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Sustainable management and improvement of genetic resources for aquaculture

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Abstract

Effective genetic management of the ~700 aquatic species cultured globally should be addressed for aquaculture to make a significant contribution towards meeting the UN's Sustainable Development Goals. This article aims to identify the current status and challenges relating to the management of farmed aquatic genetic resources (AqGR) and to make recommendations for its improvement. The lack of information on the genetic status of many farmed species is a critical constraint and there is a need to characterize these resources and develop information systems and tools to monitor farmed types used for aquaculture and their wild counterparts. Risk assessment is needed when introducing non-native species and when managing native species including developed farmed types; policies need to be improved and increased awareness and training in risk assessment are required. To increase the uptake of selective breeding in aquaculture, there is a need for the development and adoption of better and more sustainable business models, including long-term financial instruments such as public-private partnerships. Training and technology transfer between aquaculture sectors can have significant impact, especially for lower-value species. Nationally and globally

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applicable instruments and regulations need to be adapted to AqGR and become operational and be effectively implemented by countries.

KEYWORDS

aquaculture, aquatic genetic resources, conservation, invasive species, regulations

1 | INTRODUCTION

There are ~700 aquatic species that are cultured globally. There is a large variation in the degree of maturation of the respective industry sectors for these species and also in how well these industries are managed and regulated with respect to genetics, both nationally and globally. Overall, genetic management and development in the aquaculture sector is far behind that in terrestrial agriculture presenting a huge opportunity to enhance genetic management to capture and conserve the high levels of genetic diversity present in most of our wild and domesticated genetic resources, to underpin the long term future of aquaculture development and to expand the scope of genetic improvement to deliver the genetic gains that can help to ensure that aquaculture will make a significant contribution to meet the Sustainable Development Goals of the United Nations.

One special feature of farmed aquatic genetic resources (AqGR) is that they still have wild counterparts. Their genetic diversity constitutes a large reservoir that can be utilized for starting selective breeding programs, which are powerful tools to improve the performance of the aquaculture sector. Compared to terrestrial populations, genetic gains are typically larger for aquaculture species. However, the importance of this wild genetic resource also saddles us with the responsibility to manage the total (wild and farmed) genetic resources of the species in a sustainable way, technologically and with respect to policies and regulations.

In recognition of the vital importance of the effective management of genetic resources to the future of aquaculture development, Members of the Food and Agriculture Organization of the United Nations (FAO) recently adopted a Global Plan of Action for the Conservation and Sustainable Use of AqGR for Food and Agriculture (FAO, 2022) which identified some of the strategic priorities and recommended actions for the enhancement of genetic resource management.

In this context, the aim of this thematic review is to identify the current status and challenges relating to the management of farmed AqGR and to make recommendations for future improvement of this management in four specific areas identified as needing increased attention.

- 1. Genetic diversity in aquaculture: monitoring, characterization, conservation and sustainable use;
- Introduction of invasive species or farmed types (either native or non-native)-risk assessment and management;
- 3. Genetic improvement-the role of public and private sectors, dissemination, and seed supply;
- Access and Benefit Sharing (ABS) of Aquaculture Genetic Resources and Associated Traditional Knowledge (TK).

All four sections of this article have a similar structure: first reviewing the current status of the issue; identifying today's major challenges and needs; and then identifying the way forward and key recommendations. The final section summarizes the key messages from this analysis.

2 | GENETIC DIVERSITY IN AQUACULTURE: MONITORING, CHARACTERIZATION, CONSERVATION, AND SUSTAINABLE USE

2.1 | Current status

There are a few aquaculture species with a long history of domestication with perhaps the best example being the common carp (*Cyprinus carpio*) for which domestication may have occurred in China about 3000 years ago (Hu et al., 2018; Zhang et al., 2019) and in Europe during the early Roman Empire in the first and second centuries A.D. (Balon, 1995). However, for the majority of species, domestication for use in aquaculture is relatively recent. Duarte et al. (2007) report that 97% of cultured aquatic species entered domestication in the 20th Century. In consequence, most present-day cultured farmed types still retain relatively high levels of genetic diversity compared to their wild relatives (Lind et al., 2012) in contrast to the situation with terrestrial livestock. This high genetic diversity in aquaculture populations gives these populations a high potential to deliver significant gains in commercially important traits through selective breeding. Gjedrem and Rye (2016) report that a 13% genetic gains are rarely seen in terrestrial animal or plant breeding. This scenario presents the opportunity, through effective management of genetic diversity in domesticated farmed types, to retain genetic diversity for the future which will ensure the potential for long-term genetic gains and make a major contribution to securing the future supply of aquatic food.

Wild stocks (i.e., wild relatives of farmed species) still exist for all reported aquaculture species, although some are threatened, including by habitat change, aquaculture activities, and overfishing (FAO, 2019a). While we know that these wild relatives can be found in nature, we often do not know whether these wild relative genetic resources are impacted by anthropogenic activities, as we lack information on the genetic status of these stocks. An initial analysis of the conservation status of cultured species (Lucente et al., 2021) indicates that up to 5.4% of these species are listed in the CITES (Convention on International Trade in Endangered Species of Wild Fauna and FloraDAD) appendices of endangered species¹ indicating that trade is restricted in one or more countries. The same analysis identified that 9.6% of cultured species referenced by the International Union for Conservation of Nature are listed with status as vulnerable or worse² Wild-relative genetic resources are essential reservoirs of genetic diversity for future genetic management of the species in the wild and for the sustainable use and development as farmed types. We, thus, have the incentive to protect our wild relative resources and to try to ensure that none will become extinct and genetic diversity will be conserved, thereby retaining the opportunity to utilize this genetic resource now or in the future.

In the context of aquaculture and this article "conservation" and "sustainable use" of AqGR are related but distinct concepts. Conservation relates mainly to the retention of wild relative genetic resources and a subset of important domesticated farmed types. There are relatively few improved farmed types, certainly when compared to terrestrial agriculture. However, the number of farmed aquatic species (nearly 700 are reported-FAO, 2019a) is much higher than for terrestrial animal species (38) (FAO, 2017). Given that the aquaculture industry is in the relatively early stages of development of its genetic resources and breeding programs have yet to establish differentiated farmed types for most species, there are relatively few developed farmed types (e.g., strains of aquatic animals and varieties of aquatic plants and seaweeds) that must be conserved, certainly when compared to the many breeds of livestock that are threatened.

The main exceptions where there are relatively large numbers of developed farmed types are common carp (*Cyprinus carpio*) and rainbow trout (*Oncorhynchus mykiss*), which are aquatic species with relatively long histories of

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domestication and breeding. Bogeruk and Federatsii (2008) list 72 recognized breeds (farmed types) of common carp in Central and Eastern Europe alone.

Whilst there may not be a strong need for the conservation of farmed types in present-day aquaculture, especially where significant reservoirs of genetic diversity reside with wild relatives, it is nevertheless crucial that these developed farmed types are recorded and monitored to identify those that will need to be conserved. Thus, for AqGR, whilst it is important to conserve some developed farmed types, the current main priority for conservation is to preserve the wild relative genetic resources as the main reservoirs of genetic diversity for the future development of farmed types of aquatic species. These conservation efforts should focus on the important wild relative resources that are considered to be under threat. FAO (2019a) reports that most reporting countries recorded conservation efforts for AqGR, with the majority of these being in situ and/or in vivo conservation programs such as aquatic protected areas, with only 260 in vitro collections being reported globally (mostly sperm cryopreservation). However, coverage of species was very limited in most countries.

Sustainable use relates more narrowly to farmed aquatic species under domestication. For these, it is vital that we recognize the opportunity to effectively manage and thus sustainably utilize these resources and conserve this genetic diversity before it is lost. There is a wide range of different approaches to managing genetic diversity during the domestication of species for aquaculture. Generally, the initial emphasis on early domestication addresses technical issues in artificial breeding and then scaling breeding systems to produce commercial quantities of seed. Often genetic diversity is not actively considered in these early stages when the emphasis is frequently on meeting the demand for quantity of seed over quality. First, a common problem is that the genetic quality of base populations (the genetic resource on which the initial domestication process is developed) is often not adequately considered, and that base populations are often too small in both census and effective population sizes. Effective population size considers the ability of the population to maintain genetic variation based on the relationship among individuals in the population and is a function of the size of the population and the number of breeding individuals contributing to the next generation of broodstock. Second, often genetic variation is not managed well in the early stages, this being a clear problem if broodstock is large, fecund, and expensive to rear such as for several marine finfish, which can lead to loss of genetic diversity (e.g., Hansen et al., 2006, Frost et al., 2006) and inbreeding. Also, given the relative ease of mating closely related aquatic species, hybridization is often attempted. However, uncontrolled hybridization can lead to species introgression, resulting in the loss of the discrete species, for example, in Clarias catfishes Clarias macrocephalus and C. gariepinus (Na-Nakorn et al., 2004) and in Chinese carp Hypophthalmichthys molitrix and Aristichthys nobilis (Mia et al., 2005). The poor genetic management practices outlined above amount to unsustainable utilization of the genetic resource.

Typically, only when an aquaculture species sector reaches a certain scale and value, will thoughts turn to the genetic status of the domesticated farmed types and the potential for genetic improvement. There are many poorly managed aquaculture breeding populations suffering from inbreeding and genetic erosion (e.g., Evans et al., 2004; Li et al., 2007; Yue et al., 2009). The high fecundity of aquatic species and lack of managerial competencies in genetic management are major reasons for this. In these cases where genetic variation is lost through domestication, it is fortunately often possible to return to wild relative stocks to supplement genetic variation in farmed types. However, this approach can dilute the benefits of domestication selection for traits that enable farmed types to adapt and thrive in the artificial environment of aquaculture systems (Janssen et al., 2015). Sustainable use in the context of AqGR should thus apply to the effective genetic improvement is prioritized. Unfortunately, the genetic status of most farmed types of species under domestication is unknown and is not monitored. This situation encourages speculation about the genetic status when adverse production events occur. The lack of information on the genetic status of cultured species below the level of species is a pervasive problem in modern aquaculture (FAO, 2019a).

There are very few countries that have developed information systems on AqGR at species level and even fewer that maintain records or monitor the status of farmed types. This often means that planners and policymakers are attempting to develop sustainable aquaculture in an information vacuum regarding AqGR.

