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Current status and potential of genomic selection to improve selective breeding in the main aquaculture species of International Council for the Exploration of the Sea (ICES) member countries

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ABSTRACT

Selective breeding has been successfully applied to improve profitability and sustainability in numerous aquatic species. Recent developments of high throughput genotyping technology now enable the implementation of genomic selection, a method aiming to predict the breeding value of candidates based on their genotype at genome-wide markers. In this review article, we review the state of the arts, challenges and prospects for the application of genomic selection in aquaculture species. The particular focus is on the status of genomic selection in several major aquaculture species of International Council for the Exploration of the Sea (ICES) member countries: Atlantic salmon, rainbow trout, Atlantic cod, American catfish, Pacific oyster, European sea bass and gilthead sea bream. While the potential of genomic selection is clear, tailored species-specific applications will be needed to maximise its benefit for the aquaculture sector.

1. Introduction

Selective breeding is playing an ever-increasing role in aquaculture production. Although the domestication of most aquatic species is much more recent than for their terrestrial counterparts, an increasing number now benefit from the cumulative genetic improvement of well-managed selective breeding programmes. Methods have tended to evolve from the initial selection associated with domestication, to mass selection, family selection, marker-assisted selection, and now to genomic selection (GS). GS harnesses genome-wide genetic markers to accurately estimate breeding values of selection candidates for quantitative traits (Meuwissen et al., 2001). While initial studies proposing GS were theoretical,

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the advent of high-throughput sequencing and Single Nucleotide Polymorphism (SNP) arrays has made implementation of the technique a practical reality. As such, GS is now routinely applied in an increasing number of terrestrial farmed species, in particular dairy cattle (Boichard et al., 2016; Rexroad et al., 2019), pigs (Samorè and Fontanesi, 2016), and crops (Desta and Ortiz, 2014; Heslot et al., 2015), resulting in an increase in the accuracy of breeding value prediction and subsequent genetic gain.

Unlike QTL-based MAS, where the effect of each QTL is first tested for its statistical significance, GS omits significance testing and estimates the effect of all markers simultaneously through a prediction equation. GS aims to predict the breeding value of individuals based on their genotype at a large number of markers spread over the genome. This extensive genomic coverage is most commonly achieved using Single Nucleotide Polymorphism (SNP) arrays. GS consists of two main steps. The prediction equation is first established in a training population in which individuals are phenotyped (i.e. measured for target traits in the breeding goal) and genotyped. The number of markers is typically much higher than the number of individuals, therefore classical statistics cannot be applied, and the use of alternative methods is required (de los Campos et al., 2013): Genomic Best Linear Unbiased Prediction (GBLUP) - an extension of BLUP (Hayes et al., 2009), assumes all markers have the same weight - while Bayesian estimates (Daetwyler et al., 2010) allows for variation of allelic effects of each marker, and assumes that only a small number of them have a non-zero effect. Once the prediction equation is established, breeding candidates can then be selected on the basis of their estimated genomic value with or without phenotype records on those individuals. GS is of particular relevance in the case of lethal traits that cannot be recorded on live individuals (e.g. disease and parasite resistance, thermal and salinity tolerance, fillet quality and yield) (Gebreyesus et al., 2020), where phenotypes are recorded on relatives of the candidate breeders. GS is thought to be more efficient than “sib selection” (Dhillon et al., 1987), which is classically used in such cases, because sib selection results in the same breeding value for all animals in a nuclear family, while GS allows the identification of the best candidates within each family. This is because GS allows utilisation of both the between and within-family components of the genetic variation in traits of interest. In terms of its limitations, GS is driven by the quality of the phenotype and genomic resources (especially in newly domesticated species or species complexes). In addition, GS is very demanding in terms of number of individuals genotyped and the number of markers employed. Its potential is likely to vary according to the life cycle characteristics of each species and the ability of breeding companies to invest in sophisticated and potentially resource-intensive (e.g. funding, infrastructure and training) selection programmes. In this article, we review the state of the arts, challenges and prospects for the application of GS in aquaculture, focussing on several major species of International Council for the Exploration of the Sea (ICES) member countries.

2. Genotyping technology: practicalities and cost-efficiency

GS requires the availability of genome-wide SNP datasets, and therefore a means of collecting genome-wide SNP data routinely on large numbers of individuals. A number of aquaculture species already have commercially-available SNP arrays (See Table 1). In addition, SNP panels can be produced *de novo* by reduced-representation Next Generation Sequencing (NGS) approaches, such as restriction site-associated DNA (RAD) sequencing or genotyping-by-sequencing (GBS) (Robledo et al., 2018a). Such NGS approaches can identify and concurrently genotype thousands of SNPs that provide genome-wide coverage directly in target populations under study (e.g. broodstock populations of a breeding programme). Moreover, direct discovery and genotyping of SNP panels on the targeted population(s) helps to minimize both ascertainment bias and the number of potentially uninformative markers. The limitations of these NGS approaches include repeatability,

Table 1
Aquaculture species for which commercial high-density SNP chips have been recently developed.

Species	References
Salmo salar	Houston et al. (2014a, 2014b), Yanez et al. (2016)
Oncorhynchus mykiss	Palti et al. (2015a)
Oreochromis niloticus	Joshi et al. (2018); Penaloza et al. (2020); Yanez et al. (2020)
Cyprinus carpio	Xu et al. (2014)
Ictalurus punctatus; Ictalurus furcatus; Ameiurus nebulosus; Ameiurus catus	Liu et al. (2014)
Crassostrea gigas	Gutierrez et al. (2017); Qi et al. (2017)
Ostrea edulis	Gutierrez et al. (2017)
Gadus morhua	Pocwierz-Kotus et al. (2015), Aslam et al., (pers. comm.)
Litopenaeus vannamei	Jones et al. (2017); Lillehammer et al. (2020)
Dicentrarchus labrax	Faggion et al. (2019); Vandeputte et al. (2019); Griot et al (2021); Peñaloza et al. (2021)
Sparus aurata	Griot et al. (2021); Griot (2021), Peñaloza et al. (2021)
Salvelinus alpinus	Nugent et al., 2019

meaning not all markers are genotyped in every sample set, and as such training and breeding populations may need to be genotyped together to maximise shared markers. In addition, the initial NGS output is very dependent on the quality of the sampled DNA and of the amplification of the fragments. Therefore, it may yield substantially fewer high-quality, reliable SNPs from poorer quality samples which can occur under commercial aquaculture conditions. In contrast, SNP arrays are typically more repeatable, and depend less on the initial DNA quality compared to NGS approaches. However, initial development of a genome-wide array can be costly and time consuming. This investment is however likely to be prudent in the long term due to the advantages of having a standardized and robust genotyping platform across multiple reference and validation populations.

Genetic maps and reference genomes are not strictly needed for the use of GS, but they can provide greater understanding of the distribution of markers around the genome and whether any areas of the genome are underrepresented or not uniformly covered. In particular, while genomic maps are not required for the GBLUP approach, they are useful in Bayesian approaches that identify markers close to genes relevant in the selection process. Furthermore, applications of genotype imputation (discussed below) are somewhat reliant on a high quality reference genome sequence for the species of interest. Historically, the creation of genetic maps and reference genomes was a costly and time-consuming enterprise, meaning that the cost-benefit analysis would not support the investment in these resources. However, with advances in sequencing technologies such as long-read, single molecule sequencing combined with advanced scaffolding technologies, the cost and effort of creating a *de novo* reference genome assembly is now much less. As such, many high quality, chromosome-level reference genome assemblies are available for major aquaculture species, and others will rapidly follow.

