







States of development and application of genetic and genomic tools in aquaculture and conservation programs: a guide for strengthening dialogue among practitioners of aquaculture and genetics

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Abstract – Throughout all stages of fish conservation and aquaculture development, genetic and genomic approaches can be leveraged to enhance understanding of the diversity and complexity of these organisms, including the linkage between phenotype and genotype, and their adaptive and breeding potential. These approaches can inform processes ranging from the initial collection of wild broodstock to the ongoing use of genomic selection on domesticated lines. Due to the diversity in cultured fish species, small and medium enterprises (SMEs) commonly explore new species for culture, or work with species within a narrow regional conservation or commercial focus. These enterprises face obstacles in utilising genetic and genomic approaches due to development and implementation costs, specialised skill set requirements, and infrastructure and labour limitations; yet the benefits often outweigh these challenges. Choosing the best molecular genetic or genomic tools depends on programme goals and species, but small and medium enterprises may miss opportunities to acquire more information through their current approaches, or not realise what may be gained through modest investments in genomic tools. To provide better insight and promote discussion and collaboration between culturists and genomic practitioners, we define and describe five States of development and application of genetic and genomic tools frequently observed in aquaculture and conservation breeding programs. We characterise these tools, their general applications, and how current technologies allow programs to advance to higher States without following a sequential progression, a concept we refer to as “State skipping”. This document outlines the available molecular genetic and genomic tools, but does not cover animal breeding or the science behind it. Similarly, bioeconomic models are not included, although relative economic costs and benefits are highlighted. The technical considerations and limitations of various approaches are reviewed, along with available resources for those seeking further support in exploring genetic and genomic tools in breeding programmes.

Keywords: Breeding programs / genetic and genomic approaches / technical considerations / selection / broodstock / small and medium enterprise

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1 Introduction

Plant and animal agriculture have been shaped by domestication and directional selection for traits deemed beneficial to humans, dating back at least 13000 years (Diamond, 2002). While many aquaculture species have undergone selection, domestication of aquatic species began much more recently than in terrestrial plants and animals, with the earliest domestication of fish species occurring within the past 2000 years (i.e., the common carp, *Cyprinus carpio*, in south central Europe by the Romans) to 1000 years (i.e., the goldfish, *Carassius auratus*, in China; Balon, 2004). Selection methods have evolved from the initial unintentional selection associated with domestication, to phenotypic mass selection, family selection, marker-assisted selection, and now genomic selection (see Boudry et al. (2021) for a review). The adoption in animal and plant breeding of molecular genetic analysis, which we define as the genotyping of a small number of markers to assess variation in individuals or populations, quantify trait heredity, and link markers to specific traits or genes. This contrasts with molecular genomic analysis, which involves genotyping of thousands or more markers to describe genome structure, and explore the interactions of genetic elements and their functions across the genome and their relationship to traits or processes of interest. Genomic approaches have demonstrated objective, quantifiable benefits, both in general (Rexroad et al., 2019) and specifically in aquaculture (Houston et al., 2020). In this paper, we focus on the description of molecular genetic and genomic tools and analyses and their use in providing information on the genetic architecture underlying traits. The adoption of such tools enables an understanding of the composition, diversity, and adaptive and selective potential of a population or strain, as well as a linkage of genetic regions, pathways, and ultimately single genes or variants to traits of interest.

As such, the adoption of genetic and genomic tools is important at all stages of aquaculture development. This can range from descriptions of candidate species and populations, to the initial collection of broodstock, or source material collected annually from the wild, through fully domesticated broodstocks which may be exposed to selective breeding using the most sophisticated genomic selection methods (Fig. 1). Genetic and genomic tools have been successfully used in aquaculture in a number of different settings, including to assist in selection for: disease resistance (Fuji et al., 2007; Moen et al., 2009; Houston et al., 2010; Yáñez et al., 2022; AquaGen's innOva BCWD selected stock (<https://aquagen.no>)), delayed maturation (Kause et al., 2003; Moghadam et al., 2007), growth rate (Palaiokostas et al., 2013; Tsai et al., 2015; Wang et al., 2017; Garcia et al., 2018; Gutierrez et al., 2018; Yoshida et al., 2018; Yoshida et al., 2019; Joshi et al., 2020; Vu et al., 2021; Wang et al., 2021; Gong et al., 2022; Jerry et al., 2022; Ke et al., 2022; Verbyla et al., 2022), feed conversion efficiency (Besson et al., 2019; Barria et al., 2021; Besson et al., 2022), external appearance (Kause et al., 2004; Colihueque, 2010; Colihueque and Araneda, 2014), product traits, including flesh quality (Quinton et al., 2005; Kause et al., 2011; Nguyen, 2016), and survival (Vehviläinen et al., 2008; Vehviläinen et al., 2010; Vehviläinen et al., 2012).

While initial selection in a species for a few commercially most important traits typically shows large effect (e.g., Neira et al., 2006; Gjedrem et al., 2012), achieving desired results is more difficult for multi-trait selection, and especially when those traits have unfavorable genetic correlations. Moreover, where heritability is on the lower end of the useful heritability spectrum, genomic selection (Meuwissen et al., 2001) can result in greater genetic gain because the accuracy of predicted genetic values increases proportionally higher than for more heritable traits (Rexroad et al., 2019). It is for these traits with low heritability, and also in traits that require lethal measurements from sibs (e.g., disease resistance, carcass traits), where understanding and then applying the tools to target the genetic and genomic architecture of a species or breeding population (i.e., DNA-informed breeding; Peace, 2017) may lead to substantial improvements in the breeding outcome and thus economic benefit (Rexroad et al., 2019).

The genetic and genomic tools developed for commercial aquaculture species can also be used in any breeding effort targeting restocking and conservation (Casey et al., 2016; Waples et al., 2020; Wenne, 2023). For example, in modern conservation programs, genetic and genomic tools are utilised to support the sustainable reproduction of endangered species or populations. In this context, the applications of these tools include defining populations of interest, documenting genetic and genomic characteristics, assisting in the determination and tracking of pedigrees, and monitoring changes in genetic characteristics over generations (e.g., DFO, 2018).

Here, we consider small and medium enterprises (SMEs) to be programs of smaller scale, or independent operations, without pooled investment, coordinated research, or genomic resource development. This scenario is common in species whose suitability for culture is being explored, those who have not been in culture long, species of regional conservation concern, or whose distribution or culture is regionally restricted. It also may apply to more established species in which, despite the existence of genetic and/or genomic tools and information, groups must develop their own resources due to proprietary restrictions, such as when genomic resources are developed by a competitor who may not wish to make the data available. Across all scenarios, the development and application of genomic tools will require financial resources and expert personnel for their development and implementation, as well as infrastructure in which to carry out a breeding programme.

There are many possible obstacles to the adoption of these genetic and genomic approaches, particularly for SMEs with inherently limited infrastructure and research budgets focusing on aquaculture and conservation programmes. These obstacles include the cost of development and implementation of genetic technologies, the availability of specific genetic tools for the species being raised, and the specialised knowledge or expertise required to undertake laboratory, bioinformatics, and analytical work. However, without a shared understanding of the available tools and the overall complexity of their applications, it becomes challenging for SMEs to initiate the necessary internal dialogue with genetic and genomic practitioners to determine their best course of action.

and conservation breeding programs. For each State, we characterise the tools used, as well as the types of applications that may be common to that State for smaller-scale commercial aquaculture and conservation-focused programs (summarised in Fig. 2). Where possible, examples are highlighted for both commercial and conservation programs (Tab. 1). The term “State” is purposefully chosen to remove connotations or implications that a program should or must advance from one State to the next; a program may find that the tools and data available at a given State may be adequate for their needs and thus remain at that particular State. In addition, current technologies make it much easier for programs to transition directly to higher States and this is discussed in its own section below.

2.1 State 0: No previously developed DNA markers or genomic information

This State refers to species lacking any developed genetic tools or genomic resources (e.g., sequence variants, linkage maps, etc.), either for evaluating wild populations or characterising cultured programs. Programs at this State may collect and rear wild-caught individuals in cages or tanks until they reach market size, or may be in the initial stages of determining whether a species, either for commercial or conservation purposes, is amenable to culture. While many species of interest have now been subjected to study with DNA markers, triptail (*Lobotes surinamensis*), serves as an example of a candidate aquaculture species in this State. This fish is of interest for culture in the U.S.A., and wild broodstock have been collected to identify and optimise spawning techniques for the development of commercial culture (Saillant et al., 2021). To date, there are no genetic resources available for triptail, and no genetic studies have been conducted on this species other than DNA barcoding using a universal mitochondrial marker (i.e. not species-specific) approach (Sirisha et al., 2018). If a culture programme seeks to apply genetic methods for this species, then markers will need to be developed *de novo*.