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2.2 | Today's challenges and needs

With the majority of the world's aquaculture sectors lacking information about the characteristics of their genetic resources, there is a strong need to develop related information systems. The development of good information systems on these genetic resources and the targeted conservation and use of these genetic resources in the aquaculture sector would enable us to secure the future of our genetic resources more effectively, given our current level of understanding of genetic management issues (certainly relative to the levels of understanding prevalent at the time when most terrestrial species were being domesticated for agriculture). The fundamental basis of improved conservation and sustainable use of genetic resources in aquaculture must be the broader understanding and characterization of genetic resources and implementation of an information system or systems to make this information widely accessible. Several countries do have information systems at some level for their national resources (e.g., the German National Inventory on AqGR³), but each system records different information with different objectives in mind.

One issue that was noted in the preparation of *The State of the World's AqGR for Food and Agriculture* (FAO, 2019a) is the significant variation in the use and interpretation of terminology to describe AqGR, and the report identified a need to develop, harmonize and promote a standardized language for describing AqGR. FAO is developing AquaGRIS, a global information system for AqGR¹, utilizing a proposed standardized nomenclature around the concept of "farmed type" (Mair & Lucente, 2020). The adoption of more internationally standardized terminology and recording of information would greatly facilitate the organization and sharing of information on AqGR as the Domestic Animal Diversity Information System (DAD-IS)⁴ does for breeds of livestock and the Global Information System on Plant Genetic Resources for Food and Agriculture (WIEWS),⁶ Genesys,⁷ and the Union for the Protection of New Varieties of Plants (UPOV)⁸ do for crops.

While noting that some farmed types (particularly in the case of long-domesticated species) may require monitoring and a specific focus for conservation, this article identifies wild genetic resources as the principal focus of efforts to conserve AqGR that represent the future potential to develop farmed types best suited to culture. It is essential to recognize which genetic resources are under threat, particularly concerning their relevance to food supply and human nutrition, and that appropriate efforts are made to conserve these resources. Some aquatic species are listed as under various levels of threat by the International Union for the Conservation of Nature (IUCN) and trade of some aquatic species is limited by CITES. However, Lucente et al. (2021a) report that 50% of farmed species are classified by IUCN as data deficient or not assessed. The IUCN system is primarily focused on wild species and whilst it includes many aquatic species that are used as food (>8000), it does not have adequate focus on wild relatives of farmed species. Today there is no generic methodology or tools to classify the threat status of farmed types of AqGR and thus those that are deemed worthy of conservation are classified on an ad hoc basis by government technical advisers. Furthermore, the genetic resources of migratory species require coordinated transboundary approaches to their management and conservation.

Generally, in the conservation of wild relative genetic resources, where feasible, preference should be given to in situ conservation through habitat protection or restoration, effective use of aquatic protected areas, and effective fisheries management for those species that are also fished. Often, the genetic implications of such conservation approaches are unknown, and the genetic status of species conserved in situ should be considered in addition to the size of fished populations. Where in situ conservation is not feasible or can be effectively complemented by ex situ conservation, this should be considered and will become increasingly necessary as new farmed types are

⁴http://www.fao.org/dad-is/en/

- ⁶http://www.fao.org/wiews/en/
- ⁷https://www.genesys-pgr.org/
- ⁸https://www.upov.int

³https://agrdeu.genres.de/?L=2

⁵http://www.fao.org/plant-treaty/areas-of-work/global-information-system/en/

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progressively developed. However, in situ, in vivo conservation requires monitoring and management of the genetic diversity within the conserved population and, to be effective, requires long-term resourcing, and thus widespread adoption is perhaps unlikely. One of the major challenges for conserving AqGR is the limited scope for ex situ, in vitro conservation, given that, with a few exceptions, such as for bivalves and microalgae, the primary option for this is cryopreservation of male gametes, particularly fish sperm. To date, there has been little success in the cryopreservation of fish oocytes or embryos. It seems that, until such methods can be developed for multiple aquatic species, the role of ex situ in vitro conservation will remain limited.

The focus of sustainable use of AqGR is on applying established understanding and best practice methods to manage genetic variation and control inbreeding. There is considerable scope for improvement in awareness of the implications of how seed supply systems are established and managed, and particularly the mechanism for the renewal of broodstock over generations. There is a need to develop a changed mindset, in significant and emerging aquaculture sectors as well as in established aquaculture sectors, that the genetic quality of seed is as important as the quantity of seed. In the development of an aquaculture sector for a species, genetic management (including the source base populations) should be considered as soon as significant seed supply systems are initiated. The principles of management of effective population size need to be applied in relation to the fecundity and generation time of the species in question. For most aquaculture species cultured around the world today, the basic principles of genetic management of broodstock have received little attention, with the resulting risk that the genetic status of the farmed types has already been compromised. There is a tremendous opportunity to put in place or adapt breeding and seed supply systems for aquaculture species, such that they focus on maintenance of genetic diversity as well as meeting the demand for the quantity of seed.

There are also numerous examples of well managed and successful aquaculture breeding programs (controlling inbreeding) using low-tech equipment where the identification of families and pedigree is managed by physical tagging and separate rearing of families until tagging (Bentsen et al., 2017; Gjedrem, 2010). These breeding programs improve production performance, but they require careful management and infrastructure to implement effective management of families. This level of effective management of genetic diversity is far less common outside of organized breeding programs. To realize the opportunity to enhance genetic management more fully across existing seed supply systems, it is highly desirable to have a cost-effective means of assessing the genetic status of farmed types, relative to that of wild relatives, especially the wild stocks from which the farmed types were derived. Whilst such genetic technology does exist, for example through appropriate single nucleotide polymorphism (SNP) panels such as genotyping-in-Thousands by sequencing (GT-seq-Campbell et al., 2015). The access to and cost of such services could nevertheless be relatively high and prohibitive for low-value farmed species in the developing world.

Therefore, such characterization efforts remain mostly in the realm of research and development (R&D) or commercial aquaculture in the developed world. There is thus a need for the development and dissemination of costeffective genetic tools that can be applied across the seed supply chain for monitoring the genetic status of key genetic resources of major species/production systems enabling the maintenance of genetic diversity and avoidance of inbreeding. Possible options to enable this include the development of tailored marker systems and the strengthening of the necessary capacities and infrastructure, in developing countries and countries with economies in transition, for the implementation of more advanced genetic diversity within seed supply systems, possibly based on analysis of environmental DNA (eDNA) samples representing pooled DNA, using well-designed marker systems (Xiong et al., 2022). This might be best achieved with support of strong collaborative linkages between developed and developing countries.

The interaction between farmed types of cultured species and their wild relatives will be a prominent feature of the conservation, sustainable use, and development of AqGR. These interactions should be managed more effectively, including through appropriate management and conservation of wild resources, with a view to their current and potential future role in aquaculture in addition to their sustainability in the wild. Where cultured genetic resources, either derived from non-native species or farmed types of native AqGR, are potentially invasive, the harm

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they could pose to native wild genetic resources must be factored into any assessment of proposed introduction and use in aquaculture. In line with a proposed target of the Kunming-Montreal Global Biodiversity Framework,⁹ which aims to reduce the number of introductions of potentially invasive alien species, introductions of non-native species should be based on low risk of environmental harm and high potential for economic benefit. The challenge in implementing such a strategy is the relative paucity of information on the impacts of non-native species introduced for aquaculture.

Lastly, the development of new species for aquaculture often competes for the same resources available for the development of farmed types of existing culture species. It is not easy to quantify the costs of developing aquaculture of new species, but unless a species is readily adapted to culture systems developed for other species, this requires significant effort in R&D and sometimes also in developing the value chain and the market for a product. Before investing in R&D for adapting these species in aquaculture, procedures to pre-evaluate new species should be established. Sometimes the objectives of developing a new species for aquaculture could be met, perhaps more cost-effectively, by adapting an existing cultured species through a suitably targeted breeding program rather than by introducing/developing a new species. It is essential in the development of aquaculture production strategies, to set an appropriate balance between species diversification and the development and adaptation of existing cultured species. For example, rising temperatures due to climate change can challenge the tolerance ranges of existing cultured species. Such a challenge could be met by seeking a new species to farm in that environment or by developing or adapting a breeding program designed to develop farmed types with greater tolerance to higher temperatures and/or greater temperature fluctuations. The cost and benefits of both approaches should be evaluated. There is thus a need for countries to take a strategic approach and strike a balance between introducing a new species to aquaculture and developing farmed types of existing species, based on specific target objectives, including the existing and projected market demand for associated products.

2.3 | The way forward and key recommendations

There are several recommendations that address the needs and challenges in enhancing the conservation and sustainable use of AqGR.

We must identify key genetic resources (mostly wild relative stocks, although some farmed types should be included) most under threat (globally, nationally, and regionally) and develop appropriate responses using a combination of in situ (preferred) and ex situ conservation approaches. In situ conservation approaches could incorporate the inclusion of conservation in fisheries management objectives, habitat restoration, and restorative aquaculture. Genetic monitoring programs for wild populations should also be considered, even if these populations are not under threat, to better understand the genetic resource enabling reliable assessment of the future risks of genetic introgression, selection of appropriate founder stock for domestication and to establish baselines for future monitoring.

This may involve an analysis of the threat and conservation status of all major aquaculture species in all countries. Conservation efforts should be coordinated regionally for transboundary resources. Guidelines on the conservation of AqGR should be developed. Given the limitations on the maintenance of ex situ *and* in vivo gene banks, it is further recommended to expand research efforts to develop methods for cryopreservation of oocytes and zygotes, embryos or diploid cells for threatened species recovery. Such techniques, where appropriate and cost effective, could greatly facilitate ex situ conservation programs but may also enhance genetic improvement and dissemination for species with limiting reproductive characteristics.

Given the paucity of information on AqGR, the future availability of a global information system for AqGR represents an opportunity to standardize the nomenclature and terminology with which AqGR are described, promote the appropriate characterization and monitoring of these resources, facilitate the sharing of information on them, and facilitate access to them. We recommend the broad participation, by national focal points and experts, and investment of resources in the further development and utilization of a global information system and the population of this system with information on species and farmed types used in aquaculture and even the inclusion of information on wild genetic resources of the same species. The availability of this information will provide a strong basis to inform the development of strategic management approaches for AqGR nationally and regionally and would be transformative in developing governance and policies aimed at improving this management.