3. Specific considerations for application of genomic selection in aquaculture species

In aquaculture, selective breeding programmes are more recent than for most terrestrial livestock and are so far limited to relatively few species, such as salmonids, shrimps, tilapia, carp, sea bream, seabass, turbot, hirame, sturgeons, oysters, scallops, clams, catfish, and moronids. Many of these programmes started with simple mass selection for growth and appearance, but an increasing number now use family information to improve genetic gain and enable selection on traits not easily measured on breeding candidates (e.g. disease resistance, processing yields, flesh quality). However, when information from siblings

is used to select candidates on such traits, the within-family genetic variation is not exploited, and this limits the potential genetic gain. Thus, the use of GS could be especially beneficial for improving these highly-desirable traits, and especially for highly fecund aquaculture species where nuclear family sizes can be very large. A second benefit of GS for aquaculture species is that a traditional pedigree file is strictly not needed, because the relationships between individual fish are calculated based on the genetic marker information only. This means that families do not have to be kept separately until tagging as in the traditional breeding programmes for the sake of the genetic evaluation (Sonesson et al., 2010), which is relevant especially for species that reproduce in groups and physical family separation is challenging or impossible. Fortunately, in many new and developing breeding programmes, kinship information can be or has been reconstructed through microsatellite and/or SNP genotyping. As such, the infrastructure for DNA collection and fish individual tagging is already available, these programmes are good candidates for easier implementation of GS without major operational changes.

Developments in GS in aquaculture species have been recently reviewed by several authors (Norris, 2017; Hosoya et al., 2017; Palaiokostas and Houston, 2018; Zenger et al., 2018; Zenger et al., 2019; You et al., 2020; Houston et al., 2020). The overall consensus is that GS will enhance the rate of genetic gain both by increasing the accuracy of prediction of breeding values and - in some species - shortening generation intervals. To a smaller extent, increased selection intensity is also a result of GS. Achieving this requires the collection of genome-wide genetic marker datasets together with relevant trait measurements in reference populations, which in aquaculture species are typically full or half siblings of selection candidates. These same datasets can facilitate the discovery of genomic regions that contribute to the underlying genetic variation of complex traits via genome-wide association studies (GWAS). Such information on genetic architecture can inform the optimal use of statistical models for application of GS; for example whether GBLUP or Bayesian approaches are appropriate.

While the benefits of GS are undeniable, it is also important to consider and to evaluate potential challenges and pitfalls of the approach for different species and distinct breeding programmes (Ibanez-Escriche and Gonzalez-Recio, 2011). In comparison to selective breeding programmes for terrestrial species, the use of GS in both finfish and shellfish has also traditionally been limited by the lack of dense marker maps and/or high-throughput genotyping platforms. These limitations, however, are beginning to change as advances in genomic methodologies accompanied by reduced costs for analyses are enabling the increased use of GS in aquaculture. Results from recent empirical GS studies in farmed aquatic species are confirming those from early simulations and suggest an increase in the accuracy of selection for both continuous and categorical traits (Vallejo et al., 2017; Nielsen et al., 2009; Sonesson and Meuwissen, 2009; Daetwyler et al., 2010). In addition to facilitating the increase of genetic gains, GS can also be used to introgress advantageous polymorphisms into a potential target population. For instance, Ødegard et al. (2009) demonstrated that simulated backcross breeding programmes using GS provided a faster approach to developing a disease-resistant line of commercial value.

The design of GS in aquaculture breeding programmes are in general flexible. Including GS in traditional family-based breeding programmes, where families are kept separate until tagging has the advantage that the number of individuals to be genotyped per trait can be precisely planned. The genomic information is then particularly increasing the accuracy within-family term. If this is taken to an extreme, very large (~100 sibs) families can be produced and within-family GS applied (Lillehammer et al., 2013), which only uses very few markers (10) per chromosome to predict within family GEBVs. If families are mixed early, family contributions are unknown until genotype information is known and family sizes are unequal due to different early mortality per family. In general, this results in a need to genotype more fish (Sonesson et al., 2010). However, the investment in many family tanks can be omitted. GS is in this case used to predict also the between family genetic component to a larger extent than for the traditional designs. Sire:dam mating designs have little effect on the GS results (Sonesson and Ødegård, 2016).

It is important to note that most aspects of the use of genomics technologies depend on economies of scale. Aquaculture involves a large number of species farmed globally, most of which are neither model organisms themselves nor are closely related to well known model species, making it impossible to use shared genetic similarities to better known model organisms to jumpstart genomic work. This need for bespoke tools raises the costs of genomic selection, and when considered alongside the rather limited value of selection candidates for most aquaculture species, means that detailed economic evaluations will be needed for each case. While genotyping using higher density SNP arrays are typically cheaper per individual SNP marker, a key advantage of lower-density SNP panels is lower cost per individual which results in ability to genotype a much higher number of individuals. Unfortunately, the small breeding programmes often have to start their GS breeding programmes with a SNP chip with fewer markers, which results in less increase in accuracy compared to traditional BLUP breeding values and which soon will be exchanged with a larger chip. This transition to a larger SNP chip results in imputation errors. Breeding programmes for a particular species may only require genotyping at a certain SNP density, and must decide whether to purchase existing commercial SNP arrays, or to design a custom lower density array. Furthermore, generation interval is typically rather short in most aquaculture species, with most trait measurement being performed prior to sexual maturity, and few if any sex-limited traits recorded on granddaughters or grandsons such as for milk production in dairy cattle. These factors limit the potential to benefit from reduced generation interval, and mean that the primary benefit of GS in aquaculture will likely derive from the improved selection accuracy due to capitalising on within-family genetic variation. This is particularly important in aquaculture because of their typically high fecundity and the routine measurement of traits in full siblings and other close relatives of selection candidates. While improvements in prediction accuracy compared to pedigree-based approaches have been almost universal, the main practical concern for the use of GS in aquaculture is whether GS is a cost-effective selection strategy compared to pedigree-based methods. As noted above, using commercial or private SNP arrays, developing new SNP arrays, performing NGS, and then collecting extensive datasets on reference and breeding populations is typically expensive. For GS to benefit these aquaculture sectors, more cost-efficient genotyping is necessary as recently proposed by using low density SNP panels (perhaps 1000–2000 SNPs) without significant loss of prediction accuracy (Kriaridou et al., 2020).

In order to illustrate the variety of the level of implementation of GS among species of interest for aquaculture in the International Council for the Exploration of the Sea (ICES) member countries (https://www.ices.dk/about-ICES/who-we-are/Pages/Member-Countries.aspx), the following sections presents current status and developments of GS in Atlantic salmon, rainbow trout, Atlantic cod, American catfish, Pacific oyster, European sea bass and gilthead sea bream.

4. Current status and developments of genomic selection in species of interest for aquaculture in the ICES member countries

4.1. Atlantic salmon (Salmo salar)

4.1.1. General context

Modern farming of Atlantic salmon started in Norway in the beginning of the 1970s. The main producers of Atlantic salmon (*Salmo salar*) are currently based in Norway, Chile, UK, Canada and Australia. The Atlantic salmon start their lifecycle in freshwater, where they are raised in recirculating hatcheries and/or freshwater net pens, before undergoing smoltification and transfer to seawater for growing on to harvest size They are slaughtered at around 4 kg. The fillets are red and contain

high levels of fat (~13–18%), which contains omega-3 fatty acids that are known to have beneficial human health effects.

