Chapter 17

Genomic Selection in Aquaculture Species

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Abstract

To date, genomic prediction has been conducted in about 20 aquaculture species, with a preference for intra-family genomic selection (GS). For every trait under GS, the increase in accuracy obtained by genomic estimated breeding values instead of classical pedigree-based estimation of breeding values is very important in aquaculture species ranging from 15% to 89% for growth traits, and from 0% to 567% for disease resistance. Although the implementation of GS in aquaculture is of little additional investment in breeding programs already implementing sib testing on pedigree, the deployment of GS remains sparse, but could be boosted by adaptation of cost-effective imputation from low-density panels. Moreover, GS could help to anticipate the effect of climate change by improving sustainability-related traits such as production yield (e.g., carcass or fillet yields), feed efficiency or disease resistance, and by improving resistance to environmental variation (tolerance to temperature or salinity variation). This chapter synthesized the literature in applications of GS in finfish, crustaceans and molluscs aquaculture in the present and future breeding programs.

Key words Genomic selection, Aquaculture, Finfish, Crustaceans, Molluscs, Accuracy, Genotype-by-environment

1 General Introduction

Since the 1980s, seafood aquaculture production (i.e., excluding seaweeds) has been multiplied by more than ten and its economic value by more than 25 (Fig. 1). Aquaculture is today the worldwide fastest-growing food production sector now exceeding fisheries production. In 2019, aquaculture produced more than 85 million tons of seafood for a total value of over 250 million dollars [1].

However, most of the producers use wild fish and shellfish or stocks just entered in domestication for a few generations [2]. Aquaculture breeding programs are recent and limited to about 60 species [3] (out of ~1200 species reared in aquaculture—[1]). Many started with simple mass selection for growth and morphology. But, in the last decades, selective breeding demonstrated its important role in boosting the domestication of

Nourollah Ahmadi and Jérôme Bartholomé (eds.), *Genomic Prediction of Complex Traits: Methods and Protocols*, Methods in Molecular Biology, vol. 2467, https://doi.org/10.1007/978-1-0716-2205-6_17,

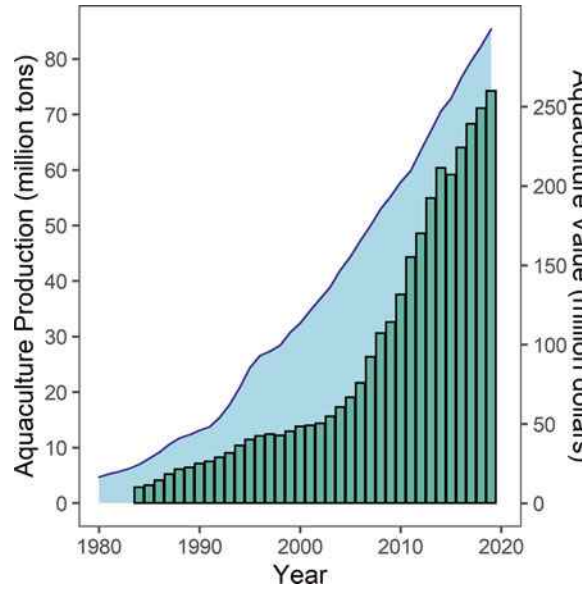

Fig. 1 Evolution of aquaculture seafood production per year in million tons and economic value in million dollars

aquaculture species and improving the performances and the sustainability of seafood production [3, 4], to meet the growing global demand for animal protein [2]. As a result, conventional genetic improvement based on pedigree and phenotype has successfully improved the productivity of many aquaculture species, with an average genetic gain of 5–18% per generation for growth traits [3, 5, 6]. Most genetic improvement programs have focused on selecting for rapid growth, mainly due to its ease of measurements and its supposed economic importance in production systems. However, several studies underline the importance to select traits linked to efficiency (feed efficiency, processing yields...) [7–11] or resilience-related traits (disease resistance [12, 13], hypoxia, or salinity tolerance...) to meet a sustainable development of aquaculture. Those traits are often lowly heritable or difficult/expensive to measure, such as disease resistance that requires challenge tests, or carcass and flesh quality that requires slaughter of siblings of breeding candidates, are not well studied [8, 14]. When genetic improvement programs are underway, the breeding objective for aquaculture species should be broadened by including new traits to meet the growing demands of the sector as well as to deal with environmental challenges (e.g., salinity, temperature, or disease tolerance). Family-based breeding programs with sib selection allowed to integrate those traits recorded on the collaterals of the selection candidates. Such breeding programs were applied either, keeping families separately (like for Atlantic salmon [4, 15], Atlantic cod [4], or Pacific oyster [4, 16]), or mixing families with a

posteriori DNA-based pedigree recovery [17] (like for European sea bass (*Dicentrarchus labrax*) [18, 19], gilthead sea bream [4], or rainbow trout [20–22]). However, quantitative genetic improvement for traits measured on siblings of the selection candidates captures only a half of their genetic variation and hence, reduces genetic progress made for these traits in commercial aquatic animal populations. Since 1990s, several attempts have been made to assess possibilities for using molecular and genomic information for the genetic improvement of such "difficult to measure" traits. Nevertheless, application of marker-assisted selection (MAS) in commercial selective breeding programs is limited across aquaculture species, primarily due to limited marker availability, the small markers effect, high genotyping cost, inconsistent associations between markers and quantitative trait loci (QTL) across populations, the interaction of marker and QTL effects with genetic background and environment, and the overestimation of QTL effects [23]. In aquaculture species, only two applications of MAS have been reported for: (1) Infectious Pancreatic Necrosis (IPN) in Atlantic salmon [12], and (2) Lymphocystis resistance in Japanese flounder [24]. However, these two cases are not representative of what is more commonly found, since single QTLs are rarely found to explain such a large proportion of the variation in quantitative traits.

Since 2001, the paradigm in animal breeding has shifted toward genomic selection (GS) which use a large number of markers across the entire genome to predict animal genetic merits (breeding values) [25]. The GS technology has been quickly adopted by the dairy industry [26] and also expanded to other farmed animal industries, including aquaculture species [27]. Despite the potential benefits of applying GS across the sectors, research in aquatic animal species has begun recently in a limited number of species. This is because not many in-depth pedigreed populations of fish, crustaceans, or mollusc are currently available. In addition, phenotypic records (needed to train the genomic models) are often not maintained and there is a lack of industry structure in terms of the sector's size and organization. Another constraint is that currently, single-nucleotide polymorphism (SNP) chips are not widely deployed for fish, crustacean, and mollusc species [28, 29], and high-density SNP panels must be developed de novo at substantial costs. The advent of high-throughput genome sequencing technologies, especially genotyping-by-sequencing (GBS) that can generate a large amount of high-quality genetic markers at a reasonable cost, opens possibilities for genomic selection in non-model aquaculture species [28].