For species in State 0, the development of genetic and genomic tools has become considerably easier, owing to advancements in techniques that now make *de novo* genetic resource development relatively straightforward. This document focuses on examples of these different types of tools and their applications, rather than focusing on the development process itself.

The development of microsatellite markers, and their application to aquaculture was reviewed by Chistiakov et al. (2006); since that time, methods to identify microsatellites and SNPs have advanced considerably. Reduced representation sequencing (e.g., RADseq, and others) has been used to discover SNPs (single nucleotide polymorphisms) (e.g., Bootsma et al., 2020; Chang et al., 2021), microsatellites (e.g., Liu et al., 2021), and haplotypes (e.g., Baetscher et al., 2018; Euclide et al., 2022), across the genome without a reference genome. However, when available, high-quality whole-genome assemblies allow for identification of SNPs and microsatellites using *in silico* methods (e.g., Marcy-Quay et al., 2023).

When deciding on the type of genetic or genomic marker development to pursue, programmes or species in State 0 should take into account both future objectives and the potential opportunity costs of limiting the number of DNA markers produced, as well as the versatility of the selected molecular tools. Therefore, even for programs that do not anticipate progressing beyond State 2, specifically, individual genetic tagging, we generally recommend developing an annotated reference genome, if feasible. This is due to the advantages it provides including relatively simple development of goal-specific molecular marker panels, as well as serving as the foundation for future efforts such as initiating marker assisted breeding and linking traits and markers to putatively causative genes (e.g., Kess et al., 2019; Kess et al., 2021; Holborn et al., 2022; Lehnert et al., 2023). Leveraging genome information will be discussed in more detail in the section on “State skipping”.

2.2 State 1: Leveraging of population genetic or genomic information

Once a candidate species for aquaculture or conservation has been identified, local regulations generally require permits or licenses for both collection of aquatic organisms from the wild, as well as the aquaculture operations themselves. In many cases, the issuance of collection permits will be contingent upon the applicant demonstrating that the collection will not result in harm to the populations or species. Part of this process may involve the delineation of population structure and determination of effective population sizes (N_e). The delineation of population structure can be accomplished using population genetics or genomics, and this is often the first opportunity to develop and employ genetic or genomic tools and collect genetic information for the species. This information can then be utilised in other States and stages of aquaculture program development.

There are myriad examples of population genetic and genomic studies in aquatic organisms. First based on allozymes, most studies now rely on microsatellite or single nucleotide polymorphisms (SNPs) as markers (see notably Wenne, 2023 for a review about the applications of SNPs in conservation and exploitation of aquatic populations). Whatever the choice of marker, the goal is typically to define population units, determine degree of differentiation between them (e.g., O’Reilly, 2006; Lehnert et al., 2023), and when collection and incorporation into an aquaculture or conservation breeding program is the goal, determine the genetic or genomic diversity within the collection (O’Reilly and Harvie, 2010).

The choice of marker type, the degree of population divergence, and the number of markers used in a study can influence the degree of genetic differentiation that is detectable. While studies historically relied on a handful of markers, advancements in genotyping technologies have made panels of tens to hundreds of microsatellites (e.g., Bradbury et al., 2018) or hundreds to thousands of SNP markers the norm (e.g., Jeffery et al., 2018).

Lehnert et al. (2023) used a weight-of-evidence approach and a combination of genetic and genomic data to identify

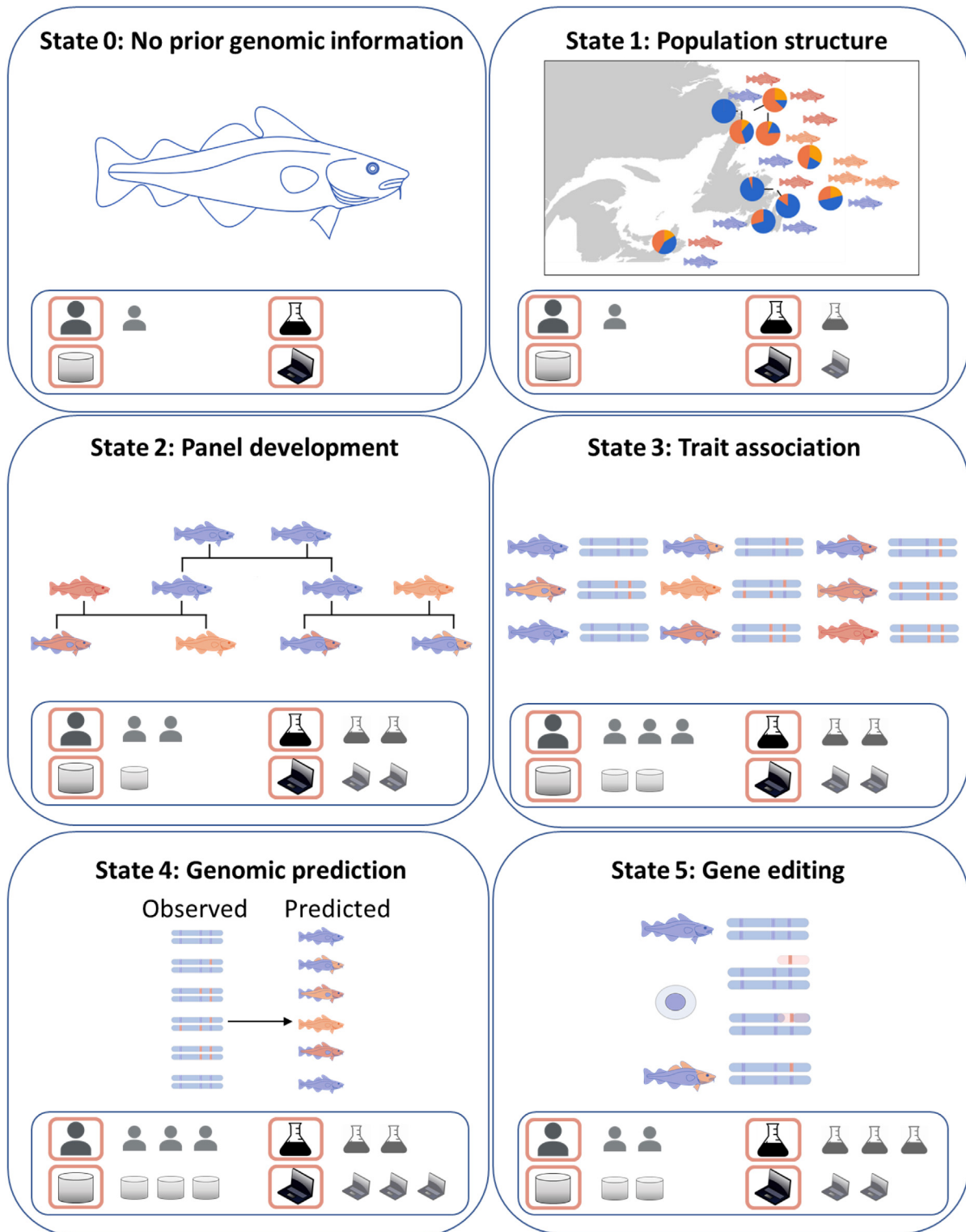


Fig. 2. The six large panels represent the States of development, the application of genetic and genomic tools, and broad research categories associated with each State. Inset are the relative levels (low, medium, or high – depicted by one, two, or three icons, respectively) of resource investment likely required to address research at each State: sampling or phenotyping labour, breeding program infrastructure (e.g., tanks, labour), genetic or genomic laboratory support (e.g., equipment and specialised labour), and bioinformatic support (e.g., computational and bioinformatics labour). While the requirements for each of these categories of resources may vary widely across different programs at each of the States, the relative levels are intended to depict a minimum level of resource investment that new adopters could expect with research or operations conducted at each of these States.

Table 1. States, and state skipping, describing the development and application of genetic and genomic tools in aquaculture and conservation breeding programs, with selected examples under each category as available.