Selective breeding programmes have been an integral part of the farming of salmon since the beginning of the modern farming practices in Norway. The first major trials of family-based breeding programmes were in the early 1970s (Gjedrem et al., 2012). These trials involved collection of populations from Atlantic salmon originating from ~40 Norwegian rivers, which were used to estimate robust genetic parameters for important production traits, and this then led to the first commercial breeding programme (Gjoen and Bentsen, 1997). Subsequent initiatives have resulted in the establishment of strains such as the Mowi, the Rauma, the Jakta and the Bolaks, and these have been established from various sampling events and locations (Glover et al., 2017). After a series of crossing and international export events, the vast majority of global salmon production derives from these original strains. The exceptions are the North American-derived Atlantic salmon aquaculture strains (predominantly farmed in the Australian and Canadian industries) which are genetically quite distinct from the European Atlantic salmon, with a distinct karyotype (Brenna-Hansen et al., 2012). There is also a small amount of production in Scotland using Scottish origin strains (Munro, 2019)

Most breeding programmes of Atlantic salmon sell fertilized 'eyed' eggs to multipliers, which in turn sell fry to producers. There are also fully-integrated companies that include their own breeding programmes and manage the fish from egg until slaughter.

4.1.2. Past and current status of selective breeding in Atlantic salmon

The first traits included in the breeding goals were mainly those that could be measured on the selection candidates themselves. This included increased growth rate, because that results in shorter production times, and has a medium to high heritability. Reduced incidence of precocious sexual maturity was also a major target, because this causes negative effects on growth, flesh quality and fish health. As breeding programmes have advanced, they have included multiple additional traits into the breeding goals, including those which can only be measured on relatives of selection candidates. These include product quality traits, e.g. fat content, pigmentation and spine deformities, and resistance to different diseases, e.g. IPN, PD and salmon lice. These traits often have medium-high heritabilities, meaning genetic gain can be relatively rapid, although it is limited by the relatively long generation interval of salmon (3–4 years).

There are two major designs of breeding programmes for salmon. One is where families (200–800 per year class) are kept separately until individual tagging can take place (using some kind of Passive Integrated Transponder (PIT)- tag). This system gives accurate pedigree and data for the genetic evaluation. However, it requires significant investment in hatchery infrastructure and PIT-tagging, and its size depends on the number of families. Genomic selection (Nielsen et al., 2009; Sonesson and Meuwissen, 2009) and mating (Sonesson and Ødegård, 2016) designs for these programmes are available, as also designs for optimum contribution selection (Nielsen et al., 2011).

The second design is where fish from different families are merged at an early stage and DNA markers are used to identify a number of pre-selected individuals (in combination with individual PIT-tags). This system requires high cost of genotyping to develop markers-based pedigree but less investment in hatchery facilities, but has less control of family contributions in different batches of fish, which may result in loss of whole or parts of families. This may lead to unbalanced data for the genetic analysis, and ultimately lower selection intensity for certain traits, and higher risks of inbreeding accumulation. Often, larger numbers of families are produced to reduce the risk of getting a too small population. Examples of genomic selection designs for these programmes are available (Sonesson et al., 2010).

Since the beginning of the modern salmon breeding programmes, the pedigree and trait data collected have been used to calculate BLUP breeding values for selection candidates (Henderson, 1973). BLUP has been extensively utilized in selection programmes of salmon, however, since the development of the first high density SNP arrays (e.g. Houston et al., 2014a; Yanez et al., 2016), genomic selection has become more commonplace. The advantages of genomic selection have been shown in several studies, in terms of improved prediction accuracies compared to pedigree methods, such as growth (Tsai et al., 2015), fatty acid composition traits (Horn et al., 2020), fillet pigmentation (Ødegård et al., 2014), resistance to sea lice (Ødegård et al., 2014; Tsai et al., 2016; Correa et al., 2017; Kjetsa and Ødegård Meuwissen, 2020), resistance to amoebic gill disease (Robledo et al., 2018b; Aslam et al., 2020b), resistance to salmon rickettsial syndrome (Bangera et al., 2017).

The large breeding programmes of salmon build up in-house R&D groups to manage data and perform the genetic evaluation, and many also collaborate with academic and private partners to develop and apply genomic tools and techniques. There are less than 10 breeding companies of salmon that have global activity. They are in Norway (Aquagen, SalmoBreed, Mowi), Chile, Canada (Cook Aquaculture, Mowi), UK (Landcatch) and Australia. They are privately owned.

4.1.3. Current/future implementation of GS in Atlantic salmon

In Atlantic salmon, GS is now routine. Traits that are not measurable on the selection candidates themselves benefit most from GS compared to pedigree selection. Most of the breeding companies have developed their own SNP chips and use them for GS in Atlantic salmon. Some of these SNP chips have already been refined several times for the quality of the SNPs, e.g. density, polymorphism rate, trait effects etc. There has been substantial interest in optimizing SNP density to reduce genotyping costs. Due to the large full-sibling families used in salmon breeding, the reference population normally contains very close relatives to the validation population. This close relationship means that relatively sparse markers can be used to accurately define genomic relationships, and much of the benefit of genomic selection is due to more accurate estimation of the within-family component of genetic variation. However, most programmes routinely use a ~50–70k SNP chip, partly due to the high volume of samples resulting in competitive prices per chip. Imputation from low to high density has also been investigated (e.g. Yoshida et al., 2018a; and 2018b; Tsairidou et al., 2020) with high prediction accuracy shown even with just several hundred markers. However, imputation to sequence data has not yet been tested with success, and may hold promise for downstream improvements in prediction accuracy.

4.1.4. Challenges for genomic selection in Atlantic salmon

Genomic selection accuracy and performance is high in the context of sib-testing schemes in salmon, due to the aforementioned close relationships between reference and validation populations. However, as that relationship becomes more distant, the accuracy drops off rapidly. For example, prediction accuracy in a specific year group of a breeding programme was shown to be near zero when another year group was used as the training population (Tsai et al., 2016). Therefore, a major challenge is to improve prediction accuracy in distant relatives, which may reduce the need for routine phenotyping. To meet this challenge, identification of functional variants impacting the trait may be key, and employing a suite of modern genomic and genome editing tools will assist with that process (Houston et al., 2020). The value of enrichment for functional variants in increasing prediction accuracy, and in the persistence of that prediction accuracy across distant relatives can then be evaluated more thoroughly, in conjunction with population-scale whole genome sequence data on the populations. Integration of interaction with triploidy by genomic selection is another field of development of genomic selection to limit impact of escapees in improving performances of triploids (Kjøglum et al., 2019; Grashei et al., 2020).

4.2. Rainbow trout (Oncorhynchus mykiss)

4.2.1. General context

The rainbow trout (also sometimes known as steelhead trout) *Oncorhynchus mykiss* (Walbaum, 1792) is a salmonid fish species native to cold waters of the Pacific Ocean in Asia and North America. Given its popularity for both recreational angling and aquaculture, since the end of the 19th century, the species has been widely introduced to suitable waters around the world (Halverson, 2010). Rainbow trout aquaculture started to substantially expand from the 1950s with the development of pelleted feeds, and it is now one of the main species cultivated in cold freshwater habitats around the world, with particular focus in Europe, the Americas and Asia (Janssen et al., 2017; D'Ambrosio et al., 2019). As a result of ongoing aquaculture efforts, several local domesticated strains have been developed, while others have been produced through mass selection and crossbreeding for improved cultural qualities (Cowx, 2009). On a country basis, Chile (currently the largest producer), Peru, Japan, Australia, Iran, and the USA are among the largest producers. In Europe, the main producers are Norway, France, Italy, Denmark, Germany, UK and Spain (Cowx, 2009). On a world scale the rainbow trout aquaculture is currently worth over USD 3.8 billion with Europe (USD ≈ 1.39 billion), Asia (USD ≈ 1.97 billion) and the Americas (USD ≈ 1.24 billion) as the major producers (source FAOSTAT database 2018).