This chapter reviews recent genomic prediction studies reported for aquaculture species. Specificities of GS implementation in aquaculture are examined. The interest of GS for increasing the accuracy of prediction of breeding values is discussed, with

examples from the most important aquaculture species. Imputation strategies applied to aquaculture as well as genotype-by-environment interactions are treated. The use of GS to reduce the time generation and the association of GS with surrogate breeders is briefly addressed. Finally, prospects of GS in aquaculture are discussed.

2 Specificities of Genomic Selection in Aquaculture Species

As for livestock, in GS applied to aquaculture, a genomic prediction equation is built from a reference population genotyped for genome-wide markers and phenotyped for desirable traits. This equation is used to predict the genomic estimated breeding values (gEBV) of the selection candidates.

Classical aquaculture selective breeding programs have allowed to improve some target traits in several finfish, crustacean, and mollusc species [3]. However, numerous desirable traits (i.e., disease resistance, feed efficiency, processing yields, flesh quality) are difficult to measure on candidates and require evaluation of siblings. With a classical pedigree-based sib selection, the genetic gain achieved is limited because the selection candidates of a given family have the same genetic value, ignoring the intra-family genetic variation due to the Mendelian sampling. The main interest of GS in aquaculture breeding programs is to improve the genetic response, enhancing the accuracy of prediction by capturing this within-family genetic variation component. A second interest is, for some species, to reduce the generation interval [4, 29–32]. Furthermore, GS can reduce the rate of inbreeding [33] and in some cases, also results in increased selection intensity.

An important specificity of aquaculture species, contrary to terrestrial animals, is the external fecundation and the extraordinary fecundity allowing large-scale artificial crossing (e.g., 50 dams by 50 sires, for 1000 families). This permits the production of thousands of animals (over 10,000) with very large sire half-sibs families and dam half-sibs families, allowing to accurately estimate the genetic parameters of traits (heritability, genetic correlations) [34]. Furthermore, animals in the reference population and the candidate population are closely related (from the same families). This allows maintaining a high selection accuracy, even at low marker density (i.e., 1000–5000 SNPs) [29]. However, the limitation of the reference population size is often linked to the genotyping costs that can be prohibitive while thousands of animals per year need to be genotyped (see the following section). Finally, such large reference populations (over 2000 animals) allow multiple phenotyping strategies: growth survey in different production facilities (e.g., sea cages, tanks, etc.) and different environmental areas (e.g., cold or warm); resistance to disease by controlled viral/bacterial/

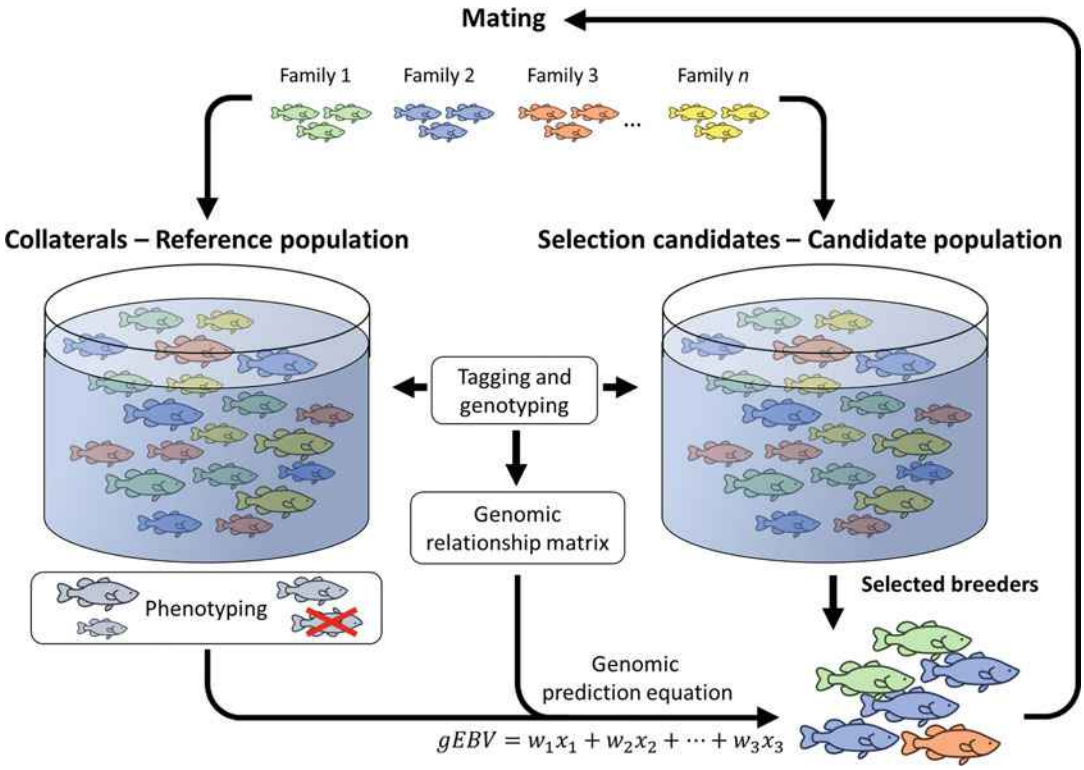

Fig. 2 Aquaculture breeding programme applying genomic selection. Hundreds of selection candidates are separated from collaterals (siblings of the selection candidates) kept for phenotypic evaluation. Collaterals are evaluated for growth in productive environments, disease resistance, lethal processing traits, or other desirable traits. All siblings are genotyped with genome-wide SNP markers. With the genomic relationship matrix and the collected phenotypes, genomic estimated breeding values (gEBV) for the selection candidates are computed using genomic selection models. Selected breeders with the highest genetic merits are used for obtaining the next generation. In the phenotyping box, on the left the big and the small fish symbolize growth survey and on the right of the box the red cross on the dead fish is for fish susceptible to a disease challenge

parasite challenges. An example of a GS breeding programme adapted from Houston et al. [29] is given in Fig. 2. Interestingly, the typical scheme of GS implementation in aquaculture programs is very similar to family-mixed selective breeding schemes with, as sole difference, the genotyping of dense genome-wide markers to estimate the genomic relationship among siblings, instead of few markers for pedigree reconstruction. Such breeding programs are good candidates for GS implementation without important operational changes. The Fig. 3 depicts a typical breeding programme for the European sea bass that have shifted to GS. In this example of breeding programme monitored by SYSAAF (Syndicat des Sélectionneurs Avicoles et Aquacoles Français), the breeding scheme has been little impacted by the evolution toward GS. The main difference is the technology used for the genotyping of the animals. In the previous traditional breeding programme (before 2017), the

animals were genotype for 14 short sequence repeats (SSR or microsatellite) markers for parentage assignment and further Best Linear Unbiased Prediction (BLUP) of the breeding values. In the current GS breeding programme the same traits are targeted including disease resistance (by controlled infectious challenges at the FORTIOR Genetics platform [36]), processing yields and growth in different environments. However, the genotyping is done with a 57,000 SNP chips [35]. This genotypic data are then used to compute the genomic relationship matrix [37] for the genomic prediction equation (genomic-BLUP–GBLUP).