State	Description of state	Applications / categories of research questions	Tools	Examples commercial aquaculture	Examples conservation aquaculture
State 0	No previously developed DNA markers or genomic information	No genetic resources exist for this species for wild or cultured programs; markers may be available in related species, or through the use of universal primers.	No species-specific tools are available to utilise for genetic / genomic projects. Newer technologies make it easier to develop these tools <i>de novo</i> .	Tripletail (<i>Lobotes surinamensis</i>) (Saillant et al., 2021); golden Shiner (<i>Notemigonus crysoleucas</i>) (Stone et al., 2016)	Dwarf oysters (<i>Ostrea stentina</i> species complex) (Prado et al., 2022)
State 1	Stock choice, use of population genetic or genomic information	Characterise the population(s) or the species of interest (e.g., determination of effective population sizes, population genetic structure, degree of differentiation, genetic diversity).	Allozymes, Sanger sequencing of small sections of nuclear or mitochondrial regions, microsatellites, SNPs	Lumpfish (<i>Cyclopterus lumpus</i>) (Jansson et al., 2023); Atlantic salmon (<i>Salmo salar</i>) (Gjedrem et al., 1991)	Atlantic salmon (Bradbury et al., 2018; Lehnert et al., 2023); Atlantic whitefish (<i>Coregonus huntsmani</i>) (Murray, 2005); eastern sand darter (<i>Ammocrypta pellucida</i>) (Ginson et al., 2015); reidside dace (<i>Clinostomus elongatus</i>) (Serrao et al., 2018)
State 2	Individual genetic tagging	Individual identification, parentage and pedigree analyses, trace the individual back to their breeding program, or origin, diversity estimates compared to wild populations.	Microsatellites, SNPs, Sanger sequencing of small sections of nuclear or mitochondrial regions, RAD-Seq, low-coverage genome sequencing	California yellowtail (<i>Seriola dorsalis</i>) (Schmidt et al., 2021); Atlantic halibut (<i>Hippoglossus hippoglossus</i>) (Jackson et al., 2003)	white abalone (<i>Haliotis sorenseni</i> ; C. Purcell, pers. inform.); Atlantic salmon (<i>S. salar</i>) (Karlsson et al., 2016; DFO, 2018); rainbow trout (<i>Oncorhynchus mykiss</i>) (Steele et al., 2013); Delta smelt (<i>Hypomesus transpacificus</i>) (Lew et al., 2015)
State 3	Linking phenotypes/traits and genotypes	Link genotypes to phenotypes for simple traits (Mendelian inheritance) or for genes (and markers) of major effect; implement marker-assisted selection to guide broodstock development or to improve traits.	Genotyping-by-sequencing approaches (e.g., RADSeq, ddRADSeq, WGS); screening using SNPs, PCR, microsatellites.	Atlantic salmon (<i>S. salar</i>) (Houston et al., 2012); rainbow trout (<i>O. mykiss</i>) (Wringe et al., 2010); Atlantic halibut (<i>H. hippoglossus</i>) (Palaikostas et al., 2013)	Chinook salmon (<i>O. tshawytscha</i>) (Waters et al., 2018); Coho salmon* (<i>O. kisutch</i>) (Horn et al., 2020)
State 4	Genomic selection and/or genomic imputation and	Implement genomic selection, utilising family- or	SNP arrays, genomic resequencing (e.g., GenCove	Atlantic salmon (<i>S. salar</i>) (Kijas et al., 2017); rainbow	

Table 1. (continued).

State	Description of state	Applications / categories of research questions	Tools	Examples commercial aquaculture	Examples conservation aquaculture
	prediction using family- or pedigree-based selection.	pedigree-based selection for complex polygenic traits, typically requiring breeding programs and/or genomic selection/imputation to improve trait outcomes.	– use resequencing for genome imputation and prediction instead of developing SNP panel)	trout (<i>O. mykiss</i>) (Vallejo et al., 2017); Pacific oyster (<i>Crassostrea gigas</i>) (Jourdan et al., 2023)	
State 5	Gene editing	Utilise gene editing to precisely modify genes already present in the organism (or from another organism – transgenic), to inactivate genes/genetic sequences or to add genetic material at specific locations of the genome.	Zinc fingers, TALENs, CRISPR-Cas	Siamese fighting fish (<i>Betta splendens</i>) (DFO, 2021); tiger barb (<i>Puntigrus tetrazona</i>) (Dietrich et al., 2022); Atlantic salmon (<i>S. salar</i>) (Du et al., 1992)	
State skipping	Beginning research at any State relevant to the needs of the breeding program.	Develop genomic resources with broad applicability (e.g., such as reference genomes) that will allow for the development of tools tailored to pressing research questions or breeding program applications.	Varied tools, but frequently <i>de novo</i> development of a high-quality reference genome.	New Zealand trevally (<i>Pseudocaranx georgianus</i>) (Catanach et al., 2021; Valenza-Troubat et al., 2022; Valenza-Troubat et al., 2022); Australasian snapper (<i>Chrysophrys auratus</i>) (Ashton et al., 2019; Sandoval-Castillo et al., 2022)	Barrens topminnow (<i>Fundulus julisia</i>) (Hurt and Harman, 2017)

* Selective breeding in this species for conservation purposes is not occurring, but has been suggested as a mechanism to benefit the population.

previously unresolved landscape-scale genetic distinction in Atlantic salmon (*Salmo salar*). Similarly, using a panel of 101 genome-wide microsatellites, Bradbury et al. (2018) resolved 26 predominantly river-level Atlantic salmon genetic reporting groups across approximately three degrees of latitude in Labrador, Canada, where previous analyses using smaller numbers of SNPs were only able to detect three groups in the same area (Jeffery et al., 2018).

Another example is seen in population genetic studies of lumpfish (*Cyclopterus lumpus*), a species where both wild-caught translocated and domesticated individuals are used in the aquaculture industry for biological control of sea lice. A study based upon 14 microsatellites indicated that interbreeding between wild and aquaculture escapes would have little impact on the genetic composition of the wild stocks in Norway (Jónsdóttir et al., 2018), while more recent genomic analyses across the Atlantic have revealed fine-scale population structure and temperature adaptation, with the risk of breakdown of local adaptation if introgressed by aquaculture escapees (Jansson et al., 2023; Langille et al., 2023).

Within conservation programs, a common goal is the maintenance of existing genetic characteristics of the species or populations of concern. This generally entails undertaking a population genetic or genomic study to determine metrics such as genetic or allelic diversity, levels of heterozygosity, and effective population size. Theoretical linkages can then be made to predict the risk to the species or population of genetic impact from inbreeding and drift over time, among other concerns (e.g., O'Reilly and Harvie, 2010). In conservation scenarios where focal population(s) has(have) been extirpated and reintroduction is desired, it is generally recommended to identify and use source populations that are genetically – and presumably adaptively – similar. These can be identified by screening nearby existing populations and, if they exist, comparing them to focal population samples (e.g., Anderson et al., 2014). An associated approach, genetic rescue, may be used for populations where reductions in genetic diversity are reducing the fitness and resilience of the population. In this scenario, individuals are intentionally translocated into the imperiled population to restore genetic variation and adaptive potential (Kovach et al., 2022). While difficult to predict, the outcome of genetic rescue may rely in part on the effective population sizes of the recipient and donor populations and their genetic divergence, metrics which can be measured using population genetics (Wells et al., 2019).

2.3 State 2: Individual genetic tagging

One of the most immediately informative genetic approaches to utilise for a breeding program is individual genetic tagging. Individual genetic tagging refers to the use of DNA markers to unambiguously identify an individual, link an individual to genetic information pertaining to family relationships (e.g., parentage and pedigree analyses) (Vandeputte and Haffray, 2014; Liu et al., 2016; Holman et al., 2017; Weng et al., 2021), and/or to trace the individual back to their breeding program, or origin (e.g., farmed versus wild, and/or location) (Norris et al., 2000; Chistiakov et al., 2006). Within selective breeding programs, this can allow (previously collected) phenotypic data to be linked to an individual, or

to their relatives, through parental assignment and pedigree reconstruction. This can enable higher resolution tracking of phenotypic heritability and inheritance through breeding lines, as well as management of ancestry and inbreeding within conservation programs (Holborn et al., 2025). Detection of linkages between DNA markers and genomic regions is discussed in more detail in States 3, 4 and 5 below.

Both parental assignment and pedigree reconstruction can be used to manage the level of inbreeding and genetic diversity in both commercial and conservation breeding programs across generations (Meuwissen and Sonesson, 2004; Vandeputte and Haffray, 2014; Wellmann et al., 2014; Gebregiwergis et al., 2020; Gautason et al., 2022). Given the importance of genetic diversity in maintaining the adaptive capacity of populations to respond to novel challenges in the environment (Tringali and Bert, 1998), in providing the variation upon which long-term selection goals in breeding programs rely on (D'Ambrosio et al., 2019), and in avoiding detrimental impacts due to inbreeding associated with a loss of genetic diversity (Kincaid, 1976), mitigating the loss of genetic diversity in breeding programs is a high priority.

