybrid offspring known as "cutbows". This interbreeding diluted the genetic integrity of native cutthroat trout populations, leading to a decline in the abundance of pure species. Moreover, the hybrid could outcompete native cutthroat trout for food and habitat, disrupting the local ecosystem. Conservation efforts were implemented to remove non-native species, restore native habitats, and employ genetic monitoring to maintain the integrity of cutthroat trout populations (Hohenlohe et al., 2013). Studies have also shown that hybridization could also rapidly reduce the fitness of native cutthroat trout, threatening their long-term survival in the wild (Muhlfeld et al., 2009).

Challenges, Solutions and Ethical Concerns

Improving our understanding of hybridization is critical for biodiversity conservation, adaptive evolution, ecological impact management, aquaculture enhancement and climate change adaptation. The resilience of aquatic ecosystems and the sustainable use of fish resources are encouraged by effective management and conservation strategies made possible by this understanding (Holsman et al., 2020; Pinna et al., 2023). While hybridization can contribute positively to species diversity and adaptation, it also poses challenges like different susceptibilities to diseases compared with parent species, potentially leading to new health challenges in aquaculture settings (Šimková et al., 2015).

Significant progress has been made, as shown by the development of chromosomal engineering, genetic engineering and cell nuclear transfer technologies (Lu and Luo, 2020; Moran et al., 2024). However, still, there are not many high-quality aquaculture fish stocks available. One of the primary reasons is the poor interaction and lack of collaboration between scientists and industry players in applying the breeding methods. Another challenge is the speed of incorporating new technologies into genetic breeding methods. The use of recent technological advancements, such as CRISPR-Cas9 in hybrid fish presents challenges, such as off-target effects and regulatory hurdles, additionally, the risk of chromothripsis, a phenomenon that can lead to genomic instability, raises concerns about the long-term implications of CRISPR-Cas9 applications in fish (Höijer et al., 2021).

Although traditional cellular engineering techniques like artificial gynogenesis and distant hybridization have been shown to be successful, the number of new varieties produced with these techniques is restricted due to the need for optimal conditions (e.g., larger aquaculture sites and advanced facilities) as well as systematic detection techniques (Pinto et al., 2004; Liu et al., 2013; Liu et al., 2024). However, efforts to resolve the aforementioned problems are encouraging. Therefore, there is a need to incorporate the application of genetic breeding techniques into the industry and adapt basic research with industry requirements. An innovative environment must be fostered to speed up the development of new technologies.

Ethical Considerations and Public Perception

Besides raising ethical concerns, Fish hybridization also creates all kinds of perception, especially when it comes to genetic modification and release of hybrids into the wild (Olesen et al., 2010; Blackwell et al., 2020; Hata et al., 2022). The process has been misunderstood for a long time due to a lack of systemic theories and knowledge to manage it effectively (Wang et al., 2019b). Without comprehensive theories and reliable technologies, hybridization efforts can lead to unpredictable and inconsistent outcomes.

The use of genetic modification in fish aquaculture has the potential to increase food security and is claimed to be the next logical step for industry. However, it requires a careful balance of maintaining the welfare of animals, the integrity of ecosystems, and the rights of local communities and consumers. Public perception of genetically modified organisms (GMOs) also significantly influences agricultural policies and practices, shaping the regulatory frameworks and market acceptance. The interplay between public sentiments and policy is critical in determining the trajectory of biotechnology in agriculture. Issues often stem from perceived risks to health and the environment, leading to stringent regulations in some regions (Dessie & Zegeye 2024; Bearth et al., 2024).

There is great concern regarding GMOs, particularly when they are incorporated into hybridization applications in aquaculture. From an ethical standpoint, questions arise about the manipulation of natural processes and the long-term impact on biodiversity. Critics argue that GMOs may disrupt ecosystems, create genetically unstable populations and blur species boundaries, besides undermining conservation efforts. Such concerns must be weighed against the potential benefits to food security and economic sustainability. Another public concern is the environmental consequences if GMOs escape or are introduced into the wild and breed with native species (Darek et al., 2011), potentially leading to the unintended spread of modified genes. GM fish that escape can also pose a threat to biodiversity, which can result in what scientists call the "Trojan gene" effect (Dowling et al., 2015; Lalyer et al., 2021). This refers to GM fish breeding with native populations, causing the genetic alterations to be increasingly passed to wild offspring (transgenic pollution). Research published in the *Proceedings of the National*

Academy of Sciences noted that the release of just 60 GM fish into a wild population of 60,000 could lead to the extinction of the wild population in less than 40 generations (Muir & Howard, 1999).

Other underlying issues are the use of antibiotic resistance markers in GMO development. Research has indicated that the use of antibiotics in aquaculture has led to the emergence of antibiotic-resistant bacteria, which can infect humans through the food chain or direct contact (Preena et al., 2020). Studies have shown that antibiotic resistance genes (ARGs) are prevalent in aquatic environments, with the potential for horizontal gene transfer to human pathogens, thereby increasing public health risks (Lazăr et al., 2021). Furthermore, the presence of transferable genetic elements. Such as plasmids and integrons in fish pathogens. Exacerbates this issue as they facilitate the spread of resistance traits among bacterial populations (Preena et al., 2020; Deekshit et al., 2022). Thus, the integration of antibiotic resistance markers in GM fish may inadvertently contribute to the growing public health crisis of antimicrobial resistance. Moreover, the long-term effects of consuming genetically modified fish are not yet to be fully understood. Some concerns relate to potential allergens or unintended consequences that may only become apparent over time.