Although the high fecundity of aquaculture species is theoretically an advantage, the required genotyping of all siblings (reference population and selection candidates) is a strong limitation for the adoption GS in aquaculture. However, the first limitation of GS deployment in aquaculture species is the lack of molecular resources and the cost of genotyping methods. For some advanced aquaculture species, low- to high-density SNP arrays were developed [29]. However, SNP arrays are expensive genotyping platform (over 40$ per animal), while a random aquatic animal often has a low individual economic value. Nevertheless, for most aquaculture species no or sparse genomic resources are available preventing the possible design of such genomic tools. To implement GS in such aquaculture species, it is crucial to develop cost-effective specific genomic tools. SNP panels can be produced de novo by NGS-based reduced-representation approaches, such as genotyping-by-sequencing (GBS) or restriction site-associated DNA (RAD) sequencing [23] or diversity array technology sequencing (DArT-seq) [38]. Although GBS, RAD, or DarT technologies allow to identify and genotype, thousands of SNPs in a target population, the repeatability of genotyping is limited and the quality of genotyping is weaker than using a proven SNP array.

3 Accuracy of Genomic Prediction for Important Traits in Aquaculture Species

Table 1 summarizes the comparison between pedigree-based and genomic-based accuracy of prediction in few important finfish (13 species), crustaceans (2 species), and molluscs (3 species) reviewed by Houston et al. [29] and completed by a recent literature review. Regarding growth-related traits, the average pedigree-base accuracy across all species is 0.48 (0.45 for finfish) but with a large range of variation depending on species and the population studied. With genomic prediction of growth trait (0.59 on average) the overall increase in accuracy is about 25% (26% for finfish) but with large intraspecific variation (e.g., increase of accuracy ranging from 15% to 89% in Nile tilapia). For instance, Tsai et al. [39] compared the accuracy of genomic prediction (GBLUP) and pedigree-BLUP (PBLUP) breeding values for growth traits

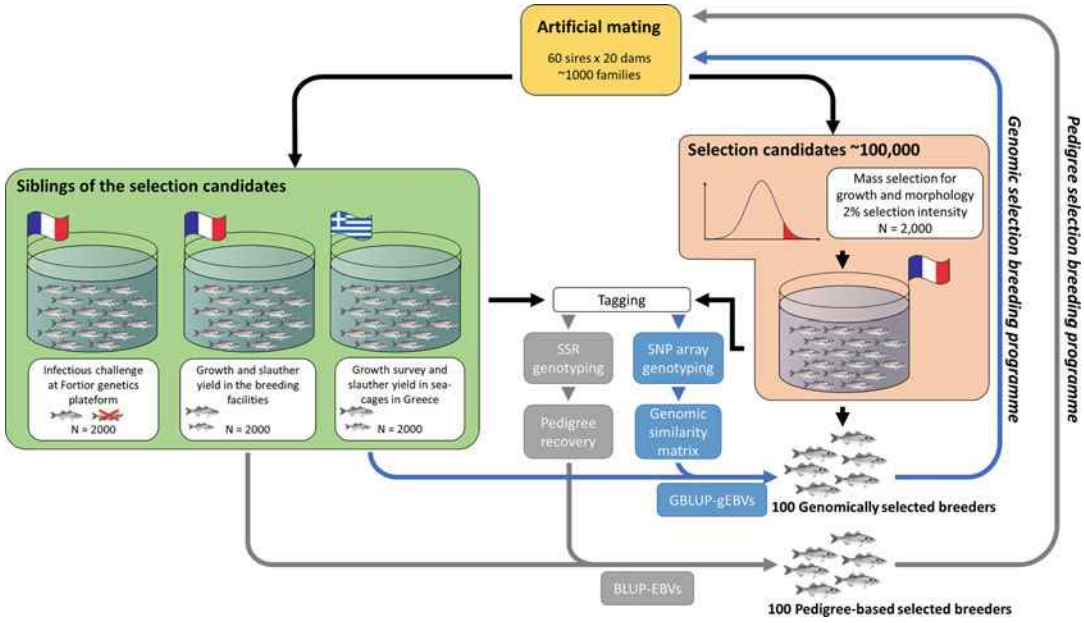

Fig. 3 Evolution of typical French European sea bass breeding programs from pedigree-based sib selection (gray boxes and arrows) to genomic selection (blue boxes and arrows). Some siblings of the selection candidates are challenged for diseases resistance (e.g., nodavirus, vibriosis, etc.), some are surveyed for growth and processing yield phenotyping in the breeding programs environment and in the typical Greek customers' environments. Mass selection for growth and morphology control is applied at a selection intensity of 2%. In the pedigree-based selection scheme, the siblings measured and the remaining selection candidates are tagged and genotyped for 14 short sequence repeats (SSR or microsatellite) markers while for genomic selection the genotyping is done by the DLabCHIP 57K SNPs array [35]. In the pedigree-based breeding programme, the genotyping is used to reconstruct the pedigree, further estimation of the breeding values (EBVs) using Best Linear Unbiased Prediction (BLUP) method. In the genomic selection, the dense genotyping is used to build the genomic similarity matrix used to estimate the genomic-EBVs by genomic-BLUP methods

(weight and length at one-year-old post-hatching) in a population of 712 fish, from 61 families reared separately, generated from Landcatch Natural Selection (LNS, Ormsary, UK) broodstock fish, and genotyped for 111,908 informative SNPs. The accuracy of EBVs for weight and length was respectively 0.58 and 0.56 for PBLUP and 0.70 and 0.66 for GBLUP, depicting a relative increase of accuracy of 21% and 18% [39]. Likewise, Griot et al. [35] compared the accuracy of GBLUP and PBLUP for predicting resistance to nodavirus in a European sea bass breeding programme managed by SYSAAF: reference population of 800 animals, phenotyped by a controlled infectious challenge at FORTIOR Genetics platform [36], and genotyped for DlabCHIP SNP array (44,772 SNPs) [35] at the GENTYANE platform (INRAE, Clermont-Ferrand, France). The accuracy of EBVs was of 0.54 for PBLUP and 0.64 for GBLUP, representing an improvement of 23% [35]. At the whole aquaculture species level, the accuracy of EBVs for diseases related traits was on average, 0.56 for genomic