Where pedigree data do not exist, genetic kinship data available across generations can be used for parental assignment (Lacy, 2012) and pedigree reconstruction (Mendes et al., 2022). Parental assignment or pedigree data can be helpful in exploring spawning dynamics and assessing individual spawning success for naturally spawning species in culture settings (Herlin et al., 2007; Herlin et al., 2008; Horreo et al., 2008). These analyses may also assist in tracing physical traits (due to genetic or non-genetic factors) back to individual broodstock. This type of application can be immensely helpful to rapidly inform breeding designs and culturing approaches.

In the California yellowtail (*Seriola dorsalis*), for example, parentage analyses using a small number of microsatellites (developed for other *Seriola* species) revealed that only one, or occasionally two, female broodfish contributed to individual spawning events and dominated spawning seasons regardless of female abundance in the tank (Schmidt et al., 2021). This discovery informed experimental approaches which used smaller breeding groups spread among an increased number of smaller spawning tanks. Parental assignment was also used to identify females contributing low-quality eggs, which informed decisions to bring in additional broodstock.

In the White Abalone (*Haliotis sorenseni*) Recovery Program (a collaborative effort with the University of California, Davis, NOAA Fisheries Southwest Fisheries Science Center, and other partners), parentage and pedigree analyses, using microsatellite markers, informed crosses of gametes for the captive breeding program to maximise genetic diversity in this endangered species. As demonstrated above, determination of broodstock breeding dynamics and quantification of the extent of unequal reproductive success can help guide targeted mitigations that include modifications to spawning groups, alterations of breeding tank designs, replenishment or rotation of broodstock individuals or populations, and help determine whether other approaches such as artificial fertilization or cryopreservation are needed.

Supplementation or conservation program effectiveness may also be evaluated using genetic marking and pedigree reconstruction (Araki et al., 2007; Horn et al., 2023). In order

for a conservation program to be successful, the individuals removed from the wild population to be bred in captivity must produce at least as many adult offspring as they would have had they been left to reproduce in the wild. Whether the program meets this objective can be evaluated by genotyping the parents in captivity and subsequently sampling and genotyping the next generation of adults and conducting genetic parentage assignments. This methodology may also reveal if the parents in captivity contribute to the next generation to such an extent that it ultimately reduces the effective population size and thus the genetic variation in wild populations (Ryman and Laikre, 1991).

For supplementation programs, providing harvest opportunities may also be among the objectives. Such is the case for Canada's West Coast Salmonid Enhancement Program, which includes among its goals both rebuilding vulnerable populations and providing harvest opportunities. The Salmonid Enhancement Program uses parentage-based tagging to track fish captured in the fishery back to their hatchery (and thus population) of origin. While technically not a breeding goal, genetic tagging can also be used for product traceability in production systems, and traceability to the producer or cage facility is a legal requirement for aquaculture in some jurisdictions (Håstein et al., 2001; Espiñeira and Vieites, 2016; Holman et al., 2017).

From a conservation perspective, the goals of captive breeding are avoiding loss of genetic variability and inbreeding, and avoiding genetic drift and accidental selection, while other program-specific targets such as retention of rare alleles or maintenance of a target effective population size may also exist (Rollinson et al., 2014; Waters et al., 2015; Attard et al., 2016; Marshall et al., 2022). Additionally, it is important to monitor both the genetic character of reintroduced populations, and the effect of those reintroduced individuals on the genetic character of the wild remnants of the species/population (Russello and Amato, 2004; Christie et al., 2012; Christie et al., 2013; Waters et al., 2015; Waters et al., 2016; Waters et al., 2018; Auld et al., 2021; Hagen et al., 2021; Marshall et al., 2022), particularly to avoid the Ryman–Laikre effect (Ryman and Laikre, 1991), where hatchery fish increase the number of spawning individuals while simultaneously decreasing the effective population size (Morvezen et al., 2016).

As an example, genetic approaches are used to determine the origin of Norwegian Atlantic salmon. Due to declines in natural populations, Atlantic salmon is being stocked for conservation purposes in multiple areas of their natural range. Genetic screening of wild-caught broodstock can be an effective tool for improving the accuracy of such programs. From a 7000 SNP array, a set of 59 SNPs have been identified with the purpose of separating Norwegian Atlantic salmon individuals of farmed vs. wild origin (Karlsson et al., 2011; Karlsson et al., 2014). Introgression of farmed salmon has been documented throughout Norway (Karlsson et al., 2016), leading not only to genetic but also phenotypic and phenological alterations in introgressed individuals (Bolstad et al., 2017; Bolstad et al., 2021; Besnier et al., 2022). It has also been documented that farmed ancestry has been unintentionally selected for in the supplementary stocking of Atlantic salmon (Hagen et al., 2019). As a result, genetic screening for introgressed individuals in broodstocks used for conservation breeding is now a routine practice in Norway.

As demonstrated in the examples above, it is still possible to use genetic tools such as microsatellites or sets of SNP markers for the applications described under this State. However, some breeding goals may benefit from the adoption of genomic technologies due to the higher potential for precision they have for estimating population parameters (Supple and Shapiro, 2018). In this State, the analytical and bioinformatic support required for these applications is not extensive, but will depend on the scale of the undertaking and the types of analyses required for the desired project.

2.4 State 3: Linkages between phenotypes and genotypes

In State 3, genotyping is used to establish associations between DNA markers and phenotypes, and these linkages are used to inform the breeding process or other aspects of the program. Implementation or description of breeding programs is beyond the scope of this paper. The focus in this State is on targeting simple traits with Mendelian inheritance or phenotypes associated with genes — and their associated DNA markers — of major effect, whereas polygenic associations and genomic imputation are discussed in State 4.

Approaches to developing linkages to phenotypes include Quantitative Trait Loci (QTL) analysis and Genome-Wide Association Studies (GWAS). QTL analysis identifies genetic DNA markers associated with the traits, primarily within pedigree studies. On the other hand, GWAS, a more recent evolution of QTL analysis, identifies QTLs using population-scale sequencing and maps phenotypes to genotypes. While linkage maps may be produced through various forms of reduced representation sequencing to obtain markers across the genome, a reference genome may also be used for this purpose. Developments of linkage associations at this level allows programs to use marker assisted selection (MAS) to identify and screen individuals at target loci associated with traits of interest. Marker assisted selection and/or application of genetic screening for these traits offers a rapid approach to make improvements in the breeding program or inform breeding decisions (Meuwissen et al., 2001).

Widespread examples exist of the use of genomic information described in State 3 in culture or study of aquatic organisms, but frequent applications include identification of genetic sex (Einfeldt et al., 2021; Holborn et al., 2022), improvements in disease resistance (Holborn et al., 2019; Holborn et al., 2020), and determining the degree of introgression by aquaculture escapees in fish destined for breeding programs (Liu et al., 2017; Bradbury et al., 2022). For example, the reference genome developed for California yellowtail (*Seriola dorsalis*) was used in conjunction with a GWAS on resequenced (i.e. low-coverage whole-genome sequencing) sexed individuals to identify a genomic region associated with sex (Purcell et al., 2018). This approach identified both a genomic region significantly associated with sex, but also an insertion/deletion within that region. PCR primers spanning this region were used to amplify and visualise fragments on an agarose gel, enabling sex identification in brood and offspring fish based on the banding pattern (e.g. presence or absence, with positive control). This

method has become a valuable tool for a species lacking external sexual dimorphism (Purcell et al., 2018).

At the NOAA Fisheries, Southwest Fisheries Science Center, in collaboration with Iowa State University, a similar approach is currently underway for the endangered white abalone (*Haliotis sorenseni*) to enhance the breeding programme. A recently assembled chromosomal-scale reference genome for this species is being used to inform a GWAS using genotyping-by-sequencing (GBS) data from sexed white abalone specimens. One highly significant genomic region associated with phenotypic sex has been identified, and genetic variants are currently being assessed and screened (as of manuscript preparation) to determine if a sex-specific marker may be developed. The development of a sex-specific marker for this species would be tremendously important to the breeding programme, as it would allow for the identification of potential broodstock without the need for extensive handling of wild abalone to determine sex. A simple swab sample followed by genotyping would be an effective method for these animals with relatively limited dispersal. Additionally, this marker could support outplanting efforts by ensuring mixed-sex groups of juvenile white abalone or facilitating the matching of known-sex individuals with wild populations in the region.

In Atlantic salmon, outbreaks of infectious pancreatic necrosis virus (IPNV) were a major concern to the aquaculture industry. Research groups identified a single major QTL that explained 80 to 100% of genetic variation in resistance to IPNV. Marker assisted selection, utilising a SNP-based genetic screening for the favorable, resistant, and dominant allele, was rapidly adopted by salmon breeding programs to help prevent further outbreaks of this virus (Houston et al., 2012).