4.2.2. Past and current status of selective breeding in rainbow trout

Rainbow trout selective breeding programmes date back from the end of the 19th century with earlier efforts orientated towards improving fecundity, delaying time to sexual maturation, and off-season spawning (Chavanne et al., 2016; Janssen et al., 2017). Following the substantial expansion of the rainbow aquaculture industry in the 1950s, hatcheries started to further develop selective breeding programmes in Norway, USA, France, Finland, Denmark and Chili aiming at the improvement of additional traits relevant to aquaculture including improved growth performance and body weight, carcass yield and fillet quality and disease resistance (D'Ambrosio et al., 2019) for different kind of products as pan size (350 g) and large trout (2−4 kg) reared in fresh water or large trout reared in brackish or sea water (2−4 kg). Recent advances in genomics resources for the species, including access to the full genome sequence information (Berthelot et al., 2014; Gao et al., 2021), detailed genetic maps (Guyomard et al., 2012, Gonzalez-Pena et al., 2016; Fraslin et al., 2018) and species-specific SNP chips (Palti et al., 2015a) are now providing the means to new and more powerful approaches to the further development and monitoring of rainbow trout breeding programmes (e.g. Reis Neto et al., 2019).

4.2.3. Current and future implementation of GS in rainbow trout

Current rainbow trout selective breeding programmes were predominantly based on mass selection for growth or and/or a combination of marker selection on growth and sib selection to improve other desirable traits for aquaculture (e.g. Palti et al., 2015b; Liu et al., 2015; D'Ambrosio et al., 2020). The difficult logistics associated with family-based breeding programmes and, the often, complex genetic architecture of many traits of interest (e.g. disease, slaughter traits, female reproduction traits) makes these selection approaches challenging regarding the market (Vallejo et al., 2017). The two breeding companies in Norway use family-based selection combined with genomic selection Aquagen and SalmoBreed. Three breeding companies also use GS in France combined by mass selection (Aqualand, Viviers de Sarrance and Bretagne Truite) and at least one in Denmark (OvaSearch) and one in the USA (Clear Spring trout Company) are also investing in GS. Implementation of genomic selection in Chili is also reported in Chili by Benchmark breeding company. For decades, these companies have been using family-based selection mainly for growth, sexual maturity, skeletal deformities, and other slaughter traits. Additionally, selection for disease resistance (e.g. infectious pancreatic necrosis, *Flavobacterium psychrophilum* VHS, *Piscirickettsia salmonis*) or robustness is also performed which may also include markers identified as linked to QTL. While global implementation of genomic selection in commercial aquaculture is in late when compared to Atlantic salmon, some early studies have been showing promising results. Vallejo et al. (2017) have shown that the accuracy of genomic prediction is significantly higher than estimates generated from traditional pedigree-based methods for bacterial cold-water resistance in rainbow trout. In a comparison involving traditional pedigree-based approaches and genomic prediction, Yoshida et al. (2019) suggested that the latter method could be used to improve the accuracy of breeding values for resistance against infectious pancreatic necrosis virus in rainbow trout. Silva et al. (2019), examining the genetic architecture of columnaris disease in rainbow trout, argued that genomic-wide selection is better to predict future performance in comparison to pedigree-based selection. D'Ambrosio et al. (2020) suggested that genomic prediction would allow significant gains of accuracy in comparison to pedigree-based approach for predicting female reproduction traits (body weight, spawning date, fecundity, and egg size). Genomic SNP array was also used to trace back population effective size from the 10 previous generations based on ROH (Run of Homozygosity) fragments in 3 commercial lines to evaluate the positive impact of introduction of optimum contribution selection on genetic management practices in France (D'Ambrosio et al., 2019).

4.2.4. Challenges for GS in rainbow trout

The ongoing implementation of GS in rainbow trout mentioned before shows that several companies have estimated that the benefits of GS offset its additional cost. This may be due to the fact that many rainbow trout breeding programmes implement selection for traits measured on sibs (disease resistance, fillet yield, fillet colour) which are the most susceptible to benefit from improved prediction accuracy with GS. The challenges are somewhat similar to Atlantic salmon, including improving persistency of prediction accuracy across generations, which may reduce the need for routine phenotyping. Furthermore, incorporating functional genomic information to enhance prediction accuracy is likely to become more routine in the coming years, including in interaction with triploidization as in salmon and will require improved knowledge of the functional variants impacting on traits of commercial interest.

4.3. Atlantic cod (Gadus morhua)

4.3.1. General context

Atlantic cod is a marine species of great commercial interest, whose distribution ranges from the East coast of the USA to Greenland, Iceland, Norway and along the west coast of Europe. Juvenile production of Atlantic cod started in the 1980s in Norway, resulting in a few 100,000 fish per year in the late 1990s. Production at this time was extensive, with no targeted breeding, and generally not profitable, resulting in closure of all companies. New attempts to produce Atlantic cod started in the early 2000s with the first successful intensive hatcheries and production. Structured breeding programmes showed potential for improvement of cultured stocks of Atlantic cod, and major improvements were made both in rearing practices as well as genetic improvement of growth traits. Production peaked at around 60 million juveniles overall. Yet, biological challenges, such as early maturation, juvenile deformities, high mortality rates in sea cages, and the financial crisis of 2008 greatly affected the industry. In 2014, commercial aquaculture of Atlantic cod was effectively shut down. Two main actors in Norway continued their breeding programmes and commercial production resumed in 2018 with improved growth rate as the result of selective breeding, improved rearing practices, diets and economics. The reduction in fishing quotas from natural populations of Atlantic cod also drove the interest for cod farming in Norway. To date there are still only a few producers, but interest for cod aquaculture is on the rise again.

4.3.2. Past and current status of selective breeding in Atlantic cod

There are two main actors of Atlantic cod breeding nowadays, both of which are located in Norway: a national programme run NOFIMA, with the aim of making cod aquaculture profitable by selective breeding based on the model of Atlantic salmon, and currently produces around 400,000 juveniles per year, and a private breeding programme Havlandet Marin Yngel that currently produces around 3 million juveniles per year. The main traits selected for in Atlantic cod have been growth rate, morphology (absence of deformity, condition factor), as well as disease resistance. The latter has not yet been successfully addressed through selective breeding and disease challenges, but is now relatively well managed with vaccines and prophylactic measures. Several selective breeding strategies have been used to date: phenotypic selection and breeding value estimation. Phenotypic selection relies on selecting the best individuals based on their phenotypes, without pedigree information. In contrast, breeding value estimates are calculated using Best Linear Unbiased Prediction (BLUP) based on pedigree information and phenotypic observations from all family members and breeding candidates. In both approaches, special care is taken to limit inbreeding, either through Optimal Contribution Selection (OCS) or through producing a very large number of families.

4.3.3. Current/future implementation of GS in Atlantic Cod

There has been no genomic selection implemented in Atlantic cod aquaculture to date. Atlantic cod aquaculture is still in its infancy, and optimal rearing techniques are now just being developed. However, Atlantic cod is in a unique position to be starting aquaculture programmes at a time where many genomic resources are already available for the species. Most of these resources have been developed in the context of wild Atlantic cod, but are directly relevant to aquaculture. In particular, the genome of Atlantic cod has been fully sequenced and is publicly available (Torresen et al., 2017) and SNP chips and linkage maps are also available (Hubert et al., 2010; Pocwierz-Kotus et al., 2015). These resources could be directly used for implementation of genomic selection in Atlantic cod aquaculture for traits of interest, such as sexual maturation – which is currently the biggest bottleneck in cod aquaculture –, feed efficiency, skin health, overall immune system and muscle mass. Family-based breeding for several generations combined with the genomic resources for Atlantic cod will provide the ideal set up for implementing genomic selection in this species. Demonstration of GS in the NOFIMA population is underway alongside the development of a SNP chip for the species.

4.3.4. Challenges for GS in Atlantic Cod

The main challenges for genomic selection in Atlantic cod aquaculture rests in the fact that this is a young industry with not many private producers whose rearing techniques and economic profitability still need to be validated. However, although costly, implementing genomic selection at such an early stage might be easier than it would be for other more established aquaculture species. Additionally, the large amount of genomic resources and the technical and scientific expertise of the actors in Atlantic cod aquaculture and Atlantic cod research in general might facilitate the implementation of GS.