Table 1
Comparison of pedigree and genomic prediction accuracy for some traits

Species	Traits	Genotyping method (number of effective SNPs)	Average pedigree accuracy (range)	Average genomic accuracy (range)	Accuracy relative increase	References
Finfish						
Atlantic salmon (*Salmo salar*)	Growth	SNP arrays (33,000–112,000)	0.57 (0.56–0.58)	0.68 (0.66–0.70)	19.5% (18–21%)	[39]
	Disease resistance	SNP arrays (7000–220,000)	0.44 (0.20–0.61)	0.53 (0.41–0.70)	23.8% (7–52%)	[40–45]
Rainbow trout (*Oncorhynchus mykiss*)	Disease resistance	SNP arrays (27,000–45,000)	0.37 (0.06–0.61)	0.53 (0.22–0.78)	70.8% (−2% to 154%)	[46–52]
Coho salmon (*Oncorhynchus kisutch*)	Disease resistance	RAD-seq (9000)	0.29 (0.27–0.31)	0.67 (0.52–0.81)	127% (93–161%)	[53]
Common carp (*Cyprinus carpio*)	Growth	RAD-seq (20,000)	0.60	0.71	18%	[54]
	Disease resistance	RAD-seq (16,000)	0.49	0.53	8%	[55]
Nile tilapia (*Oreochromis niloticus*)	Growth	SNP arrays (32,000 and 48,000)	0.37 (0.18–0.54)	0.48 (0.29–0.62)	39.8% (15–89%)	[56, 57]
European sea bass (*Dicentrarchus labrax*)	Disease resistance	SNP array (44,000), RAD-seq (9000)	0.60 (0.52–0.67)	0.64 (0.62–0.65)	9% (−7% to 25%)	[13, 58][a]
	Feed efficiency	SNP array (3000)	0.15	0.33	120%	[8][a]
Gilthead sea bream (*Sparus aurata*)	Disease resistance	SNP array (44,000), RAD-seq (22,000)	0.46 (0.30–0.61)	0.54 (0.44–0.64)	23.5% (5–47%)	[13, 59, 60][a]

Turbot (*Scophthalmus maximus*)	Disease resistance	RAD-seq (18,000)	0.46	0.42	12%	[61]
Japanese flounder (*Paralichthys olivaceus*)	Disease resistance	WGS (1,900,000)	–	0.63	–	[62]
Channel catfish (*Ictalurus punctatus*)	Growth	SNP arrays (55,000)	0.27 (0.24–0.29)	0.34 (0.31–0.37)	28.5% (28–29%)	[63]
Large yellow croaker (*Larimichthys crocea*)	Growth	RAD-seq (30,000)	–	0.37 (0.40–0.41)	–	[64]
Yellowtail kingfish (*Seriola lalandi*)	Growth	DArT-seq (14,000)	–	0.60 (0.44–0.69)	–	[65]
Yellow drum (*Nibea albiflora*)	Growth	GBS (54,000)	–	0.29 (0.17–0.38)	–	[66]
Crustaceans						
Whiteleg shrimp (*Litopenaeus vannamei*)	Growth	RAD-seq (23,000), SLAF-seq (6000)	–	0.49 (0.30–0.62)	–	[67, 68]
	Disease resistance	RAD-seq (23,000)	0.37 (0.20–0.47)	0.36 (0.21–0.50)	5.5% (5–6%)	[69]
Banana shrimp (*Fenneropenaeus merguiensis*)	Growth	DArT-seq (9000)	0.57 (0.32–0.66)	0.68 (0.42–0.76)	21.4% (17–31%)	[70]
	Disease resistance	DArT-seq (9000)	0.09	0.60	567%	[70]
Molluscs						
Pacific oyster (*Crassostrea gigas*)	Growth	SNP array (23,000)	0.52 (0.44–0.54)	0.64 (0.54–0.67)	25% (23–28%)	[71]
	Disease resistance	SNP array (23,000)	64	76	19%	[72]

(continued)

Table 1
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Species	Traits	Genotyping method (number of effective SNPs)	Average pedigree accuracy (range)	Average genomic accuracy (range)	Accuracy relative increase	References
Yesso scallop (*Patinopecten yessoensis*)	Growth	RAD-seq (2000)	–	0.51 (0.46–0.55)	–	[73]
Zhikong scallop (*Chlamys farreri*)	Growth	RAD-seq (31,000)	–	0.65 (0.63–0.70)	–	[74]

DArT-seq diversity array technology sequencing, *GBS* genotyping-by-sequencing, *RAD-seq* restriction site-associated DNA sequencing, *SLAF-seq* specific-locus amplified fragment sequencing, *SNP* single-nucleotide polymorphism, *WGS* whole-genome sequencing

[a] Recent studies added to the review of Houston et al. [29]

prediction and, 0.42 for pedigree-based prediction (Table 1). However, we notice very large variations, ranging from 0% to 567%, depending on species, disease, and measurement methods. Note that, the gains in prediction accuracy are independent of the genotyping platforms (SNP arrays, GBS, RAD, or whole-genome sequencing) involved.

Of course, accuracies of prediction depend on population structure, the density of genotyping, and the size of the reference population. For example, Griot et al. [13] analyzed the impact of marker density (from 1000 to 44,000 SNPs) and the size of the reference population (from 50 to 800 animals) on the accuracy of genomic prediction. They compare the genomic prediction of two commercial populations of European sea bass for resistance to viral nervous necrosis and vibriosis, and one commercial population of Gilthead sea bream (*Sparus aurata*) for resistance to pasteurellosis. The effect of the reference population size was important and did not reach a plateau even with 800 individuals. In contrast, from 6000 SNPs on, the genomic accuracy reached at least 90% of the accuracy obtained with the maximum density of markers.

4 Imputation as a Key for Cost-Effective GS in Aquaculture

Imputation aims usually to correct for genotyping errors and to complete missing values in genotypes. However, regarding the objective of adoption of GS for minor aquaculture species, imputation brings a novel opportunity for cheap GS development. Indeed cost-effective genotyping of low to very-low-density SNP panels are now possible using targeted GBS techniques, such as Genotyping-in-thousands by sequencing (GT-seq) [75], or specific-locus amplified fragment sequencing (SLAF-seq) [76]. Under this strategy, only the parents and the selected candidates are genotyped for the high-density SNP panel. Individuals of the reference population are genotyped for a small subset of the SNPs. Imputation is therefore used to infer the full density genotype of the siblings using the pedigree and the dense genotyping of the parents [77]. As mentioned above (Subheading 2), the very high fecundity, the ease of gamete handling, and the possible artificial mating allow producing thousands of siblings in factorial designs (several dams crossed with several males), resulting in large half-sibs families and a gradient of closely related siblings [29]. Due to this close relationship between animals in aquaculture reference populations, the imputation strategy of low-density SNP panel often allows reaching the accuracy of genomic selection with dense genotypes [77–79]. Moreover, this strategy can be adapted with little investment to existing breeding programs using a few hundred SNPs for a posteriori pedigree assignment by molecular markers [17].