Similarly, disease outbreak of Ostreid herpesvirus 1 (OsHV-1) has greatly affected aquaculture of Pacific oysters (*Crassostrea gigas*). A QTL on chromosome 8 of the Pacific oyster genome was determined to be associated with improved survival (13% phenotypic variance) to mortality events in Tomales Bay, California, USA, where OsHV-1 is endemic. Marker-assisted selection for this QTL resulted in 47% higher survival in breeding values for families undergoing MAS than based solely on pedigree selection (Divilov et al., 2023).

Developing and applying genotype-phenotype linkages may also be important for restoration-focused culture. A good example is the European flat oyster, *Ostrea edulis*, which is currently a species of limited interest in commercial aquaculture, particularly when compared with the Pacific oyster. However, there is an increasing interest in oyster bed restoration, particularly in northern Europe where populations have been severely depleted, or become extinct due to overfishing, parasites and habitat degradation (see <https://noraueurope.eu/>). Genomic tools and knowledge have been developed for European flat oyster, and these currently include several low- to medium-density SNP panels (Lapègue et al., 2014; Gutierrez et al., 2017), RAD-Seq data, three independently developed chromosome-level assemblies, and low-coverage whole-genome sequencing (Bean et al., 2022; Boutet et al., 2022; Gundappa et al., 2022; Li et al., 2023). While most studies have been dedicated to population genomics aimed at studying population structure and identifying signatures of local adaptation (e.g., Vera et al., 2019; Lapègue et al., 2023), GWAS has also been applied in hatchery-produced offspring to target

traits of interest for aquaculture (Peñaloza et al., 2022). In particular, molecular breeding to improve resistance against bonamiosis (an infection caused by a protozoan parasite that impacts wild and cultured populations) is a major objective in this species (Pouvreau et al., 2023). However, the development of selective breeding programs remains limited for *O. edulis*, notably due to the small-scale nature of the aquaculture industry, and to the constraints related to seed supply for restoration projects (Colsoul et al., 2021; Zu Ermgassen et al., 2023).

Linking single traits to DNA markers is also of consideration for conservation. Determination of what constitutes a ‘species’ is foundational to conservation as well as endangered species legislation, especially given that most programs and legislation consider subunits below the level accepted as biological species. For instance, in determining designatable units, the Committee on the Status of Endangered Wildlife in Canada assesses the proposed group’s discreteness and evolutionary significance (Lehnert et al., 2023; Lehnert et al., 2023). This is similar to the U.S. evolutionarily significant unit (ESU) being based on ‘reproductive isolation’ and ‘evolutionary legacy’ (Waples et al., 2022). These determinations are generally accomplished through investigation of population structure using panels of typically neutral markers (e.g., Lehnert et al., 2023). However, adaptive diversity at single markers exists within identified conservation units, and the appropriateness of considering designations based on variants at these markers has been debated (Waples et al., 2022).

Within salmonids, for example, variants in single genes have been detected that have a major influence on important life history traits. In Atlantic salmon, variants of the genes *six6* and *vgl3* show pronounced effects on age at maturity in some genetic and habitat backgrounds (Barson et al., 2015; Sinclair-Waters et al., 2020; Kess et al., 2024). In Pacific salmon, *six6* has also been associated with age at maturity in Steelhead (*Oncorhynchus mykiss*) and Sockeye salmon (*O. nerka*), but no association was found in Chinook (*O. tshawytscha*) or Coho salmon (*O. kisutch*) (Waters et al., 2021). Of particular note for conservation programs are the links that have been detected between an approximately 200 Kb region of the Steelhead and Chinook salmon genomes between the genes *GREB1L* and *ROCK1* (Hess et al., 2016; Narum et al., 2018). Variants at this region are associated with the propensity to exhibit ‘early’ or ‘late’ migration, where the migration type enables access to spawning habitats that are inaccessible under different flow/temperature conditions (e.g., sandbars can block river mouths during low flows). Despite being loci of large effect, the presence of both variants in a number of populations suggests that this diversity is being preserved through ongoing selection. The importance of selection in maintaining diversity is also demonstrated by changes in allele frequencies following interbreeding when habitat that was previously inaccessible to one or the other type is created through anthropogenic alteration. Waples et al. (2022) discuss loci of large effect in Pacific salmon in relation to conservation and the definition of conservation units.

The above section provides a broad spectrum of scenarios for which linkages between DNA markers and traits have been developed and utilised in both commercial and conservation focused programs. In this State, while it may be possible in some cases to utilise existing DNA markers for many species,

applications in this State may require additional steps such as developing a reference genome and using higher-resolution genotyping or sequencing for GWAS studies. A greater degree of analytical, computational and bioinformatic support will be required to accomplish these goals, but requirements for ongoing support will be largely determined by the method used to link the marker and trait.

In conclusion, it is important to note that the overwhelming majority of markers available in marker panels are not causal. Thus, while powerful, all approaches described in Stage 3 are dependent on the strength of the linkage between markers and phenotype, and the persistence of variation at markers linked to the phenotype. For linked, non-causal markers, a recombination-driven breakdown of linkage disequilibrium over generations (that is, a trend towards an independent segregation of genetic marker and causal variant), or, conversely, the loss of heterozygosity due to marker-driven selection, will make specific linked markers lose their information content, creating the need to regularly identify high-information-content markers. The level of polygenicity of the phenotype or phenotypes will influence the amount of variance any marker will be able to explain, with smaller proportions of variance attributable to any specific marker with greater polygenicity of a trait. These caveats are relevant to any genetic program that is, or has been, at a stage corresponding to Stage 3. However, this challenge is being overcome through statistical approaches that model combined sub-significant contributions of alleles to phenotypes, and ongoing reductions in sequencing cost and increases in data informativeness that have allowed the broader genotyping across large, phenotypically diverse sample sets (i.e., State 4).

2.5 State 4: Genomic selection and/or genomic imputation and prediction using family- or pedigree-based selection

In State 4, genomic selection and/or genomic imputation and prediction are applied using population- or pedigree-based selection methods. In this State, many species will have been bred in captivity and subjected to selection for multiple generations. However, genomic prediction methods are now being increasingly applied to wild populations of conservation interest as well. The common theme unifying these approaches is the leveraging of existing genomic information, typically including an annotated reference genome, to predict unobserved data. This can include traits of interest, signatures of environmental association, or the allelic state at a specific locus.

Having a high-quality genome for a species of interest also creates opportunities to generate genome-level data for individuals at considerably reduced costs through imputation or low-coverage whole genome sequencing (Lou et al., 2021). When high-density marker maps are available for the parents of the samples under investigation, it becomes possible to sequence fewer loci and then impute to the whole genome (Kijas et al., 2017). Imputation methods use missing genotype information at the pedigree or population level to assign unobserved or low-confidence genotypes, thereby reducing the amount of missing data (Marchini and Howie, 2010).

Alternatively, genotype likelihood approaches use the combined information across sequenced individuals to infer population genetic parameters (Kim et al., 2011). These methods have been generally found to outperform reduced-representation and SNP array-based approaches in terms of informativeness for detected trait-associated loci (Homburger et al., 2019; Jorsboe and Albrechtsen, 2022), and in accurately inferring population divergence (Szarmach et al., 2021). In recent years, whole-genome sequencing approaches that use low-coverage data, along with imputation or error correction approaches, have been increasingly applied in both aquaculture (Tsai et al., 2017; Gundappa et al., 2023; Kriaridou et al., 2023) and wild population studies (Kess et al., 2024), when a reference genome is available to increase the number of informative markers for genetic analyses. Imputation-based whole genome sequencing (WGS) approaches have been applied to Atlantic salmon in both aquaculture and wild population settings for marker discovery and GWAS (Kess et al., 2024). Similarly, low-coverage WGS and genotype likelihood methods have been applied to various wild species of management interest, including Atlantic silversides (*Menidia menidia*) (Therkildsen et al., 2019), European eel (*Anguilla anguilla*) (Enbody et al., 2021), northern sand lance (*Ammodytes dubius*) (Jones et al., 2023), and cunner (*Tautoglabrus adspersus*) (Nugent et al., 2023), to uncover population differentiation relevant to species management. These methods represent the forefront of WGS approaches, optimising the trade-off between marker and individual sample number, while providing robust estimates of genomic diversity, population structure, and trait association. However, reference population divergence, as well as local population structure and linkage, can bias imputation accuracy (Lou et al., 2021). In cases of low divergence and linkage, or high divergence from a reference population, genotype likelihood approaches may serve as a validation step (e.g., Kess et al., 2024).