It is recommended to strengthen the role of genetic management in the development and implementation of seed supply systems for aquaculture to promote the sustainable use of these important genetic resources. This recommendation is also valid for the management of gene banks, where currently proper management strategies and practices are often lacking. This can be achieved through effective capacity building and communication of the importance of genetic management and the consequences of poor management, including through education, training and extension and the promotion of simple guidelines. Furthermore, the development and wide availability of cost-effective genetic tools specific to cultured species (with initial prioritization on lower-value species most important to food security) could be transformative in characterizing genetic resources and preventing or identifying bot-tlenecks where intervention is necessary. For example, a species-specific SNP marker system could be applied to analyze the genetic status of farmed types at different points in the seed supply chain (e.g., breeding nucleus, multiplier hatchery, and growers) and compared to a benchmark, perhaps of wild relatives of the same species, to understand the implications of broodstock management through the chain, on the genetic diversity within the farmed type. Widespread use of such tools, combined with a broader understanding of the importance of genetic management in seed supply systems, could be a major step in securing the long-term future of our domesticated genetic resources for aquaculture.

3 | INTRODUCED SPECIES OR FARMED TYPES (EITHER NATIVE OR NON-NATIVE)-RISK ASSESSMENT AND MANAGEMENT

3.1 | Current status

AqGR commonly farmed outside their natural range, such as common carp, salmonids, tilapias, shrimps, and Pacific oysters, and developed farmed types that are differentiated from their conspecific wild types, comprise a large and growing component of global aquaculture production. Nine of the top 10 aquaculture species are farmed in more countries or ecosystems where they are non-native than where they are native (FAO, 2019a). While the development and production of genetically improved farmed types may target increased aquaculture productivity, human well-being, and economic development, they also may pose ecological hazards to native ecosystems (Costa-Pierce, 2003) and genetic hazards to native AqGR (Hallerman, 2008).

Risk analysis is the formal process of identifying, assessing, and managing factors that may jeopardize the achievement of a goal. In the context of aquaculture, the goal is to promote food security while protecting AqGR. Principles of risk analysis can be applied to manage genetic harms posed by the distribution and production of introduced species and developed farmed types (Hallerman, 2008). Risk analysis is a formal approach to estimate the likelihood of undesirable outcomes stemming from a given action. It seeks to identify risk pathways, estimate risk probabilities and consequences, develop procedures to manage risk, and communicate the results to stakeholders, thereby minimizing harm to aquatic and human populations. Principles of risk analysis have been applied to aquaculture (Bondad-Reantaso et al., 2008), including the production of introduced species and developed farmed types. The scope of existing case studies regarding the impacts of introduced aquaculture species and farmed types on AqGR is narrow, limiting our ability to predict and manage the likelihood of harms being realized from the distribution and production of introduced species and developed farmed types. However, even with limited predictive ability, risk analysis provides approaches for managing risks to acceptable levels.

3.2 | Risk analysis

3.2.1 | Risk pathways

Aquaculture has been the justification for many introductions of species to regions or ecosystems where they are not native (Bartley et al., 2009; Benzie et al., 2012). There is a large literature on harm posed by introduced species, including introductions pertinent to aquaculture. Environmental/ecological harms may be realized through competition, predation, habitat alteration, and transmission of introduced pathogens (including parasites in the term "pathogen") and pests (Table 1), which may add to and increase existing challenges from anthropogenic activities. While procedures exist for conducting risk analysis of introduced fishes (e.g., Zambrano et al., 2006), decisions on new introductions can be biased and often are based on incomplete data (Pullin et al., 1997). Hence, ecological impacts frequently are recognized only after introduction and establishment. Atalah and Sanchez-Jerez (2020) estimated that 26.5% of global aquaculture production was comprised of species not native to where they were produced, identifying southern Chile, the East China Sea, and the Yellow Sea as hot spots for the impacts of ecological invasion. Biological invasion may lead to economic as well as ecological impacts on native fishes and ecosystems. Liu et al. (2014) developed a general invasive species economic model to capture both the ecological and economic impacts of invasive species, including a bioeconomic model to assess changes in fishery yield, distribution of benefits, and overall profitability, applying the model to wild and cultured Atlantic salmon stocks in Norway. The impacts of such introductions are not adequately studied, and associated risks of aquaculture-related introductions need to be more comprehensively assessed.

Entry of farmed types into natural populations may pose genetic harm to receiving native populations. Such harm may be realized through loss of adaptation in natural populations, introgression of new genetic material into species' gene pools, and in the extreme case, loss of locally adapted populations.

3.3 | Genetic harm posed by farmed types

Interbreeding of non-native or conspecific farmed types with natural populations poses risks of genetic harm. Natural selection operates upon fitness-related loci, mediating adaptation of populations to their respective environments. Spatial heterogeneity of natural selection results in adaptive genetic divergence of populations (Hallerman, 2003). Escape of widely cultured farmed types and their interbreeding with local populations of wild relatives can homogenize genetic variation. The best-demonstrated case studies involve salmonids (reviewed by Ferguson et al., 2007), although it should be noted that salmonids have a migratory life history that contributes to their susceptibility to genetic harm. Reviewing studies of the genetic effects of cultured fish on natural salmonid populations, Hindar et al. (1991) found a wide variety of effects, from no detectable effect, to complete introgression, to complete replacement of natural populations. Interbreeding of farms with wild Atlantic salmon (Salmo salar) resulted in lowered fitness of the wild stocks, and repeated fish escapes resulted in cumulative fitness depression (McGinnity et al., 2003). Dramatic losses of fitness were observed after just two generations of captive breeding in anadromous rainbow trout (Oncorhynchus mykiss), as well as reduced fitness of their wild-born descendants (Araki et al., 2007, 2009). Glover et al. (2017) review the knowledge gained over half a century of investigating interactions between farmed and wild Atlantic salmon. Conceptual models have been developed to predict the effects of introductions of maladapted individuals into locally adapted gene pools for salmonids (Sylvester et al., 2019) and more generally (Tufto, 2001, 2010) and to predict the relative likelihoods of beneficial or negative impacts of gene flow on receiving gene pools (Garant et al., 2007). However, empirical studies of the effects of interbreeding of escaped farmed types upon populations of wild relatives are lacking for most cultured species. Hence, we lack the empirical data to parameterize models predicting the effects of introgression of farmed types into native gene pools.

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Species or farmed type	Location and documented impact	Source			
Golden apple snail (Pomacea canaliculata)	Introduced to several Asian countries from South America as a source of protein and supplementary farm income in the 1980s–1990s, the snail invaded rice fields, consuming rice seedlings. The economic cost in the Philippines alone was estimated at US\$ 420,000–1200,00 per annum in 1990.	Halwart (1994), Naylor (1996)			
Hybrid characiforms (Colossoma macropomum, Piaractus mesopotamicus and Piaractus brachypomus) and silurifomes (Pseudoplatystoma corruscans, P. reticulatum, and Phractocephalus hemioliopterus)	Produced in Colombia, Venezuela, Peru, Argentina, and chiefly in Brazil to yield genetically improved secondary farmed types, this process has resulted in fertile F_1 hybrids in aquaculture operations, which have been verified in the wild as farm escapees. In addition, assessments have reported the presence of post- F_1 , introgressed individuals, confirming genetic contamination of wild populations, jeopardizing the gene pools of the parent species.	Vaini et al. (2014), Hashimoto et al. (Hashimoto et al., 2012, Hashimoto et al., 2016)			
African catfish (Clarias gariepinus)	<i>Clarias gariepinus</i> has been introduced to various countries worldwide for aquaculture. Its adaptations include the ability to withstand low dissolved oxygen, early maturity, and primarily its voracity, which qualify this species as highly invasive. Escapes from aquaculture and deliberate releases have resulted in the establishment of <i>C. gariepinus</i> in the wild in several countries, with the potential for habitat change and impacts on native species.	Rocha (2008), Weyl et al. (2016)			
Striped catfish (Pangasianodon hypophthalmus)	Striped catfish native to Asia have been introduced in many countries as an aquaculture candidate. Despite the large fish diversity present in Neotropical countries, with many species potentially suited to aquaculture, striped catfish has been introduced to Brazil as an ornamental species and food fish. This introduction jeopardizes native fish species once escapees from aquaculture generate feral populations. The wisdom of this introduction for regional aquaculture is being questioned.	Garcia et al. (2018)			
Oreochromis species	Tilapia species are moderate to highly invasive, with a 60%–90% probability of becoming established in new open waters of tropical and subtropical regions. Tilapia introductions have led to habitat alteration, including declines in aquatic plants and decreased availability of breeding areas for native species. Africa is the center of tilapia diversity, with many species native to different countries. Since the 1950s, several waves of tilapia translocations were made to promote aquaculture and fisheries. Due to its superior cultural qualities, Nile tilapia, native to northern Africa, has been introduced into many countries across the continent. Most <i>Oreochromis</i> species will readily hybridize, resulting in fertile progeny; thus, the introduction of non-native Nile tilapia jeopardizes the natural genetic diversity of native <i>Oreochromis</i> species, some of which are themselves candidates for regional aquaculture. Wild populations of Nile tilapia can be threatened by introduced farmed types, resulting in long-term erosion of genetic variation on which breeders may rely for future tilapia breeding programs.	Pullin et al. (1997), Moreau (1983), Canonico et al. (2005), D'Amato et al. (2007), Deines et al. (2014), Shechonge et al. (2019)			

TABLE 1 Examples of ecological or environmental impacts of the introduction of non-native species for aquaculture.