5 GS to Tackle Genotype-by-Environment Interactions in Aquaculture

The environment of an aquaculture breeding programme, often in a biosecured onshore facility, differs from the environment of the operational production sites. Moreover, the breeding companies are often selling fertilized eggs, shellfish seeds, or fingerlings to grower industries located in various environments. For example, in European sea bass aquaculture, it is usual that French hatcheries implementing selective breeding sell fingerlings to be reared in on-land facilities, or sea cages all around the Mediterranean Sea (*see* Fig. 3). Those areas differ from the selection site for numerous parameters such as the water temperature (mean, range and stability) and quality (including salinity, oxygen saturation, acidity, etc.), the photoperiod (natural, artificial, etc.). The evolution of phenotypes across those environments results in reaction norms (Fig. 4). Taking into account genotype-by-environment (GxE) interactions is of major importance for aquaculture selective breeding programme. When slopes of the reaction norms are equivalent between genotypes, no interaction is concluded (Fig. 4a, b). When slopes are different, it may result in the re-ranking of the best animals (Fig. 4c) limiting the realized response to selection [14]. Such re-ranking is highly significant for growth traits and disease resistance [80], that are of major economic importance. Such interaction can be estimated as the genetic correlation between traits measured in different environments. For instance, the genetic correlation between growth at different temperatures was reported to be between 0.18 and 0.54 on Rainbow trout [80] and 0.49 for European sea bass [81]. The current context of global changes is characterized by rising seasonal temperatures, more importantly, higher frequency, intensity, and duration of summer heatwaves, and hypoxia (reduced availability of dissolved oxygen). These changes cause severe problems in many aquatic ecosystems [82, 83]. Warming and hypoxia being major physiological challenges for aquatic species [84, 85]. Therefore, it is crucial to accompany the adaptation of reared aquaculture populations to cope with these ongoing changes. Genomic selection may accelerate the breeding of more resilient animals able to cope with various and unstable environments [80, 86]. The genetic variation in the slope of a linear reaction norm model of different genotypes can be considered as genetic variation for environmental sensitivity [80]. In GS using reaction norm (RN) model, this slope becomes the trait under selection [80] to reduce the environmental sensibility. Mulder [86] compared the use of such RN models, integrating the genetic variation of the slope across environments with genomic selection, with multivariate models. The RN models with genomic selection allowed decreasing environmental sensibility 1.09–319 times better than the classical multivariate models not accounting for the slope stability.

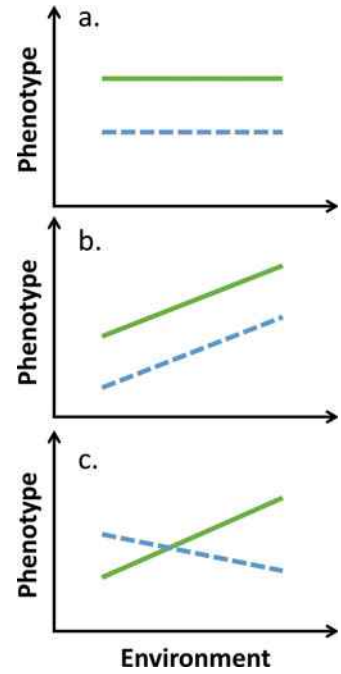

Fig. 4 Genotype-by-Environment (GxE) reaction norms. The solid green line and the dash blue line represent the phenotypic variation of two genotypes across an environmental gradient. (**a**) and (**b**) depict no GxE interaction. (**c**) indicates GxE interaction by the re-ranking of the genotype performances across the environmental gradient

6 Genomic Selection and Surrogate Breeders to Reduce Generation Time

GS contributes to increased genetic gain, and consequently, to greater productivity of an individual carrying the desired qualities. The genetic gain equation, ΔG is as follows:

$$\Delta G = \frac{i\, r\, \sigma_A}{L}$$

with σ_A as the genetic variance; r as the accuracy of selection, i as the selection intensity, and L as the generation time/interval. For boosting the genetic gain, an important way is the reduction of generation time (L) by selecting candidates early in life based on their genomic breeding value [28]. However, in aquaculture species, generation interval is typically short (2–5 years), and most trait measurements can be performed before sexual maturity. Thus, conventional reduction of generation time by estimating breeding value before the potential phenotyping has little interest and has not been applied to aquaculture breeding programs to our knowledge. Nevertheless, the reduction of generation time is expected by association with germ stem cells transplantation in short-

generation interval species [87, 88]. The principle of the method is to use a surrogate closely related species, having a shorter generation time, to produce the progeny of the desired species. In practice, primordial germ cells are collected from the selected breeders of the target species and transplanted into sterile animals of the surrogate species which thus produce gametes of the selected breeders [87]. This technic was successfully implemented in Rainbow trout using as surrogate sterile species the Masu salmon (*Oncorhynchus masou*) [88]. In the future, this method is expected to further accelerate GS for important finfish aquaculture species, with generation intervals usually between 2 to 5 years. Moreover, this will allow initiating GS in species with very long generation intervals such as Sturgeons (20 years) or Bluefin tuna (12 years).

7 Prospect of Genomic Selection in Aquaculture

7.1 Is Genomic Selection a Replacement of Conventional Pedigree- and Phenotype-Based Selection?

Although GS provides opportunities to enhance genetic gain of breeding programs, the initial expectation, discontinued phenotyping for all traits and in particular for those that are expensive or difficult to measure was not entirely realized. While some breeding programs have completely shifted to genomic selection (e.g., the European sea bass breeding programme of Ecloserie Marine de Graveline, France; the gilthead sea bream programme of Ferme Marine de Douhet, France), to date, GS is not a replacement for the conventional selection method based on phenotypic and pedigree information, but can, in conjunction with the pedigree- and phenotype-based selection approach, further improve genetic gain for disease and flesh quality traits. Furthermore, the advantages of GS need to be validated by future empirical and economic appraisal studies for alternative breeding schemes. Even when genomic selection programs are underway, re-genotyping/resequencing and continuing collection of phenotype data are also needed to maintain a high level of accuracy in breeding value estimation as well as broadening the breeding objectives when new traits are included.

7.2 Is a Genome Assembly Needed to Apply Genomic Selection?

Aquaculture species with available genome assemblies were reviewed by Abdelrahman et al. [89]. As suggested in Subheading 4, the genomic resources of the exploited species in aquaculture are sparse. In principle, genomic selection can be implemented without a reference genome, GBS providing de novo DNA markers for genomic selection. However, genome assemblies are useful tools. First, mapping the SNP panel used for GS onto a genome allows ensuring the even distribution of the SNPs. This is in particular important when a sparse genotyping is used, like in the study of Besson et al. [8] using only 3000 SNPs for the 700 Mb genome of the European sea bass. Thus, genome assembly is also important to produce SNP chips that are useful for making repeatable the

genotyping across the breeding programs and the generations. Second, with additional resequencing of many individuals at low coverage (called "1xWGS"), an imputation-like approach can be used to build consensus haplotypes and finally impute full sequence information based on the reference haplotypes [90]. The 1xWGS approach was able to detect signals in genome-wide association studies (GWAS) missed by standard imputation of SNP arrays [91]. Furthermore, well-annotated genome assemblies can allow the preselection of variants with potential causal effects to improve the accuracy of genomic prediction [92].