Genomic predictions are increasingly being used in both wild and aquaculture studies, to infer unobserved phenotypes from observed genomic data. With advances in high-throughput sequencing (HTS), genomic selection (Meuwissen et al., 2001) has emerged as a powerful tool in aquaculture to enhance selective breeding programs and improve trait outcomes. Genomic selection relies on the analysis of a large number of markers distributed genome-wide that (ideally) captures all relevant genetic variance, in order to estimate genetic potential or the genomic estimated breeding value (GEBV), of individuals for various traits, including traits with complex genetic architectures. These methods have been used for prediction and trait improvement across numerous aquaculture species (reviewed in Song and Hu, 2022). The automation of this process is also underway, with the development of reference genotype panels for many aquaculture species, as well as web-based infrastructure to support these analyses (Zeng et al., 2022).

Machine learning approaches are now also being applied to better account for the non-linearity of interactions among trait-associated loci (Brieuc et al., 2018), and have shown improvements over traditional additive genetic models under certain genetic architectures (Azodi et al., 2019; Abdollahi-Arpanahi et al., 2020). Although not universal solutions, they

have demonstrated success, and therefore, careful consideration is warranted when applying these approaches.

In wild populations, genomic vulnerability approaches provide a methodologically similar approach to using genomic information for predicting phenotypes (Bay et al., 2018; Capblancq et al., 2020), but instead phenotypic information is inferred indirectly via environmental or climatic data, which are assumed to reflect local adaptation (Hoban et al., 2016). Polygenic score approaches have been applied in this context to predict individual environmental associations in species such as the eastern oyster (*C. virginica*) (Bernatchez et al., 2019) and sea cucumber (*Parastichopus californicus*) (Xuereb et al., 2018). Additionally, genomic vulnerability estimations of future climate impacts have been conducted in Arctic charr (*Salvelinus alpinus*) (Layton et al., 2021), marine invertebrates (cape urchin (*Parechinus angulosus*), common shore crab (*Cyclograpsus punctatus*), and granular limpet (*Scutellastra granularis*) (Nielsen et al., 2021)), an additional seaweed (*Phyllospora comosa*) (Wood et al., 2021) and eelgrass (*Zostera marina*) (Jeffery et al., 2024). Likewise, all-cause decline rate risk has been estimated at the river level in Atlantic salmon (Lehnert et al., 2019), indicating that genomic prediction methods may offer utility for conservation planning and prioritisation.

2.6 State 5: Gene editing

Gene editing and genetic engineering are rapidly evolving technologies, which warrant consideration as they may see regular application in the future. While the advanced technologies used in genome editing may seem less accessible for SMEs, there could be instances where the benefits of gene editing or genetic engineering outweigh the associated costs or complexities. However, at least one aquaculture genetic/genomic service provider has already advertised gene editing as a service (e.g., <https://aquatechcenter.com/services/genome-editing/>), which could help make these technologies more accessible to smaller-scale SMEs.

One area of particular interest for smaller SMEs may include gene editing approaches aimed at developing sterile offspring, which could be used in conjunction with other selective breeding goals. This could be especially beneficial in regions where obtaining permits for the use of domesticated lines in ocean environments could be challenging, particularly without additional measures to minimise potential impacts on wild conspecifics in the event of escapes (Wong and Zohar, 2015; Güralp et al., 2020; Kleppe et al., 2022).

However, the acceptance of gene editing or genetic engineering approaches by the public, as well as the legislation governing their use in commercial, and especially conservation programs, varies considerably across the world (e.g., Qin and Brown, 2006; Dietrich et al., 2022). Therefore, it is essential to investigate local legislation and public acceptance before considering their use in a program.

There are multiple methods for performing gene editing, with Zinc fingers (ZFN) (Miller et al., 1985; Klug, 2010; Urnov et al., 2010) and TALENs (transcription activator-like effector nucleases) (Joung and Sander, 2013) being the earliest technologies developed. Today these techniques are considered to be both time consuming and expensive. The CRISPR (Clustered Regularly

Interspaced Short Palindromic Repeats)/Cas technology, first presented in 2012, is a simpler, cost-effective and efficient method for targeted gene editing, and can be used in all organisms and cells (Doudna and Charpentier, 2014). Compared to ZFN and TALENs, the CRISPR/Cas technology was identified early as a promising tool (Gaj et al., 2013). However, all three techniques are based upon the same principle: a protein that cuts DNA in a targeted place.

Compared to traditional genetic engineering methods, where whole genes (often from other organisms) are randomly inserted into the genetic material of the target organism, gene editing enables precise modification of genes already present in the organism, to inactivate (knockout) genes or genetic sequences, or to insert (knock-in) genetic material at specific locations of the genome. Thus, a prerequisite for editing genes with CRISPR/Cas is knowing the sequence of the specific piece of DNA to be edited, as well as the complete genome sequence in order to reduce the potential for off-target editing and effects. In this way, knock-in gene editing can also be used to transfer genes from other organisms to specific sections of the genome, so-called transgene knock-ins. Additionally, CRISPR technology has the potential to switch off genes without altering the genetic code, enabling epigenomic alteration (Nuñez et al., 2021), although the full potential for CRISPR-based epigenetic editing is still unknown.

As a potential solution for hindering gene flow from aquaculture escapes to wild conspecifics, the CRISPR/Cas can be used to render aquaculture fish sterile. This can be accomplished by inhibiting the function of proteins that are important for germ cell development and/or survival (Wong and Zohar, 2015), which has been demonstrated in Atlantic salmon (Wargelius et al., 2016; Güralp et al., 2020; Kleppe et al., 2022). There are also several examples where CRISPR/Cas-induced knockout of genes have been shown to improve commercially important traits, such as growth, pigmentation, disease resistance and production of omega-3 fatty acids (see Roy et al., 2022). Recently, tiger puffer (*Takifugu rubripes*) and red sea bream (*Pagrus major*) (Kishimoto et al., 2018), which were edited with CRISPR/Cas for enhanced growth, were approved for the Japanese market.

The discovery of the CRISPR/Cas system has also begun to supplant the use of random transgenesis techniques (a subset of genetic engineering). There is a relatively long history of developing and producing transgenic fish in aquaculture through various random transgenesis methods. The first transgenic aquaculture fish were produced over 35 years ago (Devlin et al., 2006), and since then, over 35 species have undergone transgenesis (Devlin et al., 2015), with the AquaAdvantage Atlantic salmon being one of the most well-known examples.

Through traditional gene modification methods transgenes have been introduced into aquaculture species to express desired traits, such as improved disease resistance, altered metabolism, and increased growth (Devlin et al., 2006). CRISPR-edited transgenes have also been produced to enhance disease resistance (Simora et al., 2020), and current efforts are directed towards identifying genes or causative mutations in Pacific salmon related to sea lice resistance (Robinson et al., 2023). If such genes are identified, they could potentially be transferred to Atlantic salmon, a species highly susceptible to sea lice, using the CRISPR/Cas technology.