(Continues)

TABLE 1 (Continued)		
Species or farmed type	Location and documented impact	Source
Introduction of oyster (Saccostrea cucullate)	Native oysters along the Brazilian coast comprise two species, <i>Crassostrea rhizophorae</i> , and <i>Crassostrea gasar</i> . Both species are essential fisheries resources for local communities. Moreover, due to its rapid growth rate, <i>C. gasar</i> is a candidate species for aquaculture. Since 2004, the presence of <i>Saccostrea cucullata</i> , native to the Indo-Pacific, has threatened populations of native oyster stocks, mostly due to competition for resources. Assessments have reported the fast establishment of this species in <i>Crassostrea</i> oyster banks, leading to decline of native <i>Crassostrea</i> populations.	Galvão et al, (2017); Amaral et al., (2020)
Introduction of common carp (Cyprinus carpio)	This is an example of a pathogen-related impact due to the introduction of common carp to various countries at the global level, both for aquaculture and ornamental purposes, which led to the introduction and spread of Koi Herpesvirus (KHV), a World Organization for Animal Health (WOAH) listed disease, with devastating economic effects.	Motohiko et al. (2004)

TABLE 1 (Continued)

Escape or release of interspecific hybrids, if fertile, pose the risk of harm due to introgressive hybridization. For example, hybrid catfish (*Clarias macrocephalus* \times *C. gariepinus*) escaping from farms in Thailand interbred with native populations of *C. macrocephalus*, causing introgressive hybridization with both wild and cultured stocks (Senanan et al., 2004). Poor management of tilapia stocks led to unwanted hybridization of previously pure populations in the wild and in culture (Macaranas et al., 1986; McAndrew & Majumdar, 1983). The genetic integrity of many Mozambique tilapia (*Oreochromis mossambicus*) populations is threatened by hybridization with Nile tilapia (*O. niloticus*) (Cambray & Swartz, 2007; Weyl, 2008). Mwanja and Kaufman (1995) showed hybridization in both directions among *O. niloticus* and *O. esculentus* in the satellite lakes of Lake Victoria, and no pure stocks of *O. esculentus* remain in these systems. In Bangladeshi hatcheries, 8.3 percent of farmed silver carp (*Hypophthalmichthys molotrix*) broodstock exhibited bighead carp (*Aristichthys nobilis*) alleles, and 23.3 percent of farmed bighead carp exhibited silver carp alleles (Sattar et al., 2005), compromising the integrity of the broodstock and their performance in aquaculture. A fulsome review of the genetic impacts of escaped farmed types is beyond the scope of this review, and interested readers are referred to Hallerman (2008).

3.3.1 | Overview of risk analysis framework

Consideration of ecological and genetic harm posed by the culture of introduced species or developed farmed types must be based on understanding of key concepts underlying the science and practice of risk analysis (Hallerman, 2008) including the following:

A *harm* is a perturbation resulting in negative impacts to a population. A *hazard* is an agent or process that has the potential to produce harm. *Risk* is the likelihood of harm resulting from exposure to the hazard.

Risk, *R*, is the product of the probability of exposure, P(*E*), and the conditional probability of harm given that exposure has occurred, P(*H*|*E*); that is, $R = P(E) \times P(H|E)$. The steps in risk analysis, then, are to:

- 1. Identify potential harms;
- 2. Identify hazards that might lead to harms;
- 3. Define and assess the likelihood of exposure, P(E);
- 4. Quantify the likelihood of harm given that exposure has occurred, P(H|E); and

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5. Multiply the resulting probabilities to yield a quantitative estimate of risk.

Furthermore, risk (*R*) is the product of the likelihood (*p*) and consequences or damage measure (*x*) of undesirable happenings or scenario(s). A common definition of risk (e.g., Kaplan and Garrick 1981) includes a set of triplets ($R = \{<s_i, p_i, x_i>\}, i = 1, 2, ..., N$), and hazard is a set of duplets (*s* and *x*). Hence, it is important to consider a risk curve (or even a risk surface) rather than a single risk measure, because the risk of a low probability and large harm is not equal to that of a high probability and small harm. Furthermore, Arthur (2008) cites the definition of risk provided by the World Organization for Animal Health (WOAH) where "Risk means the likelihood of the occurrence and the likely magnitude of the consequences of an adverse event to the public, aquatic animal or terrestrial animal health in the importing country during a specified time period."

Exact probabilities of risk are difficult or impossible to determine for all types of possible harm. Indeed, it is unlikely that all possible harms would be known a priori, particularly regarding any indirect causal pathways. Hence, it may be necessary—based on current knowledge of population genetics, population dynamics, aquatic ecology, and empirical experience with farmed types—to classify levels of concern regarding likely ecological or genetic impacts posed by farmed types into qualitative categories ranging from "low" to "high".

Risk assessment might best be considered as embedded within an interactive framework involving a range of stakeholders (Figure 1). Involvement of the full range of stakeholders will bring all existing knowledge into the process, make the process transparent to stakeholders, and enhance the understanding and acceptance of the outcome of risk analysis. Stage I involves identifying the problem at hand, engaging stakeholders, identifying possible technical solutions to the problem at hand and identifying potential harms, risk pathways, and assessment methods. Stage II is the risk assessment itself, leading to estimating the likelihood that harm could become realized should a proposed action be taken. Upon estimation of that risk, a decision is faced as to whether the risk is acceptable. If it is acceptable, the decision may be made to go forward. If the level of risk is unacceptably high, risk management measures would be identified, residual risk quantified, and the decision of whether to go forward would be reconsidered. Should the proposed action be implemented, genetic, environmental/ecological, and social outcomes should be monitored. Because all potential harms and associated pathways cannot be known and predicted a priori, it will be necessary to update the risk analysis as knowledge accumulates using an adaptive management approach (Kapuscinski et al., 1999).

3.3.2 | Step-by-step consideration of risk analysis for aquatic farm types (either native or non-native)

Harm identification

Potential harms posed by the culture of a farmed type relate to chains of events occurring after an escape or release from a culture system. Potential harm must be identified on a case-by-case basis and will depend on the phenotype of the organism, and not per se on the method used to produce the farmed type. As noted above, direct genetic harm would flow from the farmed type interbreeding or hybridizing with reproductively compatible wild stocks in the receiving ecosystem. The degree of the harm will be a function of the degree of differentiation among the two gene pools, the relative proportion of spawners from the respective groups, and the natural selective pressure imposed by the receiving ecosystem. Escape or stocking of an introduced species or developed farmed type poses the risk of interbreeding with reproductively compatible species/stocks in the receiving environment and the risk of introgressive hybridization.

Hazard identification

In this context, the hazardous agent is the farmed type because it is the entity that poses ecological or genetic harm to the receiving ecosystem or native populations.

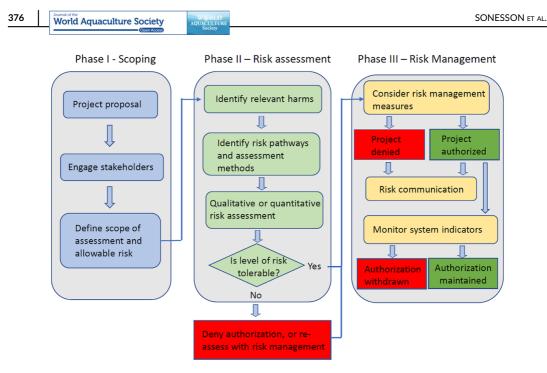


FIGURE 1 Overview of stages in the formal process of risk analysis and management.

Risk assessment

Realization of harm following exposure of a natural ecosystem or native population to a farmed type would require the occurrence of a chain of events. Aquaculture operations frequently lose small numbers of individuals to the natural environment, with occasional catastrophic losses of larger numbers due to equipment failure, storm, or flood. However, for a farmed type to prove a hazard, it must establish itself in the receiving ecosystem. The likelihood that the farmed type will become established in the receiving ecosystem, P(E), is dependent on the species' invasiveness, the fitness of the farmed type, and characteristics of the receiving ecosystem (Hallerman, 2008).

Evaluating ecological or genetic risk will have to be conducted on a case-by-case basis. The likelihood of harm being realized given exposure to a farmed type is difficult to quantify, especially given the lack of empirical data for the many farmed types at issue, resulting in this being currently the weakest aspect of applying risk analysis. Risk analysis will often be restricted to evaluating risk qualitatively based on: (1) the species, (2) the effect of genetic change on the fitness of the farmed type in the receiving ecosystem, and (3) the stability and resiliency of receiving community.

The outcome of such risk analysis will be a prediction that the likelihood of harm given exposure to a farmed type is "high", "medium", "low" or "negligible". That prediction might then be compared to the "acceptable" level of risk to determine whether to go ahead, whether to reconsider the action under conditions of risk management, or whether to reject the action at issue. As was mentioned above, the balance between possible risks and expected benefits of a certain introduction is key in decision-making. Therefore, within the risk assessment, the likelihood (introduction, survival, and spread) and the consequences are assessed; the combination of the likelihood and consequences assessment will provide the final risk rating, which is necessary for the overall risk assessment and risk management.

To summarize, the risk assessment process is based on the following steps:

- 1. Assessment of the likelihood of introduction or release.
- 2. Assessment of the likelihood of spread or exposure.
- 3. Calculation of the likelihood rating, based on the release and exposure assessment.
- 4. Assessment of the consequences derived from the release and exposure of farmed stock.
- 5. Calculation of the final risk rating, based on the likelihood rating and the consequences assessment.

TABLE 2 Risk rating matrix (ISO, 2018).

	Consequences of hazard entry, establishement, and spread					
Likelihood of hazard entry, establishment and spread	Negligible	Very low	Low	Moderate	High	Extreme/ catastrophic
High	Negligible risk	Very low risk	Low risk	Moderate risk	High risk	Extreme risk
Moderate	Negligible risk	Very low risk	Low risk	Moderate risk	High risk	Extreme risk
Low	Negligible risk	Negligible risk	Very low risk	Low risk	Moderate risk	High risk
Very low	Negligible risk	Negligible risk	Negligible risk	Very low risk	Low risk	Moderate risk
Extremely low	Negligible risk	Negligible risk	Negligible risk	Negligible risk	Very low risk	Low risk
Negligible	Negligible risk	Negligible risk	Negligible risk	Negligible risk	Negligible risk	Very low risk

The following risk rating matrix is based on the ISO 31000:2018. risk management guidelines (ISO, 2018), Table 2.

The term acceptable level of risk (ALOR) describes the likelihood of an event whose probability of occurrence is small, whose consequences are so slight, or whose benefits (perceived or real) are so great, that individuals or groups in society are willing to take or be subjected to the risk that the event might occur. Appropriate level of protection (ALOP) is the level of protection deemed appropriate by the member (country). ALOP can be regarded as an acceptable level of risk or tolerable risk.

Risk management

Should an oversight body determine that the distribution and production of a farmed type pose harm to a receiving ecosystem or native population, the question turns to managing the associated risk. Risk management is the design, selection, and implementation of a program of actions to minimize risk to an acceptable level. The best approach to minimize likelihood of harm being realized is to minimize exposure to the hazard. Four non-mutually exclusive approaches include the following: (1) geographic location, (2) physically confining the farmed type on aquaculture facilities, (3) reproductively confining farmed types and (4) operations management.

Risk communication

Risk communication transmits the ongoing process and results of risk analysis to key stakeholders, who would include international, regional, and national agency/government officials (national, regional, and international agencies, including FAO), aquaculturists, nongovernmental organizations, academic researchers, and the general public. Different groups of stakeholders will be reached most effectively by different means.