7.3 Can Genomic Selection be Combined with Other "omics" Approaches?

Integration of multi-omics approaches to improve genomic prediction accuracy has not been reported for aquaculture species. However, functional genomics of alternate genotypes, by means of transcriptomic approaches, have proven to improve genome-wide prediction of genes of aquaculture species [93] and to identify causative genetic variants to be used in marker-assisted selection [94]. Incorporation of such functional genomic information into genomic prediction, including the potential use of intermediate phenotypes such as gene expression or DNA methylation, may further improve prediction accuracy. The breeding environment may imprint epigenetic marks (cytosine methylation, histone modifications, chromatin accessibility state) due to breeding environmental conditions, as reported by Luyer et al. in Pacific salmon in hatchery facilities [95]. This may result in a variable phenotypic response of a single genotype, affecting the realized genetic response [29]. Epigenetic programming may also be an opportunity to drive the selected population toward better performances [96–98]. As an example, the early nutritional programming of Rainbow trouts induced better growth under plant-based sustainable diets [99]. An alternate example is the use of epigenetic marks to predict the sex of European sea bass individuals [100], constituting an important issue for European sea bass aquaculture [18]. Finally, microbiota evaluation constitutes a promising field of research to improve the genetic gain in breeding programs, by improving the performances and health of farmed animals [101, 102]. All these, "omics" evaluations may be used as alternate or intermediate phenotypes for improvement of GS.

7.4 Can Genomic Selection be Combined with Genome Editing?

Genomic selection can be combined with genome editing to increase the rate of genetic gain through two main mechanisms: (1) deletions (knockouts) to turn off or deactivate genes and (2) insertions (knock-ins) and replacement to introduce new alleles. Jenko et al. theoretically compared a standard genomic selection (GS) scheme with the promotion of alleles by genome editing (PAGE) and reported that PAGE produced four times greater genetic gain than GS [103]. Recently Johnsson et al. [104] compared two scenarios: selection against carriers (SAC) of deleterious

alleles and removal of those alleles by genome editing (RAGE) on the fitness of the animals. The authors reported large advantages of RAGE to SAC especially when multiple edits were made, regardless of the inheritance mode of the variants (codominant or recessive). In aquaculture species, genome editing has been reported for a range of traits (e.g., disease resistance) in grass carp or salmonids, see a review by Gratacap et al. [105]. The future potential of the practical combination of genome editing and GS could concern the Rainbow trout and the resistance to infectious pancreatic necrosis (IPN). In the close salmonid species, Atlantic salmon a major QTL explaining up 80–100% of the genetic variation in resistance to IPN was discovered [106]. An interspecific transfer from Atlantic salmon to Rainbow trout by genome editing, associated with the ongoing GS programs [50] could boost the genetic response to selection. However, the benefits of combined GS and gene editing need further studies in practical breeding programs for aquaculture species.

7.5 Will Remote High-Throughput Phenotyping be the Next Revolution for Breeding Programs?

Inaccurate measurement of a trait in a breeding programme leads to a reduced genetic variance, a lower heritability estimate, and thus to smaller genetic progress. In any aquaculture breeding programme, the handling of aquatic animals is particularly sensitive, including the netting (for finfish and crustaceans), anesthesia (for finfish), and the upkeep of animals outside water during few minutes, this even for simple weight and length recording. Moreover, sibs-testing strategies to improve lethal traits (disease resistance or processing yields) or to estimate GxE interaction, require a large number of animals [28]. Therefore, to benefit from the potential of GS in aquaculture, developing cost-effective high-throughput phenotyping methods in aquaculture is a major critical point. Regarding disease resistance, phenotyping platforms have been raised such as FORTIOR Genetics [36], ensuring ethical procedures, accurate and repeatable phenotyping. In addition, developing in situ surveys of growth, behavior, and health of the animals by associating optical sensors (surface camera, stereo video, sonar, and acoustic telemetry) and machine vision system (MVS) [107] provides a good opportunity for precision farming [108] and accurate assessment of phenotypes for cheap high-throughput phenotyping [28]. Such approaches, also able to assess fillet quality [109], allows sea lice monitoring in Atlantic salmon farms [108]. Another recent innovation that could improve fish phenotyping is the development of sensors. As an example, Martos-Sitcha et al. [110] developed a device attachable to fish operculum allowing to monitor physical activity and respiratory frequency. In a near future, the remote monitoring of the animals and the rearing converted into intelligible data is expected to develop and to improve aquatic species survey for breeding programs.

This phenomic evaluation, defined as "the high-dimensional phenotypic data recorded on an organism-wide scale," may be the next paradigm [111]. Indeed, the phenomic selection was theorized and tested on wheat and poplar by Rincent et al. [112] using near-infrared spectroscopy (NIRS) variation as a cheap alternative to genomic markers genotype to compute relationship matrices for predicting complex traits.

8 Conclusion

Contrasting to most agricultural species, the domestication of aquaculture species is recent. Although GS in aquaculture concerns only a dozen of species, the emergence of cost-effective genotyping methods foresees a rapid deployment of GS in multiple aquaculture species. Presently, GS exploits mainly the intra-family genetic variation by estimating Mendelian sampling to improve growth traits, disease resistance traits, and quality traits. Facing the global need in protein supply as well as the ongoing climate change, it is expected that GS will allow to improve fish to be more robust and sober. GS gives the possibility to better control the genotype-by-environment interactions that, when not accounted for, limit the genetic gain. Moreover, it is anticipated that GS could help to select animals with less sensitivity to environmental variation, and therefore more resilient. Associating recent biotechnological innovations (such as genome editing or stem cell drafting into receiver species) to GS in the breeding programs will constitute valuable ways to improve the sustainability of aquaculture production.

Acknowledgments

This study is supported by the mixed unit of research MARBEC (Université de Montpellier, CNRS, Ifremer, IRD, France) and the University of the Sunshine Coast, Australia.