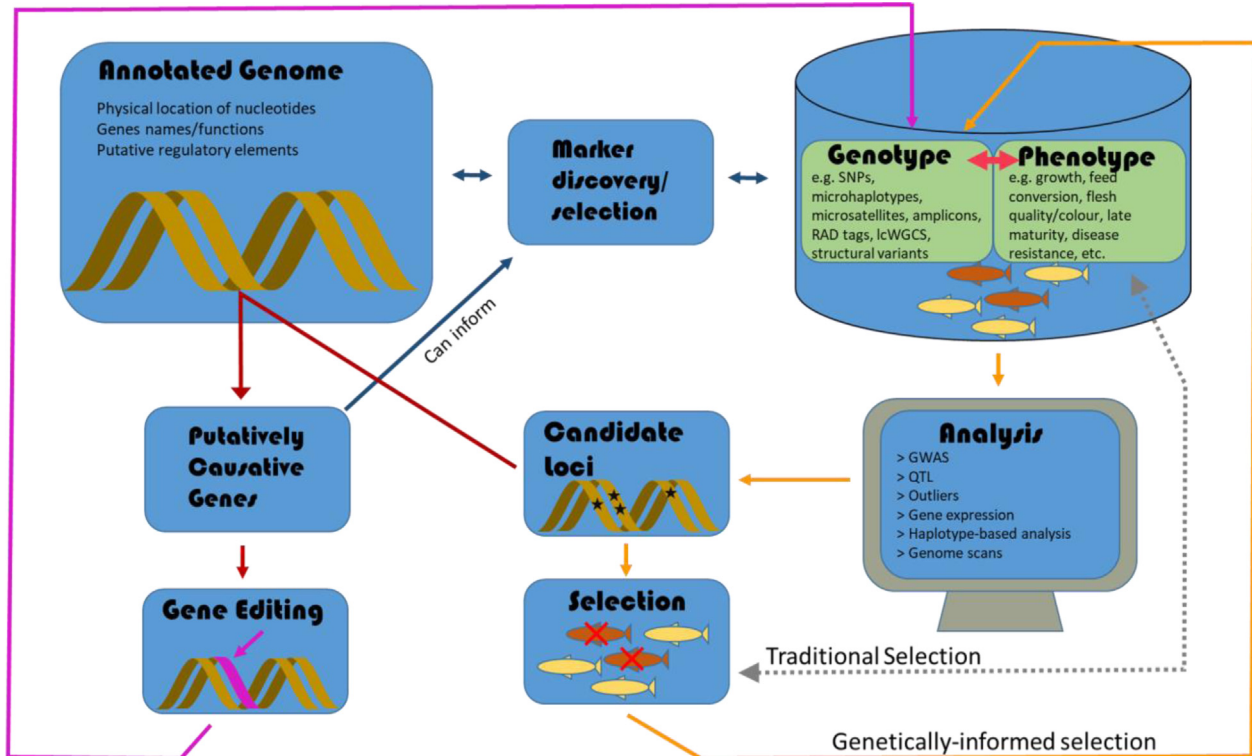


Fig. 3. Schematic illustration of the utility of an annotated, whole genome in aquaculture or conservation breeding programs. Solid arrows represent directionality of information or activity with colours denoting common pathways. The grey dashed line, representing traditional selection, is included to reinforce that it operates primarily based on phenotypes and that it can occur while genomic tools are being developed.

The transition from using random transgenesis techniques to achieving transgenesis through CRISPR/Cas is also evident in the ornamental fish trade and supporting commercial culture systems. The incorporation of transgenes that express different fluorescent colour proteins, producing novel colour phenotypes, has been conducted through random transgenesis techniques for several species including the Black tetra (*Gymnocorymbus ternetzi*) and Zebrafish (*Danio rerio*) (DFO, 2018a; 2019, 2020a, b) (DFO, 2018; DFO, 2019; DFO, 2020; DFO, 2020).

More recently, CRISPR/Cas has been used to introduce the same genes and achieve similar colour phenotypes in Siamese fighting fish (*Betta splendens*) (DFO, 2021) and a species of Barb (*Puntigrus tetrazona*) (Dietrich et al., 2022). The single gene to single trait nature of these modifications make the development of these types of ornamental fish relatively straightforward. As these technologies advance, the development of fish that incorporate more sites of modification, and thus greater complexity in trait modification, is likely.

Although few commercial CRISPR-edited species are available for human consumption at present (e.g., Kishimoto et al., 2018), this number may increase because regulations regarding their use are being evaluated in multiple geographic regions. In parallel, more commercial entities are increasing their research efforts related to this powerful technique.

The commercial applications of gene editing are clearer than its use in conservation programs. Moreover, implications to legal conservation status notwithstanding, public and legislative acceptance is more likely for gene editing in commercial settings

than for conservation purposes, particularly when the program will result in the release of gene-edited individuals into the wild.

That said, the use of gene editing in conservation programs has been proposed, though primarily in theory. For instance, a scenario could be envisioned where changes to a single region of the genome results in increased immunity to a disease agent that is endangering a species. Alternatively, gene editing could be used in species where genetic rescue is needed, allowing for the identification and targeting of lethal recessive alleles in a genome where genetic diversity has largely been lost and genetic drift has resulted in detrimental effects on the remaining individuals (Segelbacher et al., 2022).

Phelps et al. (2020), outline additional potential applications of gene editing in conservation, ranging from simpler applications (e.g., inducing neutral changes to a single base pair for marking) to significantly more complex and controversial (e.g., utilising synthetic biology to recreate genomes and species that have been lost through extinction).

2.7 State Skipping

In many ways the States presented here are a product of the history of the development of genetic and, subsequently, genomic tools in non-model species. While it is understood that aquaculture has been practiced for thousands of years, the broad adoption of selective breeding and expansion of aquaculture programs began during the latter half of the 20th century. This time period also coincided with the early

development and application of genetic tools in non-model species.

A prime example is Atlantic salmon; collections of wild salmon in the 1970s were used to form large-scale family-based breeding programs in Norway (State 0; Gjedrem, 1985). Around this time, descriptions of genetic variation and population genetic studies began to emerge, including hatchery-reared populations (State 1; e.g., McKenzie and Paim, 1969; Moller, 1970; Payne, 1974; Davidson et al., 1989). This was followed by the development of DNA markers for individual and population identification (State 2; e.g., Davidson et al., 1989; Taggart and Ferguson, 1990), the linkage of traits of interest to gene regions (State 3; e.g., Reid et al., 2005), and more recently, the use of genome-scale data in breeding programs (State 4; e.g., D'Agaro et al., 2021) and the development of transgenic lines and gene-edited variants (State 5; e.g., Wargelius et al., 2016; Güralp et al., 2020; Kleppe et al., 2022). However, this transition through stages has been more a consequence of scientific advancements and technology than a deliberate process.

Due to the relative ease with which a *de novo*, chromosome-level, fully annotated genome can now be produced – from which most commonly used genetic and genomic tools can be developed – new programmes can now rapidly begin at any desired State, effectively skipping those States below the chosen State. State skipping, as we have termed this, has advantages in terms of cost (developing only tools needed), efficiency (tools optimally designed to the problem at hand), and time (application of tools nearly immediately; optimised tools enable faster outcomes). As such, we would recommend that new programs seek to develop genomic resources of broad utility, such as whole-genome assemblies, that will allow for the development of tailored tools. At the same time, developing program goals (e.g., testing for the maintenance of genetic diversity in a conservation program, undertaking genomic selection in an aquaculture strain, etc.) will facilitate conversations with experts to help determine the best set of tools to develop given the goal.

Put another way, the advances in genotyping technology and the reduction in genotyping per-base sequencing costs mean that a candidate species can be moved from State 0 to practically any State of a researcher or SME's choosing with relative ease. For example, cunner is a temperate reef fish native to the northwest Atlantic, that is currently being considered as a candidate species to be used as cleaner fish in Atlantic salmon aquaculture in Atlantic Canada, and for which, until recently, few genetic tools existed (Costa et al., 2016; Monk et al., 2016; Chen, 2020).

Nugent et al. (2023), describe the production and annotation of a chromosome-level genome assembly for this species, as well as the characterisation of genetic population structure in Atlantic Canada. This genome will allow the development of many diverse genetic and genomic tools (e.g., microsatellites, SNPs, copy number variants, etc.). Because the genome is annotated, functional relationships may be determined between traits of interest and DNA markers. Annotated reference genomes can improve the quality of genomic tools by allowing users to avoid repetitive genomic elements and evenly distribute markers across the genome. Moreover, an annotated reference genome allows for the transfer of data and information between projects or groups by

referencing standardised genomic coordinates and names for genetic loci.

Finally, comparisons can be made between annotated reference genomes of different species to identify loci or ecologically relevant genes that have been identified as being important in a given species, habitat, or context. An excellent example of the use of a *de novo* generated annotated genome alongside data from another project is described in Gao et al. (2023). These researchers outline the development of a 50K SNP array designed for North American Atlantic salmon based on SNPs identified in the North American salmon genome they developed, with the European salmon genome's annotation used to approximate the locations of genic regions.

A schematic example of how an annotated genome can be used to develop and apply genomic tools in a breeding program is shown in Figure 3. In this figure the genome is used to enable: marker discovery and selection based on population genotypes and putatively causative genes (blue arrows); changes in population phenotype and genotype as the result of genetically informed selection (orange arrows); the identification of putatively causative genes (gamet arrows); and changes in genotype and phenotype as a result of gene editing (fuchsia arrows).

3 Considerations and constraints of genetic and genomic methods

The widespread adoption of genetic methods is constrained by economic and practical considerations. The economic considerations are centered on the overall costs associated with the use of these approaches, and whether the expected outcome or improvement will result in a net economic gain or reaching a conservation goal. These types of considerations and analyses should be specific to the producer and rely on the most current economic data to be meaningful. The practical considerations range from what State the species of interest currently is in, to availability of all ancillary genomic (such as bioinformatic and analysis pipelines, data storage and management), phenotyping (e.g., measurement equipment, personnel, etc.) and facility (e.g., experimental tanks or cages, separate production and selected lines, etc.) resources required to actually translate raw genotype and phenotypic data into actionable breeding or conservation information.