3.4 | Today's challenges and needs

There is a need to raise the debate among fish farmers about the importance of AqGR to the sustainability of fish production in the long term. Greater application of risk analysis is needed in aquaculture, research, and government sectors are given that introductions of either native or non-native species and farmed types that can become

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invasive is a common practice in many countries and these genetic resources continue to make large contributions to aquaculture production. Policymakers must have the necessary tools and scientific information derived from a well-developed risk analysis to balance benefits and risks associated with the introduction of native and non-native AqGR that can become invasive in a specific context. Concerns regarding genetic harm apply to non-native species and developed farmed types of native species.

Improving the confinement of farmed types at aquaculture operations is necessary to promote the protection of native AqGR in adjacent aquatic ecosystems. There are existing related models for the development, implementation, and verification of best management practices for aquaculture operations (Tuckett et al., 2016).

Aquaculture risk assessment, risk management and risk communication (which are three pillars of the risk analysis process) are emerging areas in aquaculture science. While the risk pathways are reasonably well known, the associated risks are not well quantified. Much information potentially useful for risk analysis of farmed types is scattered across the scientific and gray literature. Understanding of some key issues—for example, fitness of farmed types—is still emerging. Furthermore, many wild populations are not well characterized genetically, plus wild populations previously thought to be undifferentiated have turned out to be differentiated when SNPs are used as opposed to microsatellites, uncovering evidence of local adaptation. In practice, it is more difficult to assess the risk of introducing a non-native species than that of a developed farmed type. Development of quantitative risk analysis, especially regarding the estimation of the likelihood of harm becoming realized given exposure to a farmed type, is incomplete.

While the application of principles of risk analysis to issues pertaining to farmed types has been described conceptually, there are relatively few empirical case studies. Leading examples include the assessment of risks posed by field testing of transgenic common carp at Auburn University (OAB, 1990) and introduction of triploid Asian oysters into Chesapeake Bay (Dew et al., 2003; NRC, 2004). Risk management, while widely applied in research facilities, is not widely applied in commercial aquaculture operations. We need risk assessments of farmed-type escapes and introgression with wild relatives and synthesis of findings from such studies. We do not yet have a body of case studies to exemplify effective communication of aquaculture risk management.

Operation-level practice of risk assessment and management will not become commonplace unless required. There is a need for the incorporation and implementation of risk assessment and management in aquaculture development policy.

Considering the uncertainty surrounding the impacts of non-native species and farmed types on native ecosystems, a precautionary approach has been recommended by FAO and others (FAO, 1995). The precautionary approach calls for establishment of target and limit reference points, pre-agreed actions when reference points are reached or breached, and a monitoring system. The precautionary approach allows development to continue in the face of uncertainty. The establishment of reference points and pre- agreed actions needs to involve key stakeholders and sectors, for example, from private industry, government, academic, and conservation. Reference points generally have not been established for genetic parameters, but they can be formulated. In general, the approach has not been widely used in natural resources management and monitoring the ecological and genetic impacts from introductions is very uncommon (Bartley & Funge-Smith, 2018).

3.5 | The way forward and key recommendations

There is a need for developing or strengthening national policies regulating introduced species and protection of indigenous AqGR. Such policy frameworks should make provision for the decision on introduced species or specific farmed types of native species based on science-based evaluation and consideration of potential risks and benefits. The potential need for introduced species and developed farmed types for aquaculture production must be balanced with concerns for conserving native AqGR. Alternatives to introduced species, that is, development of genetically

improved farmed types of native species (recognizing that these may in turn present their own risks), must be considered, perhaps based in part on the strategic appeal of introducing new products into the marketplace.

Because aquaculture risk assessment and risk management are emerging areas, we need further risk assessment studies of farmed-type escapes and introgression with wild relatives and synthesis of findings among such studies. We need further effort in communication of aquaculture risk management to governments and aquaculturists. As examples of international guidelines and standards related to the risks associated with the introduction of AqGR, The International Council for the Exploration of the Sea has established protocols for governments to follow when considering the introduction of non-native species and farmed types (ICES, 2012) that can be used. Furthermore, the WOAH has specific guidelines and standards on the introduction of introduced aquatic species and farmed types from the pathogen-related perspective (OIE 2019), and FAO has FAO Fisheries and Aquaculture Technical Paper. No. 519 Understanding and Applying Risk Analysis in Aquaculture (Bondad-Reantaso et al., 2008).

In the context of risk management, while reliable confinement can be achieved for capital-intensive aquaculture systems, more effort must be directed to developing and demonstrating cost-effective confinement systems for reducing escapes from small aquaculture operations. Among measures for reducing wild spawning, the utility of triploid-farmed types for aquaculture varies among species and should be more widely assessed. Gene editing could offer the potential for inducing reversible sterility (Wargelius et al., 2016), although it is still a technical possibility needing further development, especially for other species.

The principles of risk analysis are established, and governments and non-governmental organizations need to apply them routinely to oversight of aquaculture. FAO can play a leading role in capacity building by training responsible parties, especially in the public sector, to raise awareness of risk perception, assessment, management, and communication. FAO can present reports of case studies of successful implementation of policies promoting risk analysis in the aquaculture sector. FAO and regional bodies can also play role in developing harmonized policies on introduction of species, among the countries which share water flows.

4 | GENETIC IMPROVEMENT- THE ROLE OF PUBLIC AND PRIVATE SECTORS, DISSEMINATION, AND SEED SUPPLY

4.1 | Current status

Selective breeding is an important contributor to advancing global aquaculture for addressing the Sustainable Development Goals of the UN. For example, the WorldFish and partners created an improved strain of Nile tilapia, called the Genetically Improved Farmed Tilapia (GIFT), by pioneering a systematic breeding method. This program was based on selective breeding for salmon and trout established in Norway in the 1970s. By selecting broodstocks that are superior for important traits, the performance of the entire population is improved. This process of selective breeding is a proven and powerful tool to improve traits such as production efficiency, product quality, and disease resistance in domesticated farmed types of cultured species (Gjedrem, 2012), in the whole world. Selective breeding is also an important approach to adapt populations to a changing climate, for example, through selection for temperature/hypoxia tolerance. Similarly, increased genetic gain for feed efficiency will reduce the required amount of feed for the same product output. Selective breeding is a cumulative process, where the genetic gains of the current generation build on the genetic gains of the previous generation, and where the natural additive genetic diversity in the population is utilized to attain genetic improvements. Genetic improvement thus has a very major role to play in the sustainable growth and increased efficiency of aquaculture.

Selective breeding is a technology applied to virtually all terrestrial-farmed animals and certain plant genetic resources. However, reproductive specificities, degree of technology development, and industrial maturation impact the cost and benefits of breeding programs. Properties specific to aquaculture breeding programs include the potentially very large number of individuals that can be produced from each family given the high fecundity of many

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cultured species. Also, in most cases, individuals cannot be tagged with individual identifiers until later in life when they have reached a sufficiently large size. These specificities in aquaculture breeding programs generate certain requirements for infrastructure, often in the form of multiple smaller holding units where families can be reared until tagging. It also results in unwanted structure in the data used for genetic analysis. An alternative system can be used, where large mixed-sex groups of broodstock are spawned in a few large tanks or individuals in early life stages from several families are pooled (Dupont-Nivet et al., 2006). These systems have less precise control of the family contribution in a population and need to be compensated by increasing the number of individuals that need to be tested for different traits and genotyped to track pedigree and calculate genomic breeding values.

There also exist low-cost options of mass selection programs as presented by Gjedrem (2005) and Sonesson (2005). In general, for aquaculture breeding programs high fecundity and large family sizes enable high selection intensities to be applied and when combined with the high levels of genetic variation, often present in recently domesticated farmed types, results in very high rates of genetic gain.

Aquaculture breeding programs can have large effects upon aquaculture production systems, with genetic gains of, on average, 13% per generation for growth rate (Gjedrem & Rye, 2016) for all aquaculture species. Genetic gains valued at 0.2 (kg fish produced have been reported after one round of selection of gilthead seabream (Janssen et al., 2018), and Atlantic salmon (Wu, 2021). However, selective breeding technologies are far from being fully utilized in the aquaculture industry. Zhou & Gui, 2018 reported that 156 strains had been developed in China using, for example, selective breeding and hybridization, but in The State of the World's AgGR for Food and Agriculture, FAO (2019a) it is reported that over 40% of all aquaculture species were produced from unimproved wild types globally. Furthermore, 45% of reporting countries noted that genetic improvement is still not significantly impacting aquaculture production in their countries. In an older reference, Gjedrem et al. (2012) reported that less than 10% of the global aquaculture production was based on wellmanaged selective breeding programs. Whilst it is likely that this proportion may have increased slightly, in general, the adoption of selective breeding to date is slowly taking into consideration its proven cost-benefit and its potential to substantially enhance production efficiency in aquaculture. Table 3, which is adapted from FAO (2019a) and Hallerman et al. (2021) shows the top fifteen species or species groups (by production) and a subjective assessment of the global status of their genetic improvement listed in order of their production in tonnes. These species account for 62.5% of global production (by volume).

The main components of a breeding program are the three following tiers: (i) a breeding nucleus that manages and develops the elite brood stock; (ii) multipliers that propagate and disseminate improved seed to tier (iii) consisting of farmers or growers. The multiplier tier is typical for lower-fecundity species such as salmonids and shrimps but is not prevalent for less-developed sectors and highly fecund marine species. Sometimes, the breeding programs operate as specialized entities, but mostly the breeding activities are integrated within the farming enterprise among activities covering the value chain from reproduction to consumer product, thereby completing the value chain for that company.

Technological development differs greatly between breeding programs, between species, and even within species, and reflects the degree of development of the breeding program. Most aquaculture selective breeding programs start with very simple breeding goals, most commonly increased weight at a certain age. This is the development stage and most present-day breeding programs are at this stage, for example programs for shrimp, some tilapias, and carps. As the production systems mature, they tend to expand and intensify, and the breeding programs expand correspondingly to include more traits, such as disease resistance. A large differentiating factor for the technological development of a breeding program is whether the traits can be recorded on the individual selection candidates themselves, for example, weight of the fish, versus on their siblings. In the case of the latter, sibling/family means are used for traits that are not easily measured on breeding candidates, for example, disease resistance (because of infection risks) or carcass traits such as flesh quality or texture (requires slaughter). A breeding program with the capacity to test for sibling traits is more sustainable, because it can include a larger spectrum of traits, and therefore can take into account genetic correlations between

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TABLE 3 The top fifteen cultured species or species groups (by production volume) and the estimated status of their genetic improvement at a global industry level (expert opinion of the authors). Nei-not elsewhere identified.