4.4. American catfish (channel catfish: Ictalurus punctatus and blue catfish: Ictalurus furcatus)

4.4.1. General context

The closely related Ictalurid catfish species *Ictalurus punctatus* (channel catfish) and *Ictalurus furcatus* (blue catfish) are native to North America and have long been used as a source of dietary protein in the United States. The farm-raised catfish industry accounts for more than half of total U.S. aquaculture production, and approximately half the total value. The 2018 Census of Aquaculture (USDA, 2018) reported catfish sales of $367 million (USD) from 531 farms, with 93 % of production based in the states of Alabama, Arkansas, and Mississippi. The regional economic impact exceeds $4 billion and the industry employs more than 10,000 people in the Deep South, the most economically underdeveloped region of the United States. Catfish are primarily raised in earthen ponds and recent advances in production systems have increased production in fewer acres of water. The success of the catfish aquaculture industry depends on a consistent supply of a high-quality product that meets consumer expectations for flavor, color, texture, and firmness.

4.4.2. Past and current status of selective breeding in American catfish

The first catfish genetics and breeding programmes started at Auburn University in the 1950s and 1960s (Dunham, 2006). In the decades since, breeding programmes for North American ictalurid catfish have developed and diminished at various institutions (e.g. University of Georgia, Mississippi State University, U.S. Fish and Wildlife Service) however, these programmes did identify the blue and channel catfish as the best species for use in commercial culture. They also established the blue x channel F1 hybrid as the best interspecific hybrid (Dunham, 2006). In the past ten years, commercial producers have increased their production of F1 channel-blue hybrids (female channel x male blue) which have the characteristics of faster growth, improved disease resistance, and larger fillet yields (Geng et al., 2016; Dunham et al., 2008). Based on reported acreage (USDA, 2018), hybrid production now comprises approximately 50 % of US catfish production. Most producers are small, family-owned operations, so genetic improvement endeavors have primarily been conducted by public entities (Abdelrahman et al., 2017). At present, institutions with major involvement in genetic enhancement are Auburn University and the U.S. Department of Agriculture (USDA), Agricultural Research Service (ARS), Warmwater Aquaculture Research Unit (WARU) in Stoneville, Mississippi (Dunham, 2006). Researchers at the University of Georgia have also recently collaborated with WARU to test genomic selection (Garcia et al., 2018). Genomic resources for these species include a high-quality reference genome for the channel catfish; 98 % of the 783 Mb genome is captured in 594 scaffolds (scaffold N50 = 7.73 Mb), genetic mapping of over 250, 000 SNPs has validated the assembly, and 99.1 % of the reference genome has been anchored to chromosomes (Zeng et al., 2017; Liu et al., 2016). A reference genome for blue catfish has also been produced (Waldbieser and Liu, in preparation). Currently, four commercial catfish Affymetrix Axiom arrays are available, a 250 K array (Liu et al., 2014), a 690 K array (Zeng et al., 2017), a 660 K array and a 57 K arrays (Waldbieser, unpublished). Several studies have also identified QTL for several important traits in catfish culture (e.g., disease resistance, hypoxia tolerance, heat stress).

4.4.3. Current and future implementation of GS in American catfish

To support the long-term sustainability of catfish aquaculture, ARS WARU is conducting a genomic selection programme for channel and blue catfish. A synthetic line of channel catfish, “Delta Select”, was produced from a base population of fish obtained from ten commercial farms. Microsatellite markers were used to determine spawn parentage, and the pedigreed population underwent two generations of selection for increased growth and carcass yield using estimated breeding values derived from standard animal breeding approaches. Early in the genomic selection programme, preliminary research revealed that existing SNP genotyping platforms showed an ascertainment bias in SNP polymorphism. Therefore, genomic DNA was re-sequenced from 49 founder individuals to a depth of 5X genome coverage, the sequences were mapped to the channel catfish reference genome (Liu et al., 2016), and 7.4 million putative SNP loci were identified in silico. After screening 660,056 SNP loci for polymorphism and Mendelian transmission, a subset of 57,354 Delta Select SNPs were arrayed that were separated by an average distance of 13.3 kb. The 2015 year-class Delta Select broodfish were selected based on the same index for growth and carcass yield, except that EBVs were replaced with genomic estimated breeding values (GEBVs). The GEBVs were derived based on growth and

carcass yield phenotypes, pedigree information and SNP genotypes using the single-step methodology developed at the University of Georgia (Misztal et al., 2016). The analysis indicated that whole genome selection based on GEBVs would increase accuracy of breeding value estimates for growth by 28 % and carcass yield by 36 % (Garcia et al., 2018). Comparison of the Delta Select line to an unselected control line, developed from the same base population, indicated response to selection after 3 generations of selection, and led to a 25 % increase in growth rate and 0.9 % increase in carcass yield (Bosworth et al., 2020). It is estimated that an increased growth rate of 14–20 % and an increased filet yield of 0.3−0.6% over two generations of channel catfish would add $7−12 million annual profit to the catfish industry above current production costs. Additional phenotypic data has been collected on body composition and reproductive traits; heritabilities and genetic correlations for these traits will be estimated to determine if they warrant inclusion in a selection index. The WARU released Delta Select germplasm to U.S. catfish producers in February 2020.

A GS programme for blue catfish was recently initiated. Preliminary performance trials of a diverse collection of blue catfish germplasm has revealed founder broodstock. A team from WARU and Auburn produced a chromosome-level blue catfish reference genome (Waldbieser and Liu, unpublished), identified 2.1 million putative SNP loci in the blue catfish breeding population, and assembled 660,000 SNP loci onto an array for genotype validation (Waldbieser and Bosworth, unpublished). Blue catfish will be selected with a focus on improving the performance of F1 hybrid offspring of blue catfish sires and channel catfish dams. Hybrid fish are valued by catfish producers for their superior performance in commercial culture. The WARU released blue catfish germplasm to U.S. catfish producers in April 2020.

4.4.4. Challenges for GS in American catfish

Challenges to implementing genomic selection include the costs associated with developing the genotyping array and the costs of genotyping a sufficient number of individuals to obtain enough individuals as selected broodstock without significantly increasing inbreeding in the population. Toward that end, continued genomic selection of the Delta Select channel catfish population will include addition of new germplasm from commercial sources. Genomic selection of blue catfish is beginning, and will demand a longer-term investment as blue catfish require one or two more years to mature compared with channel catfish. Along with addition of new phenotypes to selection indices, new genomic selection strategies must be developed to select purebred catfish for optimal F1 hybrid performance, and here the industry can learn from genomic selection approaches used in terrestrial livestock (e.g. pigs) cross-breeding programmes.

4.5. Pacific oyster (Crassostrea gigas)

4.5.1. General context

Pacific oyster is the primary farmed mollusc species in many regions of the world, due to its fast growth and robustness to diverse environments (FAO, 2005). Originally from the North West Pacific, it has been widely introduced to North America (since 1920s), Australia and New Zealand, and Europe (since 1960s), either to replace depleted native stocks or to instigate new industry. Since then, further introductions and distribution across countries has resulted in the species being one of the most farmed aquaculture species globally, with 574 K tonnes produced in 2016 (FAO, 2005). Pacific oyster is also been listed as invasive in an increasing number of countries (FAO, 2005). While initial culture methods in Japan, Korea and China were typically entirely reliant on settlement of wild spat, which remains the main source of juveniles in numerous countries, control of reproduction has allowed the development of hatcheries, allowing the production of seed outside of optimal environmental conditions and increasingly from selective breeding programmes (reviewed by Hollenbeck and Johnston, 2018), and/or using polyploids.