Another critical issue concerns regulatory trust and transparency. Public demand for clear labeling of GM fish is often driven by the desire for informed decision-making. Studies suggest that transparency in decision-making processes can significantly enhance public trust in regulatory bodies, especially when the rationale behind regulatory actions is explicitly communicated (Grimmelikhuijsen et al., 2021). In the context of food safety, stringent regulations and transparent labeling practices have been shown to increase consumer confidence by promoting both accountability and the ability to make informed choices (Adams, 2024). The ongoing debate over GM food labeling highlights the importance of providing consumers with not only product information, but also insights into labeling policies (Dixon et al., 2016). However, transparency must be meaningful; merely providing access to raw data without proper context may lead to confusion and loss of trust (Löfstedt & Wardman, 2016). Therefore, enhancing transparency within regulatory frameworks, particularly those concerning food safety, is crucial for building consumer trust and making informed decisions regarding the consumption of GM products (de Boer, 2019).

Regulatory and Policy Considerations

Regulatory frameworks play a crucial role in ensuring that hybridization is carried out responsibly in the industry. Policies may vary by region, affecting the approval process for new hybrid species and the use of genetic modification technologies. Understanding and navigating these regulatory landscapes is essential for researchers and industry players to successfully develop and commercialize hybrid fish.

In the European Union (EU), there are strict regulations governing GMOs, with priority on safety and transparency, besides the mandatory labeling requirements (Jha et al., 2021). In contrast, the US employs a more flexible approach, integrating existing frameworks to assess emerging genetic technologies such as genome editing, which encourages innovation while mitigating risks (Marden et al., 2023). Similarly, Canada evaluates these technologies by emphasizing the importance of adapting policies to keep pace with scientific advancements (Marden et al., 2023). The EU's comprehensive system has fostered public trust through rigorous safety evaluations and stakeholder engagement (Mbaya et al., 2022).

In the developing world, South Africa's evolving seafood regulations offer a glimpse on how the country is working to align with international standards, employing DNA analysis mostly for traceability and regulatory compliance (Naaum and Hanner, 2016). While there are ongoing efforts to harmonize regulations globally, significant discrepancies remain, highlighting the need for localized approaches that account for regional contexts and public perceptions (Marden et al., 2023).

Collaborative and Interdisciplinary Research

Interdisciplinary and collaborative research offers significant advantages and challenges. On the positive side, interdisciplinary research can lead to innovative solutions that address the challenges of hybridization, from improving breeding techniques to managing ecological impacts. Collaborative approaches also facilitate the exchange of knowledge between academia and industry, ensuring that research findings are translated into practical applications that benefit both the environment and the economy. Moreover, such collaboration enhances research outcomes by providing nuanced insights that single-discipline approaches might miss, particularly in complex biological systems like fish hybridization (Lanterman & Blithe, 2019). By combining expertise from various fields, researchers can achieve a more comprehensive analysis of hybridization phenomena, as demonstrated in studies of sympatric fish species (Pinheiro et al., 2019).

One the other hand, challenges include extended working timelines due to the need for consensus among diverse team members and difficulties in publication, which can arise from disciplinary biases and editorial preferences (Lanterman & Blithe, 2019). Additionally, embracing diverse methodologies can result in epistemological friction, where productive yet complex interactions may be seen as obstacles rather than assets (Laborde et al., 2019). Despite these challenges, interdisciplinary research remains a crucial driver of innovation in understanding fish hybridization, necessitating careful navigation of its complex dynamics to mitigate potential hindrances to progress.

Importance of Data Sharing and Open Access

Data sharing and open access to research findings are critical for accelerating progress in fish hybridization. These are crucial in advancing collaboration and knowledge dissemination in fish hybridization research. By making data and publications freely available, researchers can build on each other's work, avoid duplication of efforts and foster innovation. Open access also ensures that the benefits of hybridization research are widely disseminated, reaching stakeholders across the globe, including scientists, policymakers, and aquaculture practitioners. Promoting a culture of transparency and collaboration in research will drive the development of more effective and sustainable hybridization practices.

These practices facilitate universal access to datasets and research findings, thereby creating a collaborative environment that promotes innovation and collective problem-solving. Open access articles have been associated with increased citation rates, which indicates that heightened visibility may lead to greater engagement and interaction among researchers (Clements, 2017).

Moreover, implementing a structured data sharing model can significantly enhance the management and reutilization of research data, helping researchers conserve time and resources while fostering collaborative initiatives (Jusoh et al., 2019). Effective collaboration in this field depends on open communication and trust among stakeholders, which can be strengthened through shared data initiatives (Calderwood et al., 2023). The distinction between data sharing and collaborative efforts underscores the importance of coordinating concurrent operations on shared data, which can lead to more effective and impactful research outcomes (Perrino et al., 2013). Despite these benefits, challenges such as trust issues and barriers to effective communication remain, highlighting the need for ongoing efforts to improve collaborative frameworks.

Conclusion

Fish hybridization offers significant potential to enhance aquaculture by producing genetically diverse and superior offspring. However, the process also presents challenges related to genetic diversity, ecological balance and ethical considerations. A thorough understanding of hybridization techniques and their implications is essential for responsible and sustainable development of aquaculture practices. Ongoing research and careful management are necessary to maximize the benefits of hybridization while minimizing its potential risks. Although hybridization brings huge benefits to fish aquaculture, it appears to have far-reaching ramifications in biodiversity, ecological dynamics and evolutionary processes. It is crucial to adhere to local and international regulations and obtain necessary approvals to ensure ethical standards are met and promote responsible hybridization practices.

Additionally, data sharing and open access are essential for fostering collaboration and innovation. By providing universal access to research data and findings, these practices support effective problem-solving and resource optimization. Therefore, a comprehensive approach that combines interdisciplinary collaboration with robust data sharing frameworks is crucial for the responsible and sustainable development of aquaculture practices. Continued research and strategic management are necessary to fully realize the benefits of fish hybridization and mitigating its potential risks.

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