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important traits, but it also has higher operating costs. The largest modern aquaculture breeding programs today record up to 20 traits, each with a different weighting within the overall breeding goal.

The use of genomic information in the breeding programme is another differentiating factor and is a means to enhance traditional selective breeding and add value and accuracy to the existing breeding programme (see review by Houston et al., 2020 and Houston et al., 2022). By including individual genomic information in the prediction of genetic values, the accuracy of selection of parents and genetic gain can be increased up to 100%, even for traits that cannot be measured on the breeding candidates themselves.

There are two main ways to include genomic information in the prediction of breeding values:

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- Marker-assisted selection, where genetic markers, that are closely linked to the quantitative trait loci (QTL), are used. Marker-assisted selection assumes that a thorough, sometimes time-consuming and expensive, gene mapping study identifies the genetic markers that should be included in the selection programme (Dekkers & Hospital, 2002). Once identified, only a small number of genetic markers may need to be assayed, which makes it very cost-efficient once the markers have been identified. However, many traits are polygenic and there are only a few examples of marker-assisted selection in aquaculture, given the difficulty of identifying markers linked to the QTL for complex traits. The QTL for resistance to Infectious Pancreatic Necrosis in Atlantic salmon (Houston et al., 2008; Moen et al., 2009) is the most well-known example.
- Genomic selection (Meuwissen et al., 2001) does not assume that the linkage between a marker and a single QTL is known. Instead, it utilizes dense SNPs distributed across the whole genome (put on an SNP array or obtained using genotyping-by-sequencing) to predict genetic values of the selection candidates based on a prediction model developed in a training population. This typically consists of siblings or other relatives of the selection candidates. Genomic selection today is increasingly being applied in well-developed and well-resourced breeding programs, see for example, Zenger et al. (2019) for more details. The genomic selection designs of breeding programs may differ (Nielsen et al., 2009; Sonesson et al, 2009).

Business models, including cost-benefit analysis and financial instruments, are already established for mature commercial aquaculture sectors, but not in the less-mature or less commercialized sectors in both developing and developed countries. Many successful aquaculture breeding programs receive public funding for their initial selective breeding activities (Hallerman et al., 2021). Often the selective breeding activity is integrated with the production activity in the company, although there are also many examples of breeding companies focused on management of broodstock and the commercialization of fertilized eggs or juveniles.

Whereas selective breeding is the basic technique to attain genetic gain over generations, there are related genetic and reproductive methods in use to achieve specific goals. Firstly, hybrid crossing between species, for example, Carassius auratus \times Cyprinus carpio, C. auratus \times Megalobrama amblycephala, Oreochromis niloticus \times O. aureus and Clarias gariepinus \times C. macrocephalus is used to exploit heterosis, also called hybrid vigor and/or to combine specific and commercially important traits of both species. Whilst these breeding programs are technically simple, they do require maintenance of two viable, well-managed and pure breeding populations of the respective species. Also, the genetic gains produced with hybrids are non-cumulative, and therefore need to be repeated at every crossing of parents. An advantage of hybrid crossing is the possibility to protect the intellectual property (IP) of the broodstock of the pure-breeding populations by controlling access to the parental farmed types. Secondly, monosex populations can be produced in some species, for example, of Japanese flounders Paralichthys sp., yellow catfish, and tilapias, because of benefits associated with sexual dimorphism, mainly in growth and sexual maturity; see for example, review Li et al., 2022. Thirdly, certain species, for example, blue mussels (Mytilus edulis), Pacific oysters (Magallana gigas), and salmonids, sterile individuals are produced through ploidy manipulation. Reasons for producing sterile individuals include the investment of production into somatic tissues and not in reproduction, reduced risk of genetic interaction between wild and farmed populations, sometimes for improved product quality, and IP protection of the broodstock. Monosex and triploid production can be applied independently of selective breeding activities, and they do not result in cumulative genetic gains.

Selective breeding is a technology that utilizes the natural genetic variation in each population to select the individuals that will become parents of the next generation, based on their own performance and on the performance of their siblings and other family members. The frequency changes of important gene variants are made relatively slowly over generations and cover the whole genome simultaneously. This approach should not be confused with production of genetically modified organisms (GMOs), where directed changes are made in the DNA of the fish, and the whole lineage could potentially be changed within one generation. Today, the AquaAdvantage[®] Atlantic salmon developed by AquaBounty (www.aquabounty.com) is a well-known example of a transgenic fish, where an additional copy of the growth hormone gene from Pacific Chinook salmon, under the control of a different expressionregulating promoter, was introduced in 2025-16. This fish is on the market in the USA and Canada, the only example of a transgenic animal product available for human consumption.

4.2 | Today's challenges and needs

Today's challenges and needs are to a large extent related to the low uptake of selective breeding by certain aquaculture industry sectors, especially for low-value species, small-scale farming systems, and developing countries/ countries in transition. This low rate of adoption of selective breeding in global aquaculture is a missed opportunity to increase production, efficiency, disease resistance, and product and nutritional quality with the potential to significantly improve the sustainability of aquaculture and increase its contributions to the SDGs and, among other benefits, enhance mitigation of and adaption to climate change.

Financing the selective breeding activity is pivotal, and (Olesen et al., 2015) identified the development of appropriate business models for benefit sharing between the breeding, multiplier and grow-out operators as one out of three key factors for developing improved stocks. Especially for small sectors, the financial needs, and risks can be too big, for an SME for example, to carry alone. For specialized breeding programs, high initial investment costs can include building hatcheries and related facilities and forming a biologically sound base population for the breeding activities. For the breeding programs that are integrated into the production of a company, expansion of facilities is usually needed, for example, to handle broodstock from different age classes. Long-term investments are also needed to manage a more complex infrastructure to support selective breeding activities. These short- and long-term financial commitments provide a challenge for (small) private aquaculture companies to include selective breeding activities in their portfolio. There are many examples of publicly and privately owned breeding programs supported by public financing in the early phases, which ceased when the initial public funding ended (Hallerman et al., 2021) because of poor transition plans.

The difficulty of IP protection of the developed farmed types is a second pivotal constraint for the adoption of selective breeding in aquaculture, which discourages initial investments in new programs (Rosendal et al., 2006). There are currently few legal instruments to protect IP in developed farmed types of aquatic species, as exist for newly bred plant varieties in the form of plant breeders' rights. The most common protection is a statement in the purchasing contract that the genetic material may not be propagated and used for purposes other than as food, which often proves difficult to enforce. However, with the genotyping of all parents in the nucleus with (high-density) genetic markers, it is possible to identify at least the population origin and even individual parent origin if desired using a tracing/tracking scheme through the production chain.¹⁰ Whilst such traceability markers do exist, they are rarely applied for commercial IP protection in the aquaculture sector.

A second option is to sell sterile fish to the market. At present, the main approach to generating sterility in aquaculture species is the production of triploids, and while this is feasible in many aquaculture species, it is not applied at a large scale, because of technological issues, biological challenges such as health and animal welfare issues and/or because of consumer acceptance issues.

Gene editing is a group of genomic techniques that are used to alter the genome of individuals. In many countries, there are discussions in relation to the classification of GMO on whether gene-edited animals should be allowed for human consumption.¹¹ A global map of gene editing regulation can be seen here.¹² Issues under discussion include animal integrity (unknown risk for individual animals related to the technology itself or the effects of the genes that are edited) and environmental impact (e.g., what are the effects on the wild populations if the gene-edited individuals escape and mate with or compete with their wild counterparts and the possible negative impacts of diseased farmed fish on their wild counterparts when using gene-edited disease-resistant fish). Arguments in support of gene editing is that it is unethical to not use the powerful gene-editing technique to improve animal welfare traits or to make sterile fish that can reduce the potential environmental harms of escapes or releases from aquaculture (see Section 2). Another issue is whether the technology itself or its effects should be regulated. For the aquaculture production industries, including breeding, gene-editing technology has a huge potential with the possibility of changing frequencies of important gene variants in a short time, although this is not that feasible for complex traits at the moment, with corresponding effects at the phenotypic level. In addition to legal regulations with which the breeding industry must comply, the acceptance of gene-edited products among consumers is an important prerequisite to consider before adopting this technology on a routine basis in breeding activities and production. Genetic modification is an emotive topic and often elicits strong sentiments which can translate to negative perspectives on other forms of genetic improvement. Given the low production of genetically modified fish and livestock, debate on this issue often detracts from the more urgent and important need to expand and accelerate the application of selective breeding.

Selective breeding is a technology, which requires a high understanding of quantitative genetics and know-how of management of genetic variation, that is, for controlling inbreeding. In integrated companies, the selective breeding activities increase the logistical challenges of fish holding, because (groups of) individual fish must be traceable. Personnel must have the skills to manage and analyze large data sets with thousands of fish and records on many traits. Additional specific skills are needed when including genomics data, for example, for genomic selection or gene mapping. Few companies have in-house competence in quantitative and genomics analysis, and hence hire consultants. Overall, there is a lack of these competencies at the industry level. For almost all species in aquaculture, there are also large knowledge gaps in fields related to selective breeding, such as genomics (gene mapping, available reference genomes, and genetic marker arrays), as well as in reproductive techniques and sex determination. Control of the reproductive cycle is pivotal for the success of selective breeding programs. Although selective breeding techniques are known in general, different species and production systems require their specific adaptation, which is often unexplored.

4.3 | The way forward and key recommendations

Acknowledgment of selective breeding as a fundamental genetic improvement technology and a main driver for a sustainable and productive aquaculture sector and awareness of its benefits needs to be enhanced at global, regional, and national levels. Producers need to be aware of the genetic qualities of the farmed types they buy, policymakers need to set up guidelines that are relevant and accurate for each sector. A major role of private and public funding bodies should be to initiate breeding programs for currently unimproved stocks, being aware of the potential and risks of selective breeding programs, and to secure long-term financing (Hallerman et al., 2021; Olesen et al., 2015). Targeted communication is needed to disseminate the benefits of genetically improved farmed types to these stakeholder groups.