Historically, European broodstock originated either directly from Japanese populations, or populations sourced from British Columbia, Canada (Troost, 2010). However, during the following years there was substantial movement and sharing of stock between European nations to the extent that direct tracing of broodstock origin has become impractical, although population genetic studies clearly distinguish two main clusters (Lallias et al., 2015). Contemporary hatchery practice involves ownership of unique broodstock, and as such it is now possible to identify northern and southern hatchery populations, reflecting the historical introduction routes of the species in Europe. However, there continues to be mixing of stocks throughout Europe, between both hatchery and naturalized populations, alongside additional smaller scale introductions from Japan (Vendrami et al., 2019). In Australia and New Zealand, more direct links can be made between original broodstock introductions and source populations in Japan (Kijas et al., 2019).

4.5.2. Past and current status of selective breeding in Pacific oyster

A primary focal trait for oyster selective breeding programmes has been increased growth rate, which is straightforward to measure on selection candidates themselves. In oysters, growth rate and weight traits can refer to the animal including the shell, but the weight of the oyster without the shell (‘wet weight’), or meat to shell ratio, is also a target for improvement. Superior growth of triploid oysters is one of the main reasons why they have been increasingly produced since the 1900′s.

Disease resistance became the key target trait for improvement in Pacific oyster, primarily due to the global disease outbreak caused by ostreid herpesvirus 1 (OsHV-1) µVar, which severely affected the industry in most oyster producing countries (Pernet et al., 2016). Promisingly, host resistance to OsHV-1 is heritable and over 60 % improvement in survival was observed with mass selection versus unselected controls in response to OsHV-1 exposure after four generations (Degremont et al., 2015). Since then most oyster producing nations have rolled out successful programmes breeding to improve resistance to OsHV-1; either via family based or mass selection techniques. One of the reasons that genetic improvement of disease resistance is so important in oysters is that often alternative means of disease prevention are lacking, and traditional vaccination approaches are impossible in molluscan aquaculture due to the lack of an adaptive immune system (Wang et al., 2013).

Genotype by environment interaction (GxE) is an important consideration for target traits in oyster breeding. Since individuals from a breeding nucleus are likely to be distributed from hatcheries and breeding programmes to multiple, diverse environments, the robustness of their performance for traits of interest across these environments is an important consideration (reviewed by Hollenbeck and Johnston, 2018). However, most studies report limited GxE effects.

Mass selection has been performed in Pacific oyster (as highlighted above for resistance to OsHV-1), but while effective in the short term it is unlikely to be sustainable due to a lack of control of inbreeding. Therefore, several countries have established well-managed family-based breeding programmes, including in Australia, New Zealand, the USA, and France (reviewed by Hollenbeck and Johnston, 2018). Family-based selection enables the incorporation of multiple traits into the breeding goal (in contrast to mass selection), and also to include traits that are not measurable on the selection candidates themselves. This is particularly relevant to Pacific oyster breeding because disease resistance is a key trait, and often such traits are measured on relatives of selection candidates. However, in some cases (e.g. in New Zealand) breeding from survivors has been successfully practiced (Azema et al., 2017; Gutierrez et al., 2020).

Almost all breeding programmes were initially publicly funded. Some programmes, for example in France, USA, New Zealand and Australia, have now been taken on by industry-led bodies or private companies. There are also genetic services companies that provide breeding programme support and management to hatcheries and

producers.

4.5.3. Current/future implementation of GS in Pacific oyster

One prerequisite for genomic selection is the availability of genotyping technology for reliable genome-wide typing of large numbers of individuals. Two medium-high density SNP arrays have been developed for Pacific oyster (Gutierrez et al., 2017; Qi et al., 2017) which are suitable tools for testing genomic selection. While it is unclear whether genomic selection is operational in oyster selective breeding currently, there are studies highlighting its potential. For example, the accuracy of prediction of breeding values for growth-related traits was shown to be 25–30 % higher using genomic prediction than using pedigree-based prediction in a UK oyster population (Gutierrez et al., 2018). Furthermore, the advantages of genomic prediction were also highlighted for disease resistance, with approximately 19 % higher accuracy compared to pedigree methods (Gutierrez et al., 2020). Interestingly, in both studies, the marker density required to achieve this increase in accuracy over pedigree methods was only approximately 1000 SNPs. This is likely to be due to the fact that most of the benefit comes from capturing the within-family component of genetic variation for large full sibling families, and therefore the training and reference populations share long genomic segments captured effectively by few markers. However, further testing of this theory would require additional studies, including in larger populations under selection.

GS implementation is still in its infancy when compared to salmon or trout. First implementation are reported in New-Zealand by the Cawthron Institute for the industry (Gutierrez et al., 2020) France by Vendée Naissain breeding company in using the 57 K SNP chip developed by Gutierrez et al., (2018). An alternative was also proposed in using DArT-Seq Technology in Vietnam in another closely-related species Crassostrea angulata (Vu et al., 2021) to improve morphometric traits, shell length, shell width, shell depth and shell weight with estimated genomic heritabilities ranging from 0.28 to 0.55. At this date, the estimation of genomic accuracy is still limited to only few traits.

GS is particularly useful for traits that are expensive or difficult to measure on the selection candidates themselves. In family–based selective breeding programmes, routine testing of siblings is performed. This is usually the case in oysters, although sometimes breeding populations themselves are phenotyped directly (Symonds et al., 2019). Genomic selection enables breeding values to be estimated more accurately, as described above, by capturing the within-family component of genetic variation. Therefore, such traits may include disease resistance (field trials and experimental challenges) and invasive traits such as meat quantity or quality.

GS therefore improves accuracy of selection, especially for traits measured on sibs, due to capturing both within and between family genetic variation in the traits. The higher accuracy leads to equivalent improvement in genetic gain in the breeding programmes. Possibility of predicting breeding values across generations without additional phenotyping needed to be estimated as the the genomic diversity of haplotypes that segregates (and their recombination at each generation) in this species may rapidly blur the relationship between phenotypes and genotypes.

To fully capitalize on the benefits of genomic selection in oyster breeding it is necessary to genotype many selection candidates and test populations (e.g. siblings), and this is very expensive using currently available genotyping technologies (SNP arrays or genotyping by sequencing). Very cost-effective genotyping and phenotyping solutions are needed. The use of polyploids complicates applications of genomic selection but some methodologies used in plant breeding could be adapted to oysters.

4.5.4. Challenges for GS in Pacific oyster

An economic assessment of the benefits offered by genomic selection relative to the extra costs of genotyping needs to be undertaken. This is particularly the case for the highly fecund Pacific oyster which can produce tens of millions of offspring per single cross, and the value of any individual offspring is very low. New genotyping techniques such as genotype imputation, where parents are genotyped at high density and offspring are genotyped at low density and imputed to high density, may be more cost-effective. Optimized molecular protocols: standard molecular biology techniques such as obtaining high quality DNA and genotyping are more challenging in oysters than for other species, and the process of reliable sampling and processing for genotyping from commercial operations will need optimized. This will be particularly the case for high-throughput sequencing (e.g. if genotyping by sequencing is used rather than SNP arrays).

Detailed understanding of how hatchery practices impact inheritance, larval survival and in particular the potential of introducing artificial selective bias (see (Plough, 2016) that may later be a cause of GxE and reduce the field accuracy of GS is needed.

Shellfish farming has historically been an industry made of many small businesses based on wild seed. This model previously left minimal capital for investment. Some of the contemporary larger hatchery companies are testing application of genomic selection. Adaptation of genomic selection methods for improvement of triploid or tetraploid performance is needed, since current studies and theory are largely based on diploids.