Expense considerations will need to take into account the total cost of genetic/genomic approaches, including both genotypic and phenotypic data collection, data analysis, and data storage, on top of the actual cost of genotyping, animal rearing and husbandry. Part of this consideration should be the development of a breeding objective which should note the traits that influence income, expenses, or both; where the goal is to improve multiple traits, traits should be prioritised based on economic importance (Kankainen et al., 2016; Lhorente et al., 2019). It is worth noting that any cost-benefit analysis regarding the adoption of genetic and/or genomic tools will depend on the species and the technological stage at which the work is conducted. For instance, moving from a high-throughput sequencing approach to an off-the-shelf genotyping solution, or shifting from a dense genome-wide marker set to a low-density marker set with genome-wide imputation,

could substantially decrease costs and thus substantially change medium- and long-term cost-benefit projections.

Technical constraints, especially regarding data and sample collection and processing, may hamper the ability of some programs to State Skip. Depending on the specific goals being pursued, different types, and different quantities of data will need to be collected and handled, starting from tissue sample collection for genotyping, up to full phenotypic and genotypic characterisation of hundreds or thousands of samples, potentially over multiple generations. For applications in State 1 and 2, the infrastructure requirements are generally lower as the focus is on sampling wild individuals or broodstock and offspring. Tissue sampling tools and preservation methods are typically inexpensive; methods are available to preserve tissue samples for DNA extraction at room temperature, although in some cases, DNA storage may require freezing, including flash-freezing (e.g., liquid nitrogen). The best approach will depend on the species and on the genetic application. In most instances, staff can be easily trained to collect tissue samples for DNA extraction and processing. However, careful record keeping is essential to match genetic samples back to individual organisms (e.g., utilising physical tags) or families, and phenotype and genotype data.

Beginning in State 3, and more so in State 4, a combination of trained staff and infrastructure investment in phenomics technologies, which allow for the collection of large amounts of phenotypic data, will be necessary to accurately phenotype the animals, depending on the number and complexity of phenotypes. The importance of precise and standardised phenotyping approaches for *any* State targeting traits cannot be overstated. To a large extent, the success in associating traits to genotypes will depend on the ability to reliably collect accurate phenotypic information. In State 3, phenotypes are often easier to collect (e.g., sex based on gonads, fish length, presence of deformities), but become more complex in State 4 (e.g., fillet yield, color, lipid content, feed conversion rates, disease/parasite resistance), and require not only more highly trained staff, but may also require specialised equipment and infrastructure for measuring some traits. As mentioned above, applications in State 3 and State 4 also require a large number of individuals to be phenotyped and genotyped, and as trait complexity or the number of targeted traits increases, a greater number of samples are needed for analyses. The time, labour, and (if needed) equipment necessary to phenotype large numbers of animals (and repeatedly phenotype in successive generations – as is the case in State 4) should be considered. Often in State 3 and State 4, family and/or selected lines also need to be maintained, which increases the infrastructure required to maintain these populations within the aquaculture program. State 5 has similar infrastructure requirements as State 4; however, the intensiveness of phenotyping will depend on the specific target(s) of gene editing. In addition, State 5 may require close coordination between genomic scientists and breeders to obtain gametes, fertilised eggs, or larval stages required for genome editing approaches, as well as engagement with policy experts on conditions governing gene editing approval. Therefore, the availability of both a skilled workforce, and access to a sufficiently large sampling population (and the capacity to maintain the population) needs to be addressed before any further action is taken. In these considerations, it is assumed that genetic sample processing occurs externally (*see section 4.0 Resources*) since

it is unusual for SME or conservation aquaculture programs to have their own genetic laboratory capacity.

Once costs and practical considerations have been addressed, it is also important to understand the limitations of different genomic approaches. Individual DNA-based identification using DNA barcoding requires a set of informative markers, but the marker informativeness depends on polymorphism rates, a parameter itself dependent on population inbreeding and actual sample size. The information content of markers used for individual identification is therefore not stable across either time or space, requiring regular testing against a known standard to assess the usefulness of the markers used. Small marker panels can capture a high percentage of the genetic variance if the markers have been preselected (Vallejo et al., 2018), but only if they have been preselected based on previous, genome-wide analyses, noting that selected marker informativeness declines with selection (which brings these markers to fixation). Imputation partially mitigates these constraints, because it requires the genotyping of the parents, or the availability of a reference panel consisting of many individuals with a known genetic relationship between the panels and the samples that will undergo imputation (Marchini and Howie, 2010; Verbyla et al., 2022).

GWAS can provide an understanding of the genetic architecture of a trait, but sample size and marker density must be adequate to identify loci associated with a phenotype. If the marker set is too sparse, or if the sample size is too small, power might not be sufficient to identify loci that are associated with the phenotype. It is also important to remember that GWAS identify genomic locations associated with a phenotype, generally covering many loci, and that the association may be indirect between a marker locus and trait, and thus any locus identified in a GWAS cannot be assumed causal for a phenotype. Further steps, such as fine mapping, would likely be required to identify genetic variant(s) responsible for a trait, assuming one exists (Schaid et al., 2018). Independent GWAS, conducted on the same trait(s) but on different populations can also help to validate the effect of a locus on a phenotype, with associated additional costs to support these experiments.

4 Resources for implementing genetic/genomic work

SMEs and conservation programmes interested in the adoption of genomic technologies may find support through contact and/or partnership with aquaculture societies and organisations, research consortia, governmental institutes and academic institutions, and fee-for-service providers. Support from these partners or partnerships range from advice, to access, to development and implementation of genetic and genomic tools and information, to funding dedicated to breeding or conservation. For instance, in Canada, the Fundy Salmon Recovery program is supported in part by aquaculture companies and via an aquaculture association (https://www.canada.ca/en/parks-canada/news/2017/10/fundy_salmon_recovery.html).

Aquaculture societies, both national and international, (for example in the ICES region, the European Aquaculture Society (<https://aquaeas.eu>); the World Aquaculture Society

(<https://www.was.org>); the U.S. Aquaculture Society (<https://www.usaquaculture.org/>); the American Fisheries Society (<https://fishculture.fisheries.org/>), can provide specific know-how, recommendations on service providers, and information about available funding. While the focus of aquaculture societies might be primarily business related, the importance of sustainability and conservation in the aquaculture sector means that aquaculture societies may support collaboration or supporting conservation programs, especially those focused on the wild counterparts of farmed species.

Another source of support for SME and conservation programs are research consortia. Research consortia might be permanent bodies akin to aquaculture societies, organisations and projects, or might be limited in time and scope, and specifically created to apply for domestic or international funding opportunities. Drivers of the latter type of consortia is the availability of national or international funding, such as the EU Horizon funding instruments, which require the involvement of industrial/non-academic partners in consortia applying for funding. Active involvement in research or trade consortia could allow SMEs and conservation programmes to increase their visibility and their professional network, facilitating their inclusion in consortia responding to funding calls.

Academic, institutional research organisations or institutes, government agencies, and intergovernmental organisations often have a sustained interest in aquaculture and/or conservation breeding, and thus a partnership with these research institutions can facilitate access to the pertinent know-how concerning the acquisition, use, and analysis of genomic data. Depending on funding, research institutes can provide access to specific infrastructure, and grant agreements may cover specific costs (such as genotyping, personnel, data analysis), decreasing the investment required by the SME. It is important to remember that, unless working as service providers, research institutes and funding agencies expect dissemination of results, the details of which should be agreed upon before work commences.

In addition to these resources, fee-for-service providers are also available to help guide, develop, and implement the use of genomic approaches within the breeding programs. There are several that have extensive experience in, or are specifically focused on, the aquaculture sector, and many of these companies have worked on a broad array of species. Because providers may vary by region or change rapidly within this growing field, specific providers are not listed here. However, many of the above resources would be able to provide information on service providers working in a region or on a specific species. If financial resources permit, progress is likely to be the quickest through this route. This investment may be particularly worthwhile for emerging aquaculture species, which may not yet attract attention from major funding bodies. This can lead to challenges in acquiring funding and developing institutional or academic collaborations, as well as in achieving the critical mass required to establish research consortia focused on that species. It should be noted, however, that there may be funding opportunities specifically geared towards development of newer species for both commercial and conservation programs.

5 Summary

Ultimately, the argument for the use of genetic and genomic tools and approaches by SME was stated succinctly

by Gjedrem et al. (2012): “investments in well planned and managed breeding programs are unique, because genetic gains obtained in such programs are eternal and cumulative”.

Significant genetic gains are possible and can be achieved more rapidly through the use of DNA-informed breeding, which is broadly defined to include any DNA-based information, from low-coverage markers through genomic selection and genome-wide selection, to inform breeding decisions (Peace, 2017).

Long-term conservation of threatened aquatic species cannot be achieved without considering genetic diversity and proper broodstock management (Kozfkay et al., 2008). In some cases, with extremely threatened species, what is lost from genetic diversity in captive supportive breeding due to inadequate measures, is lost forever (Frankham, 2010; Bossu et al., 2023).

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Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this review.

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