¹¹See (https://sites.google.com/a/vt.edu/animalbiotechresources/2020-online-workshops) for an example of a discussion on gene editing in animals ¹²See https://crispr-gene-editing-regs-tracker.geneticliteracyproject.org/#jet-tabs-control-1403 for a global map of gene editing regulation

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Improved business and innovation plans and financial support are needed. These plans should acknowledge different phases of the development of breeding companies, and transitions from one phase to the next. The breeding programs are mostly initiated because there is a market potential rather than from a "top-down decision" and some are still at a phase where they are being surveyed on their effectiveness, some are at an expanding phase, and some are at an optimization phase. Short- and long-term financing instruments are needed, sometimes in a structure of a public-private partnership (PPP). PPP programs should target effective engagement with the private sector from the beginning with a view to long-term (20-year) sustainability and effective uptake of improved farmed types. Technical support needs to be given to resource managers and policymakers to plan appropriately and facilitate private-sector investments. IP protection plans and devoted regulatory frameworks with appropriate enforcement for AgGR are needed (see also Section 4).

Greater focus needs to be on capacity-building. Personnel educated on quantitative genetics and selective breeding are needed at all levels, for example, farmers, hatchery managers, bioinformatics and data analysists, and policymakers. Although the fundamentals of selective breeding are known for the aquaculture sectors, there is a need to increase the knowledge on how to run long-term breeding programs, using experience from successful existing examples and developing new systems and concepts. The examples should cover the following: the developed and developing parts of the world; different (groups of) species; both specialized and integrated breeding programs; and include basic and more complex programs.

Technology transfer from established breeding programs should be facilitated. It can be seen that established breeding programs generally pass through a number of developmental stages. Future evolution of applied genetic technology should comply with and reflect the needs and requirements relevant to the maturity and economic value of each sector. In addition, infrastructure needs to be built for breeding programs, which usually differ among aquatic species.

Along with the development of selective breeding programs, R&D activities should follow on using and optimizing selective breeding as well as related technologies and methodologies. The R&D plans should be part of the business and innovation plans for each species. Some of this R&D is more fundamental, for example, specific biological knowledge of each species, gene mapping, and gene editing. Some are more applied, for example, defining breeding objectives (that should be aligned with the market demand and farmers' needs) and breeding strategies and uptake of genomics techniques in traditional selective breeding activities.

The number of species and sectors with selective breeding programs needs to increase to utilize the full potential of the genetic diversity in aquaculture species. Obviously, not all of the approximately 700 species used in aquaculture can and should be developed simultaneously, and not all of them have a future as a farmed species and thus many do not warrant investment in selective breeding programs. Important criteria for prioritization of species are as follows: (1) market (current and future size and accessibility); (2) price (product, production cost); (3) biological constraints (poor survival, disease susceptibility, stress tolerance) and; (4) reproductive traits (control, generation interval, sex ratios). A balance needs to be found among efforts on existing and emerging species. While breeding designs with combined selection with large number of families are ideal there are options for lower-cost breeding program designs, acknowledging that these will deliver lower genetic gains. The latter can be integrated into production systems when based on good genetic management with some selection pressure applied. Such breeding programs can be advanced over time to deliver larger genetic gains or to increase the number of traits such as disease resistance and product quality.

5 | ACCESS AND BENEFIT SHARING OF AQUACULTURE GENETIC RESOURCES AND ASSOCIATED TRADITIONAL KNOWLEDGE

5.1 | Current status

Many countries have adopted or are in the process of adopting Access and Benefit Sharing (ABS) measures relevant to aquaculture genetic resources and associated Traditional Knowledge (TK). But there is a large variation in existing ABS measures, and there is a lack of knowledge on how ABS measures and patents affect aquaculture genetic resources R&D, including selective breeding. There is also a lack of information about TK associated with the use of AqGR (Nandeesha et al., 2012) and how ABS measures support or hinder the use and protection of TK relevant to aquaculture activities.

There are several international ABS frameworks that are relevant to aquatic resources. The Convention on Biological Diversity (CBD) and the Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilization to the CBD (NP) apply to genetic resources, including AqGR and TK.¹³ The Draft Agreement under the United Nations Convention on the Law of the Sea on the Conservation and Sustainable Use of Marine Biological Diversity of Areas Beyond National Jurisdiction of March 4, 2023, provides a framework for aquatic (marine) genetic resources from the high seas and the seabed below.¹⁴ These international ABS frameworks target biological resources used for their genetic material potential in R&D, rather than for other attributes, such as using them for consumption as food. The focus of this section is on the access, use, and benefit sharing from the use of AqGR obtained from within national jurisdiction.

The CBD and NP explicitly recognize the sovereign rights of states over their natural resources and the authority of national governments to determine access to and benefit-sharing from the use of genetic resources within their jurisdiction. Parties to the CBD must endeavor to create conditions to facilitate access to genetic resources for environmentally sound uses by other Parties and not impose restrictions that run counter to the objectives of the CBD.¹⁵ Similarly, Parties to the NP shall take measures "as appropriate" and "in accordance with domestic law", with the aim of ensuring that TK is accessed with the prior and informed consent (PIC) or approval and involvement of the communities holding the TK. However, access to genetic resources as well as subsequent applications and commercialization must be fairly and equitably shared with the Party providing such resources and/or the TK holders (CBD articles 1 & 15; NP articles 5,6 &7).

The NP provides that in developing and implementing ABS measures, Parties shall consider the importance of genetic resources for food and agriculture and their special role for food security" (NP article 8(c)). While this does not specifically require special measures or simplified arrangements for aquaculture activities, it does suggest that countries consider ways to accommodate the "special nature of agricultural biodiversity, its distinctive features and problems needing distinctive solutions" (NP, Preamble) in their ABS regimes and tailor ABS measures accordingly. The NP also acknowledges "the potential role of ABS to contribute to the conservation and sustainable use of biological diversity, poverty eradication, and environmental sustainability" (NP, Preamble).

ABS obligations are increasingly relevant for users and providers of AqGR that are globally exchanged for R&D, including selective breeding and other genetic improvement technologies. As has been mentioned above, currently there is a low uptake of selective breeding in aquaculture production. However, the situation is expected to change with the growing importance of aquaculture production and the increasingly important role of genetic improvement in this sector (see Section 3). The need for access to AqGR to breed new farmed types and to promote genetic diversity is particularly acute for aquaculture as a relatively new production sector with increasing relevance for global trade.

A key rationale for introducing international access and benefit-sharing frameworks was to address conflicts arising from the exploitation of genetic resources originating from "mega-diverse" countries (predominantly from the South) by technology-rich countries (predominantly from the North) by providing a system for the fair and equitable sharing of benefits derived from the utilization of the genetic resources. The idea was that benefit-sharing may compensate biodiverse countries for the costs of the conservation of the resources in situ and create an incentive for

¹³As a special agreement, the International Treaty on Plant Genetic Resources for Food and Agriculture applies to plant, including aquatic plant, genetic resources for food and agriculture.

¹⁴The draft agreement is subject to editing, translation and formal adoption of the final translated text. See https://www.un.org/bbnj/

¹⁵The objectives of the CBD, to be pursued in accordance with its relevant provisions, are the conservation of biological diversity, the sustainable use of its components, and the fair and equitable sharing of the benefits arising out of the utilization of genetic resources, including by appropriate access to genetic resources and by appropriate transfer of relevant technologies, taking into account all rights over those resources and to technologies, and by appropriate funding.

them to continue with these conservation efforts (Lawson, 2012). While the current gene flow (meaning the exchange of AqGR between different regions or zones) for aquaculture purposes is primarily North-North (e.g., salmonids, marine finfish temperate species such as seabass and seabream), North-South (e.g., common carp, salmonids) and South-South (e.g., tilapia, shrimp), similar conflicts (as seen in the case of plant genetic resources-Pistorius, 1998; Wallbott, 2014) may arise as R&D and global exchange of AqGR increase along with an increasing commercial interest from the private sector in accessing AqGR from all regions of the world, including South to North (Olesen et al., 2007).

There is a diversity of national ABS measures that implement international obligations but there is little information or guidance available about how these measures apply in practice to AqGR and TK of AqGR. While several countries have opted not to restrict access to genetic resources within their jurisdiction, nor enacted ABS measures to regulate the access and benefit-sharing abroad (and therefore do not require that benefits derived from their or other countries' resources be shared), many other countries have established ABS measures, most of which include in their scope AqGR and associated TK of AqGR (Humphries et al., 2021).

With the entry into force of the NP as recently as 2014, experience with the implementation of ABS laws is still limited and there is little empirical evidence of the positive or negative effects of ABS measures (or their absence) on aquaculture R&D, or on the conservation and sustainable use of AqGR or the aquaculture sector in general (Humphries et al., 2018). There is also little awareness of ABS issues among the variety of AqGR stakeholders, which include small- to large-scale farms, public and private facilities, and subsistence to commercial production facilities (FAO, 2019a; 2019c).

There is a wide variation in the scope of subject matter in national ABS laws, according to domestic and various stakeholder needs¹⁶: wild and/or domesticated resources; native and/or non-native species; resources in situ, ex situ and/or in silico (e.g., digital sequence information) conditions; and resources from private, public and/or communal lands and facilities. Relatively few laws (e.g., Australia's Northern Territory) exclude resources collected for aquaculture under certain circumstances. The scope of TK falling under ABS obligations is also varied under national laws. Many national laws do not define the scope of TK, others confine it to knowledge concerning genetic material uses or biological resources, while others extend obligations to knowledge concerning the aquatic environment and ecosystems more generally.

The activities triggering the requirement for PIC under the NP is access for their "utilization", meaning "to conduct R&D on the genetic and/or biochemical composition of genetic resources, including through the application of biotechnology" (NP, article 2). However, ABS measures vary as to what "access", "utilization" and "R&D" mean in practice.¹⁷ ABS measures are ultimately meant to capture and share monetary and non-monetary benefits derived from the commercialization of products. Some ABS laws, therefore, distinguish between commercial and noncommercial R&D. It is, however, often difficult in practice to distinguish between commercial and non-commercial R&D activities, which may partly explain the variety of ABS measures. Some ABS obligations apply to the "collection" of AqGR, and others apply to their "transfer" and/or export. Some ABS measures require PIC for access to R&D and commercialization relating to genetic resources (e.g., breeding and biotechnology), while fewer measures (perhaps unintentionally) appear to apply more broadly to grow out and/or conservation and taxonomic research. Some laws require PIC only for activities, such as R&D, as of a specific date or the date of collection, while others require PIC for new and continuing uses of previously accessed materials.

The fair and equitable sharing of benefits arising from the utilization of genetic resources, as well as subsequent applications and commercialization, is foremost a matter for the provider and user to agree upon. The NP includes in its Annex a non-exhaustive list of monetary and non-monetary benefits that may inform benefit-sharing negotiations. Benefit users and providers may agree to share include capacity building, technology/information transfer, payments of royalties, and license fees from intellectual property rights.