4.6. European sea bass (Dicentrarchus labrax)

4.6.1. General context

Aquaculture of European sea bass has been traditional in “valli” (lagoon enclosures) in Italy, but the onset of large-scale production came when controlled reproduction, hatchery and cage ongrowing methods were developed in the early 1980′s. Cultured sea bass production exceeded capture for the first time in 1991, and now represents 96 % of the total production of this species, which reached 221,000 t in 2017 (FAO).

The first captive broodstock of European sea bass were established in France and Italy in the 1990′s, based on fish sampled in West-Mediterranean and Adriatic Sea. Since then, other broodstock populations have been established from both Eastern Mediterranean and Atlantic populations. The oldest domesticated stocks had been bred in captivity for 8 generations without input from wild stocks in 2016 (Chavanne et al., 2016).

4.6.2. Past and current status of selective breeding in European sea bass

The first trait of interest has been growth rate, similar to other fish selective breeding programmes (for a review, see Vandeputte et al., 2019). Avoidance of deformities, which can reach a high incidence as in many marine species, have also been a trait of interest (Bardon et al., 2009). Disease resistance is also a key trait, with the main disease targeted being viral nervous necrosis as it is the primary disease problem for Mediterranean aquaculture (Griot et al., 2021). Other important diseases for which selective breeding is now investigated as a possible solution are vibriosis and diseases caused by parasites such as *Diplectanum spp*. and isopods. Recent traits of interest for genetic improvement include feed efficiency (Besson et al., 2019) and processing yields.

Individual selection has been and remains the main selection method used in sea bass breeding programmes. However, family selection, including BLUP using molecular pedigrees or separate rearing of families is used in several programmes, in some cases including testing of full siblings of the selection candidates for disease resistance traits (Chavanne et al., 2016). Genomic selection has been trailed (see below), and the fist sea bass selected using genomic selection are on the market since 2019.

Companies with breeding programmes for sea bass are located in France (Ecloserie marine de Graveline, Ferme Marine du Douhet), Greece (Nireus), Italy and Turkey. They are all private companies that are selling juveniles or fertilized eggs to on-growers or hatcheries. There are also genetic services companies that provide breeding programme

support and management to hatcheries and producers.

4.6.3. Current/future implementation of GS in European sea bass

Initially, genome-wide genotyping studies in sea bass have been initiated using a genotyping by sequencing method known as RAD-sequencing as part of the European Union FP7 project FISHBOOST (Palaiokostas et al., 2018). However, SNP arrays are likely to be the standard genotyping method for commercial application of genomic selection. In 2017, a 3 K Illumina SNP Chip was developed (Faggion et al., 2019), and in 2018 a 57 K Thermofisher SNP-Chip was developed by a French consortium (Griot et al., 2021). Two EU projects, MedAid and Performfish have also developed a combined-species (European sea bass, gilthead sea bream) with 35 K SNPs of each species included (Penaloza et al., 2020). GS is now applied at least by two breeding companies in France Ecloserie marine de Graveline and Ferme Marine du Douhet since 2018 (Aquaculture Europe, 2019).

Genomic selection is most suitable for traits that are difficult or expensive to measure directly on the selection candidates themselves, such as disease resistance, feed efficiency, or fillet traits. Genomic selection has been shown to improve the accuracy of prediction of VNN resistant and susceptible sea bass by approximately 13 % (Palaiokostas et al., 2018), and is thus a suitable technique to improve genetic gain for this trait. A new technique to evaluate individual feed efficiency in individual aquaria has recently been developed in sea bass, and it was shown that the reliability of EBVs was 10–125% better with genomic selection, with a reference population of limited size (<350 individuals), which is of special interest as individual phenotyping of fish for feed efficiency is costly and tedious (Besson et al., 2019). For this trait, GS could be an attractive option, as an important selection pressure could be applied on candidates not genotyped for feed efficiency, using a prediction equation established on a limited number of phenotyped siblings.

4.6.4. Challenges for GS in European sea bass

As in all species, the cost of implementation is of course a challenge, however several sea bass breeding programmes already use marker-based parentage assignment to establish pedigrees. In that sense, the step is smaller for them, as DNA collection and some genotyping costs are already routinely implemented in those breeding programmes. One challenge which is not specific to GS is the fact that sea bass sex determination is polygenic and influenced by temperature, resulting in often unpredictable and imbalanced sex-ratios, which prevent optimal use of resources by restricting the possibility to apply similar selection pressures on both sexes. In addition, it is generally difficult to obtain synchronized spawns from all females in a broodstock and thus female broodstock census size is generally at least twice larger than the effective number of females used, leading to extra costs, especially if selection implies expensive genotyping. This could make it challenging to perform crosses from targeted individuals with the highest breeding values identified using GS approaches, and therefore reduce the additional genetic gain and control of inbreeding.

4.7. Gilthead sea bream (Sparus aurata)

4.7.1. General context

The gilthead sea bream is an important migratory and demersal commercial species, highly appreciated as food fish. It prefers warm coastal euryhaline waters and its life-cycle is determined by protandrous hermaphroditism. It is reared both in sea cages and in land based farms. Global production has reached 185,980 metric tonnes in 2016, primarily from aquaculture. It is the main premium marine aquaculture species in the Mediterranean region.

Gilthead sea bream has been cultured in Mediterranean coastal lagoons and brackish/salt water ponds for centuries, especially confined areas, such as the northern Adriatic valli in Italy and the Egyptian hosha. These extensive fish rearing systems act as natural fish traps, taking advantage of the natural trophic migration of juveniles from the sea, though often restocking has been performed with wild fry and juveniles to enhance production. However by the late 1970s the reduced and irregular availability of wild fry and the increasing demand of juveniles for intensive culture accelerated the development and the implementation of induced spawning techniques. The mass production of gilthead sea bream, based on a reliable and consistent supply of hatchery fry and juveniles, started in the late 1980s. Broodstocks were established independently in various hatcheries in several countries, often mixing up fish from different geographic origins. A population genetic survey based on a medium SNP panel (approximately 1500 loci) was carried out within the framework of the EU-funded project AquaTrace revealed limited genetic differentiation between natural populations across the entire distribution range of the species. Likewise, most broodstock populations were genetically similar to wild ones, although those putatively being subject to genetic selection for several generations showed higher divergence (Maroso et al., 2020)).

4.7.2. Past and current status of selective breeding in gilthead sea bream

The first trait of interest has been growth rate, as is typical for early breeding programmes for fish species (for review see Vandeputte et al., 2019). The first trials on selective breeding of sea bream were carried out in the mid-1990s and it was only in the early 2000s that the first commercial breeding programmes of seabream were initiated (Chavanne et al., 2016; Janssen et al., 2017). Deformities, which can reach a high incidence as in many marine species, have also been a trait of interest. Disease resistance is also a key trait, with the main disease targeted being pasteurellosis (photobacteriosis). Heritability for resistance to this bacterial infection was reported to be moderate (0.18−0.45) (Antonello et al., 2009). Other important diseases for which selective breeding is now investigated as a possible solution are those caused by parasites such as *Sparicotyle chrysophrii*. Low heritability for resistance to *S. chrysophrii* has been reported, but GS showed increased prediction accuracy compared to pedigree BLUP (Aslam et al., 2020a). Recent traits of interest are feed efficiency and processing yields.

Mass selection remains the main selection method used in gilthead sea bream breeding programmes. However, family selection including BLUP using molecular pedigrees or separate rearing of families is used in several programmes. Artificial fertilization is less well established in the gilthead sea bream compared to other marine species, while its sequential hermaphroditism represents an additional issue to be considered in any breeding programme. Genomic selection has been shown to be potentially effective in controlled experiments, but it remains to be implemented in an industrial context.

Companies with breeding programmes for sea bream are located in France, Greece, Italy, Spain, Croatia, Israel, and Turkey. They are all private companies and are selling juveniles or fertilized eggs to ongrowers or hatcheries. There are also genetic services companies that provide breeding programme support and management to hatcheries and producers.