References

1. FAO (2020) The state of world fisheries and aquaculture 2020: sustainability in action. FAO, Rome
2. Gjedrem T, Robinson N, Rye M (2012) The importance of selective breeding in aquaculture to meet future demands for animal protein: a review. Aquaculture 350–353: 117–129. https://doi.org/10.1016/j.aquaculture.2012.04.008
3. Gjedrem T, Rye M (2018) Selection response in fish and shellfish: a review. Rev Aquacult 10:168–179. https://doi.org/10.1111/raq.12154
4. Boudry P, Allal F, Aslam ML et al (2021) 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. Aquacult Report 20:100700. https://doi.org/10.1016/j.aqrep.2021.100700

5. Vu NT, Van Sang N, Phuc TH et al (2019) Genetic evaluation of a 15-year selection program for high growth in striped catfish Pangasianodon hypophthalmus. Aquaculture 509:221–226. https://doi.org/10.1016/j.aquaculture.2019.05.034
6. Janssen K, Chavanne H, Berentsen P, Komen H (2017) Impact of selective breeding on European aquaculture. Aquaculture 472: 8–16. https://doi.org/10.1016/j.aquaculture.2016.03.012
7. Besson M, Aubin J, Komen H et al (2016) Environmental impacts of genetic improvement of growth rate and feed conversion ratio in fish farming under rearing density and nitrogen output limitations. J Clean Prod 116:100–109. https://doi.org/10.1016/j.jclepro.2015.12.084
8. Besson M, Allal F, Chatain B et al (2019) Combining individual phenotypes of feed intake with genomic data to improve feed efficiency in sea bass. Front Genet 10:219
9. Vandeputte M, Bugeon J, Bestin A et al (2019) First evidence of realized selection response on fillet yield in rainbow trout Oncorhynchus mykiss, using sib selection or based on correlated ultrasound measurements. Front Genet 10:1225
10. Prchal M, Kocour M, Vandeputte M et al (2020) Morphological predictors of slaughter yields using 3D digitizer and their use in a common carp breeding program. Aquaculture 520:734993. https://doi.org/10.1016/j.aquaculture.2020.734993
11. De Verdal H, Komen H, Quillet E et al (2018) Improving feed efficiency in fish using selective breeding: a review. Rev Aquac 10:833–851
12. Houston RD, Haley CS, Hamilton A et al (2010) The susceptibility of Atlantic salmon fry to freshwater infectious pancreatic necrosis is largely explained by a major QTL. Heredity 105:318–327. https://doi.org/10.1038/hdy.2009.171
13. Griot R, Allal F, Phocas F et al (2021) Optimization of genomic selection to improve disease resistance in two marine fishes, the European Sea Bass (Dicentrarchus labrax) and the Gilthead Sea Bream (Sparus aurata). Front Genet 12:665920. https://doi.org/10.3389/fgene.2021.665920
14. Nguyen NH (2016) Genetic improvement for important farmed aquaculture species with a reference to carp, tilapia and prawns in Asia: achievements, lessons and challenges. Fish Fish 17:483–506. https://doi.org/10.1111/faf.12122
15. Sonesson AK, Meuwissen TH, Goddard ME (2010) The use of communal rearing of families and DNA pooling in aquaculture genomic selection schemes. Genet Sel Evol 42:41. https://doi.org/10.1186/1297-9686-42-41
16. Hollenbeck CM, Johnston IA (2018) Genomic tools and selective breeding in molluscs. Front Genet 9:253. https://doi.org/10.3389/fgene.2018.00253
17. Vandeputte M, Haffray P (2014) Parentage assignment with genomic markers: a major advance for understanding and exploiting genetic variation of quantitative traits in farmed aquatic animals. Front Genet 5:432. https://doi.org/10.3389/fgene.2014.00432
18. Vandeputte M, Gagnaire P-A, Allal F (2019) The European sea bass: a key marine fish model in the wild and in aquaculture. Anim Genet 50:195–206
19. Chavanne H, Janssen K, Hofherr J et al (2016) A comprehensive survey on selective breeding programs and seed market in the European aquaculture fish industry. Aquacult Int 24:1287–1307. https://doi.org/10.1007/s10499-016-9985-0
20. Liu S, Vallejo RL, Palti Y et al (2015) Identification of single nucleotide polymorphism markers associated with bacterial cold water disease resistance and spleen size in rainbow trout. Front Genet 6:298. https://doi.org/10.3389/fgene.2015.00298
21. D'Ambrosio J, Morvezen R, Brard-Fudulea S et al (2020) Genetic architecture and genomic selection of female reproduction traits in rainbow trout. BMC Genomics 21:558. https://doi.org/10.1186/s12864-020-06955-7
22. Palti Y, Vallejo RL, Gao G et al (2015) Detection and validation of QTL affecting bacterial cold water disease resistance in rainbow trout using restriction-site associated DNA sequencing. PLoS One 10:e0138435. https://doi.org/10.1371/journal.pone.0138435
23. Robledo D, Palaiokostas C, Bargelloni L et al (2018) Applications of genotyping by sequencing in aquaculture breeding and genetics. Rev Aquac 10:670–682. https://doi.org/10.1111/raq.12193
24. Fuji K, Hasegawa O, Honda K et al (2007) Marker-assisted breeding of a lymphocystis disease-resistant Japanese flounder (Paralichthys olivaceus). Aquaculture 272: 291–295. https://doi.org/10.1016/j.aquaculture.2007.07.210