¹⁷See Humphries et al., 2021 expanding on the examples below.

¹⁶See Humphries et al., 2021 expanding on the examples below.

Whereas for many years, living material was excluded from patentability, patent authorities, and the courts began in the 1980s to increasingly accept patents relating to biotechnological innovations, using DNA sequences, micro-organisms, plants, and animals. Although most of these patents are still granted to patent holders situated in the Northern hemisphere, the material in genetic inventions often has its origin in the Southern hemisphere. ABS aims to strike a balance between the interests of providers/holders and users of genetic resources and associated TK (Esquinas-Alcazar, 2005; Pavoni, 2013). Striking the right balance between users and providers of genetic resources may become increasingly relevant with the consolidation of the aquaculture industry, including for AqGR originating in the South, such as growing external interest in tilapia genetic resources (Joshi et al., 2020; Rosendal et al., 2012). With the increasing interest of the private sector in aquaculture, including aquaculture R&D, patents might play an increasingly important role in this sector.

ABS-patent linkages may nowadays be found in patent laws as well as ABS measures of some countries. Some countries require patent applicants to disclose in their patent applications the country of origin of any material they used while developing their innovation (WIPO, 2020). Such disclosure in patent applications may assist in monitoring the utilization of genetic resources and therefore function as a "checkpoint" for ABS. ABS administrators may then use the information disclosed in patent applications to check compliance of patent applicants with relevant ABS measures. While this potential is there, there are very few countries that have made the relevant changes to their patent legislation, and hence the check-point effect is still small.

5.2 | Today's challenges and needs

There is an urgent need to raise the awareness among all relevant stakeholders of ABS and its potential implications for the future use and exchange of AqGR, including seed supply, breeding, and R&D. Capacity building is needed as a result of the rapidly changing context of actors and their responsibilities in the aquaculture sector (Ponzoni et al., 2010; Ramanna Pathak, 2012). While ABS has generated less conflict between users and providers of AqGR in the past when compared with terrestrial genetic resources, this may be changing with altered structures in the aquaculture sector (Greer and Harvey, 2004, Olesen et al., 2007; Rosendal & Olesen, 2022). The corporate structure in aquaculture is rapidly changing, as evidenced by the privatization of the Norwegian public breeding program for salmon (Rosendal et al., 2013).

There is a need to develop ABS measures that accommodate the distinctive features of AqGR. In 2013, the Commission on Genetic Resources for Food and Agriculture developed *Elements to Facilitate Domestic Implementation of Access and Benefit-Sharing for Different Subsectors of Genetic Resources for Food and Agriculture* (ABS Elements), including AqGR (FAO., 2019c). The ABS Elements aim to assist governments considering developing, adapting, or implementing ABS measures to consider the importance of genetic resources for food and agriculture, including AqGR, their special role for food security, as well as the distinctive features of the different subsectors of genetic resources, while complying, as applicable, with international instruments (FAO, 2019c). The next phase of the work is to explore the effects and impact of ABS implementation on the use and exchange of AqGR (Humphries et al., 2021). Distinctive features of AqGR and TK of AqGR policy- and decision-makers may wish to consider when developing and implementing ABS measures include the following: the degree of incremental improvement of AqGR; the dependency on multiple sources; the interdependence among users and providers (Chiarolla, 2011; Medaglia et al., 2013; Schloen et al., 2011); international gene flow and the traceability of AqGR (FAO, 2019a).

There is a need to understand the effects of ABS measures and patents on aquaculture sectors. This includes a need to systematically collect information on the real or potential positive and negative effects of compliance with national ABS measures and patents on the collection, use, movement, open access (where relevant), and the equitable sharing of benefits from use of AqGR, associated information (e.g., digital sequence information) and TK of AqGR. The collection of this information can start with key aquaculture-producing countries. There is a need to forecast future global movements of aquaculture-farmed types for R&D, including those that incorporate genetic materials

from several countries of origin, for which prior informed consent and MAT may then be required from several countries. There is also a need for systematic studies that determine the origin of the materials in patented genetic resource inventions relevant to aquaculture and to determine their effect on the conservation and sustainable use of AqGR.

5.3 | The way forward and key recommendations

For aquaculture actors, including farmers, businesses, and bioprospectors, building understanding of and capacity for carrying out ABS concerning AqGR and TK of AqGR are key steps for promoting certainty for the use and exchange of materials, information, and knowledge in aquaculture sectors, and equitable benefit-sharing from use of AqGR. Sources of information include the ABS Clearinghouse¹⁸ as well as National Focal Points, which Parties of the Nagoya Protocol must establish, as well as patent offices if they constitute a checkpoint under national law. Various capacity-building initiatives that aim to inform stakeholders as well as policymakers on ABS and patent issues (CBD, 2019; WIPO, 2018) could be expanded and targeted specifically to aquaculture sectors.

Policymakers need to take into account the distinctive characteristics of AqGR and TK of AqGR when developing, adapting, or implementing ABS and other measures. A central normative objective is maintaining affordable access to breeding material given that such access is essential for progress in R&D for food security. Another objective is to share lessons learned from aquaculture-specific benefit-sharing examples. A common concern among all actors involved should therefore be to maintain affordable access to breeding material and promote the sharing of benefits arising from the utilization of AqGR if ABS measures are in place.

Policymakers may wish to take into account the actual gene flows of AqGR and the fact that many AqGR are currently primarily exchanged among countries of the same region or the same hemisphere. For such cases, ABS policymakers could consider regional or special ABS arrangements, that facilitate the exchange of AqGR for R&D within a specific region or group of countries under pre-agreed terms of reference, including those concerning benefit-sharing.

While facilitating access and exchange may be important in regional cases, the facilitation of equitable benefit sharing may be more important in circumstances of access by external corporate users. As the effects and impact of ABS measures on sustainable aquaculture development are still poorly understood, national or local case studies could help to better understand whether and how ABS measures may contribute to: (a) the conservation and sustainable use of AqGR and TK of AqGR in aquaculture; (b) the fair and equitable sharing of benefits from their use with provider countries/communities (e.g., evidence of successful benefit-sharing agreements in aquaculture); (c) poverty eradication (e.g., contribution to aquaculture livelihoods); and (d) food security. Case studies on the impact of patents on the use and exchange of AqGR and TK of AqGR are also essential for the development of aquaculture sectors. However, it should be noted that the effects or impacts on the use, exchange, and R&D of AqGRs are usually caused by a multiplicity of factors, and it will often be difficult to identify with any degree of accuracy the proportional impact of an ABS measure as opposed to other factors, including the availability of research funds, adequate infrastructure, qualified workforce, and incentives.

6 | CONCLUSION

The conservation status of wild relatives of farmed AqGR is threatened for some species, but there is an overall lack of information on the genetic status of most wild relative stocks. For most cultured aquatic species there is a similar lack of information on their genetic status, particularly below the level of species (i.e. farmed types). This lack of AQUACULTUR

information constrains the implementation of effective conservation and genetic management for their long-term sustainable use. To enhance understanding of the genetic status of key farmed types and plan necessary interventions to conserve genetic variation for the future, there is a need to identify key threatened genetic resources, with a focus on wild relatives, and to develop information systems that will enhance the monitoring of farmed types and the identification of threatened wild relative genetic resources. Based on this identification, specific *in situ* and/or *ex situ* conservation programmes should be developed. With regard to the sustainable use of AqGR in aquaculture, cost effective molecular tools to enable widespread monitoring of the genetic status of domesticated farmed types should be developed and applied within major seed supply systems, enabling targeted interventions to secure the future potential for development and conservation of these resources.

Culture of non-native species and well-developed farmed types delivers economic benefit to aquaculture and underpins significant aquaculture production in many countries, but also can pose environmental/ecological risks to natural ecosystems and genetic risks to native AqGR, including conspecifics. There is a need to apply existing frame-works to assess, communicate and manage risks of the culture of non-native species and developed farmed types, and also to assess the possibilities of expanded culture of native species. Responsible stakeholders in member countries should develop and apply policies and provide training to promote utilization of the risk assessment framework to the culture of non-native and developed farmed types of native species to promote sustainability of their aquaculture sector.

Selective breeding is a proven and powerful tool to increase production efficiency, product quality and disease resistance, among other traits, and has the potential to deliver large and long-term benefits for the aquaculture industry. The principles of selective breeding are well established and transferrable with adaptation to the reproductive specificities and production systems of any species. There is a low uptake of selective breeding in global aquaculture, and it is evident that the potential of selective breeding is heavily underutilised. To increase the uptake of selective breeding in domesticated farmed types, especially for incipient farming systems and aquaculture activities producing low-value species in both developing and developed countries, it is necessary to develop applicable business plans, with appropriate timelines and long-term financial support instruments. Strategies for developing successful long-term selective breeding programmes must be implemented, including partnerships between public and private players, to execute the breeding programmes and should include plans to effectively disseminate the selectively bred material, including cost recovery approaches. These strategies should be supported by education and raised awareness of the costs, risks and benefits of long-term selective breeding and related techniques among aquaculture producers and other stakeholders.

There is a need to ensure access to AqGR for research and development as well as to share the benefits arising from the utilisation of these resources. Countries that decide to adopt ABS measures need to be aware of the distinctive features of AqGR. Many countries have adopted or are in the process of adopting ABS measures relevant to AqGR and associated traditional knowledge. However, there is large variation in existing ABS measures, and there is a lack of knowledge on how ABS measures and patents affect AqGR research and development, including in selective breeding. The awareness and understanding of stakeholders of ABS and patents and their capacity to operate within this legal environment at national, regional and global levels need to be improved. A way forward includes building capacity among relevant stakeholders concerning how to accommodate the distinctive features of aquaculture AqGR and associated traditional knowledge subject matter and activities, when developing, implementing and reviewing national ABS measures.

Overall, AqGR in aquaculture retains much of the genetic variation present in wild stocks due to the availability of wild counterparts and because most aquaculture industries are still relatively young. This situation creates both responsibility and opportunity. Effective action now can ensure conservation and sustainable use of genetic resources into the future and can target the effective development of farmed types, primarily through selective breeding, that will significantly enhance production efficiency in aquaculture. It is beholden on the aquaculture community to develop and implement effective strategies, risk and policy management and long-term solutions for the conservation, sustainable use and development of AqGR into the future.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

DISCLAIMER

The views expressed in this publication are those of the author(s) and do not necessarily reflect the views or policies of the Food and Agriculture Organization of the United Nations.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the authors upon reasonable request.

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