4.7.3. Current/future implementation of GS in gilthead sea bream

Initially, genome-wide genotyping studies in gilthead sea bream have been conducted using a genotyping by sequencing method (Robledo et al., 2018a) known as 2bRAD-sequencing (Palaiokostas et al., 2016; Aslam et al., 2018). However, SNP arrays are likely to be the standard genotyping method for commercial application of genomic selection. In 2019, a 57 K Thermofisher SNP-Chip was developed by a French consortium. Two EU projects, MedAid and Performfish have also developed a combined-species (European sea bass, Gilthead sea bream) with 35 K SNPs of each species included (Peñaloza et al., 2021). GS is now applied at least by one breeding company.

Genomic selection is most suitable for traits that are difficult or expensive to measure directly on the selection candidates themselves, such as disease resistance, feed efficiency, or fillet traits. Genomic selection has been shown to improve the accuracy of prediction of

pasteurellosis resistant and susceptible sea bream up to 24 % (Palaiokostas et al., 2016; Aslam et al., 2018), and is thus a suitable technique to improve genetic gain for this trait. Genomic selection applied since 2018 in France by one breeding company (FMD, Aquaculture Europe, 2019) and project are planned at last in Greece and Spain. The future will involve translation of this research to practical applications in the industry, and is likely to also include development of more cost-effective approaches to both genotyping and phenotyping.

4.7.4. Challenges for GS in gilthead sea bream

As in other marine farmed species, economic sustainability of GS should be carefully evaluated. Due to the challenging reproductive characteristics of the species, the application of genomic selection will have to be tailored to account for the species biology. For example, if broodstock are typically mated in groups, this creates challenges and limitations to the application of genomic selection, which tends to focus on selection based on individual EBVs. Therefore, the practical implementation of GS in the industry will face certain logistical challenges which must be overcome to benefit from GS.

5. Potential and challenges for further implementation and optimization of GS in the aquaculture breeding industry

Compared to most terrestrial farmed animal species, an advantage for selective breeding of aquaculture species is the possibility to produce very large families and different kinds of mating designs from hierarchical to factorial designs. This can increase the accuracy of the within-family component significantly.

Genotyping costs are an important limitation for implementing GS, because in addition to genotyping a large number of selection candidates, representatives from all families must be genotyped for all traits that are measured on the sibs instead of on the candidates. In the case of disease traits, this means one group per trait. In the case of slaughter traits, one group can be used for recording several traits. There are several ways to reduce genotyping costs in breeding programmes for aquaculture species. Within-family GS is a special case that can utilize these large family sizes effectively, while using very low genetic marker densities (Lillehammer et al., 2013). Genotyping of pooled DNA sib groups is one way to reduce genotyping costs (e.g. Alexandre et al., 2019), albeit with a reduced selection accuracy compared to a full GS. Genotype imputation is another promising approach which involves genotyping of key individuals (e.g. parents) at high density, and most individuals (e.g. reference populations and selection candidates) at low density, then imputing these individuals to high density. Promising results have been observed for imputation in Atlantic salmon populations, demonstrating that low density panels (down to a few hundred SNPs) combined with imputation can offer similar genomic prediction accuracy to high density panels such as SNP arrays (Kijas et al., 2016; Tsai et al., 2017; Yoshida et al., 2018a et b, Dufflocq et al., 2019; Tsairidou et al., 2020).

Many of the current challenges to the widespread implementing genomic selection-based approaches are common among aquaculture species. Among these, are the costs associated with the development of informative genotyping arrays and the subsequent genotyping of many individuals. The limitations of NGS (as an alternative genotyping approach) in terms of repeatability across generations make this approach less desirable, especially in view of a long term selection strategy. The genotyping costs are highly variable depending on the bulk of samples genotyped annually, and therefore causing relatively more challenges for the small and medium-sized enterprises (SMEs) in terms of adoptability of genomic selection than the bigger companies. Most of the breeding companies are undertaking the development of their own SNP arrays for genomic prediction due to privacy/IP issues. The huge number of arrays used/bought by bigger companies cause significant reduction in genotyping cost per samples compared to relatively small-scale operators. As the cost of arrays is dependent on the bulk of samples genotyped, the price is higher and the feasibility lower for SMEs. Therefore, the SMEs may require the technology to become cheaper or for the availability of the low-cost innovative technology. Hence, there is a danger that they may be left behind in getting timely advantage from the state-of-the-art technologies, ultimately resulting in a difference in product cost and/or quality. One of the solutions could be the development of multispecies genotyping arrays which could be used by multiple companies with joint agreement. This will increase per annum purchase of arrays, and ultimately lead to reduction in cost. Other possible ways which can make SMEs to stay competitive include smart genotyping and application of within family genomic selection (Lillehammer et al., 2013), using genotype imputation (Tsairidou et al., 2020), and/or applying combined 'single-step' relationship matrix which could link genotyped and ungenotyped individuals (Legarra et al., 2009). As suggested by Yoshida et al. (2018a; and 2018b), genomic prediction could provide an alternative approach to improve the accuracy of breeding values for complex traits for which more traditional methods have not been effective. In addition, rapid developments in genomics now allow for incorporation of functional genomic information into genomic prediction, including potential use of intermediate phenotypes such as gene expression or DNA methylation, which may further improve prediction accuracy (Houston et al., 2020).

While genotyping technology is key to advancing GS in aquaculture, it must occur alongside developments in high-throughput phenotyping at individual level. This is likely to include significant technological advances in the coming years, including increased automation and use of machine learning approaches. For example, when considering phenotypes relating to fillet quality taken from tissue samples, there are options for both invasive and non-invasive measurements at scale. phenomic selection (PS) was recently proposed as an alternative (or complement) to GS (Rincent et al., 2018). The proposed method is based on the use of near-infrared (NIR) vibrational spectroscopy. Vibrational spectroscopy allows to characterize the fundamental absorption bands of the functional groups of biochemical substances that make up a sample under study and are therefore specific to an individual (i.e. chemical fingerprint or "super-phenotype"). A large number of vibration studies have been carried out to evaluate the feasibility of prediction for a number of biochemical molecules. NIR spectroscopy first became widely used in the food industry with pioneering analyses in cereals and fruits. In their proof of concept article, Rincent et al. (2018) carried out work in wheat and poplar, showing that it is possible to estimate genetic values that are as precise (or even more precise) in PS as in GS. The advantages attributed to this spectroscopic technique are the speed and simplicity of measurement, the absence of solvent use, the low cost of implementation and the repeatability of measurements. The transfer of this principle to aquatic species presents several scientific and technical challenges. The results presented by Rincent et al. (2018) were acquired from NIR spectra of lignified tissues whereas biological samples of aquaculture species are very rich in water, which might be problematic. An alternative to NIR spectroscopy could be the use of Raman scattering spectrometry. Feasibility and potential of PS in sea bream and Pacific oyster is currently explored in France.

Such novel genomics and phenotyping technologies, combined with associated advances in both statistical methodology and computing, are likely to result in significant new opportunities to improve GS in aquaculture. Furthermore, as the genomics and phenotyping technologies become more affordable, combined with tailored methods to apply low-cost methods to smaller-scale aquaculture species, GS will become much more widely applied. The power of GS to dramatically increase genetic gain, while simultaneously offering improved control of inbreeding, means that its potential is now widely recognised and much research is underway across the world. As this research develops and translates into novel commercial applications, the benefits of GS are going to translate to a much larger proportion of global aquaculture species and production. This will have significant downstream benefits for the sustainability of aquaculture and its future role in meeting the global animal

protein demands of the 21 st century.

Author statement

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Declaration of Competing Interest

None.

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