25. Meuwissen THE, Hayes BJ, Goddard ME (2001) Prediction of total genetic value using genome-wide dense marker maps. Genetics 157:1819
26. Hayes BJ, Bowman PJ, Chamberlain AC et al (2009) Accuracy of genomic breeding values in multi-breed dairy cattle populations. Genet Sel Evol 41:51. https://doi.org/10.1186/1297-9686-41-51
27. Yáñez JM, Newman S, Houston RD (2015) Genomics in aquaculture to better understand species biology and accelerate genetic progress. Front Genet 6:128. https://doi.org/10.3389/fgene.2015.00128
28. Zenger KR, Khatkar MS, Jones DB et al (2019) Genomic selection in aquaculture: application, limitations and opportunities with special reference to marine shrimp and pearl oysters. Front Genet 9:693. https://doi.org/10.3389/fgene.2018.00693
29. Houston RD, Bean TP, Macqueen DJ et al (2020) Harnessing genomics to fast-track genetic improvement in aquaculture. Nat Rev Genet 21:389–409. https://doi.org/10.1038/s41576-020-0227-y
30. Hosoya S, Kikuchi K, Nagashima H et al (2017) Genomic selection in aquaculture. Bull Japan Fish Res Edu Agency 45:35–39
31. Palaiokostas C, Houston RD (2017) Genome-wide approaches to understanding and improving complex traits in aquaculture species. CAB Rev 12:1–10
32. You X, Shan X, Shi Q (2020) Research advances in the genomics and applications for molecular breeding of aquaculture animals. Aquaculture 526:735357. https://doi.org/10.1016/j.aquaculture.2020.735357
33. de Roos APW, Schrooten C, Veerkamp RF, van Arendonk JAM (2011) Effects of genomic selection on genetic improvement, inbreeding, and merit of young versus proven bulls. J Dairy Sci 94:1559–1567. https://doi.org/10.3168/jds.2010-3354
34. Dupont-Nivet M, Vandeputte M, Haffray P, Chevassus B (2006) Effect of different mating designs on inbreeding, genetic variance and response to selection when applying individual selection in fish breeding programs. Aquaculture 252:161–170. https://doi.org/10.1016/j.aquaculture.2005.07.005
35. Griot R, Allal F, Phocas F et al (2020) Genome-wide association studies for resistance to viral nervous necrosis in three populations of European sea bass (Dicentrarchus labrax) using a novel 57 k SNP array DlabChip. Aquaculture 530:735930
36. François Y, Cabon J, Morin T et al (2019) FORTIOR genetics, a platform to enhance disease resistance by genetic selection in aquaculture. In: 19th international conference on diseases of fish and shellfish, Porto, Portugal
37. VanRaden PM (2008) Efficient methods to compute genomic predictions. J Dairy Sci 91:4414–4423. https://doi.org/10.3168/jds.2007-0980
38. Kilian A, Wenzl P, Huttner E et al (2012) Diversity arrays technology: a generic genome profiling technology on open platforms. Methods Mol Biol 888:67–89. https://doi.org/10.1007/978-1-61779-870-2_5
39. Tsai H-Y, Hamilton A, Tinch AE et al (2015) Genome wide association and genomic prediction for growth traits in juvenile farmed Atlantic salmon using a high density SNP array. BMC Genomics 16:569. https://doi.org/10.1186/s12864-015-2117-9
40. Tsai H-Y, Hamilton A, Tinch AE et al (2016) Genomic prediction of host resistance to sea lice in farmed Atlantic salmon populations. Genet Sel Evol 48:47. https://doi.org/10.1186/s12711-016-0226-9
41. Correa K, Bangera R, Figueroa R et al (2017) The use of genomic information increases the accuracy of breeding value predictions for sea louse (Caligus rogercresseyi) resistance in Atlantic salmon (Salmo salar). Genet Sel Evol 49:15. https://doi.org/10.1186/s12711-017-0291-8
42. Ødegård J, Moen T, Santi N et al (2014) Genomic prediction in an admixed population of Atlantic salmon (Salmo salar). Front Genet 5:402. https://doi.org/10.3389/fgene.2014.00402
43. Robledo D, Matika O, Hamilton A, Houston RD (2018) Genome-wide association and genomic selection for resistance to amoebic gill disease in Atlantic salmon. G3 8:1195–1203. https://doi.org/10.1534/g3.118.200075
44. Boison SA, Gjerde B, Hillestad B et al (2019) Genomic and transcriptomic analysis of amoebic gill disease resistance in Atlantic salmon (Salmo salar L.). Front Genet 10:68. https://doi.org/10.3389/fgene.2019.00068
45. Bangera R, Correa K, Lhorente JP et al (2017) Genomic predictions can accelerate selection for resistance against Piscirickettsia salmonis in Atlantic salmon (Salmo salar). BMC Genomics 18:121. https://doi.org/10.1186/s12864-017-3487-y

46. Vallejo RL, Leeds TD, Fragomeni BO et al (2016) Evaluation of genome-enabled selection for bacterial cold water disease resistance using progeny performance data in rainbow trout: insights on genotyping methods and genomic prediction models. Front Genet 7: 96. https://doi.org/10.3389/fgene.2016.00096
47. Vallejo RL, Leeds TD, Gao G et al (2017) Genomic selection models double the accuracy of predicted breeding values for bacterial cold water disease resistance compared to a traditional pedigree-based model in rainbow trout aquaculture. Genet Sel Evol 49:17. https://doi.org/10.1186/s12711-017-0293-6
48. Vallejo RL, Silva RMO, Evenhuis JP et al (2018) Accurate genomic predictions for BCWD resistance in rainbow trout are achieved using low-density SNP panels: evidence that long-range LD is a major contributing factor. J Anim Breed Genet. https://doi.org/10.1111/jbg.12335
49. Vallejo RL, Cheng H, Fragomeni BO et al (2019) Genome-wide association analysis and accuracy of genome-enabled breeding value predictions for resistance to infectious hematopoietic necrosis virus in a commercial rainbow trout breeding population. Genet Sel Evol 51:47. https://doi.org/10.1186/s12711-019-0489-z
50. Yoshida GM, Carvalheiro R, Rodríguez FH et al (2019) Single-step genomic evaluation improves accuracy of breeding value predictions for resistance to infectious pancreatic necrosis virus in rainbow trout. Genomics 111:127–132. https://doi.org/10.1016/j.ygeno.2018.01.008
51. Yoshida GM, Bangera R, Carvalheiro R et al (2018) Genomic prediction accuracy for resistance against Piscirickettsia salmonis in farmed rainbow trout. G3 8:719–726. https://doi.org/10.1534/g3.117.300499
52. Silva RMO, Evenhuis JP, Vallejo RL et al (2019) Whole-genome mapping of quantitative trait loci and accuracy of genomic predictions for resistance to columnaris disease in two rainbow trout breeding populations. Genet Sel Evol 51:42. https://doi.org/10.1186/s12711-019-0484-4
53. Barría A, Christensen KA, Yoshida GM et al (2018) Genomic predictions and genome-wide association study of resistance against Piscirickettsia salmonis in Coho Salmon (Oncorhynchus kisutch) using ddRAD sequencing. G3 8:1183–1194. https://doi.org/10.1534/g3.118.200053
54. Palaiokostas C, Kocour M, Prchal M, Houston RD (2018) Accuracy of genomic evaluations of juvenile growth rate in common carp (Cyprinus carpio) using genotyping by sequencing. Front Genet 9:82. https://doi.org/10.3389/fgene.2018.00082
55. Palaiokostas C, Vesely T, Kocour M et al (2019) Optimizing genomic prediction of host resistance to koi herpesvirus disease in carp. Front Genet 10:543. https://doi.org/10.3389/fgene.2019.00543
56. Joshi R, Skaarud A, de Vera M et al (2020) Genomic prediction for commercial traits using univariate and multivariate approaches in Nile tilapia (Oreochromis niloticus). Aquaculture 516:734641. https://doi.org/10.1016/j.aquaculture.2019.734641
57. Yoshida GM, Lhorente JP, Correa K et al (2019) Genome-wide association study and cost-efficient genomic predictions for growth and fillet yield in Nile Tilapia (Oreochromis niloticus). G3 9:2597–2607. https://doi.org/10.1534/g3.119.400116
58. Palaiokostas C, Cariou S, Bestin A et al (2018) Genome-wide association and genomic prediction of resistance to viral nervous necrosis in European sea bass (Dicentrarchus labrax) using RAD sequencing. Genet Sel Evol 50: 30. https://doi.org/10.1186/s12711-018-0401-2
59. Palaiokostas C, Ferraresso S, Franch R et al (2016) Genomic prediction of resistance to pasteurellosis in Gilthead Sea Bream (Sparus aurata) using 2b-RAD sequencing. G3 6: 3693–3700. https://doi.org/10.1534/g3.116.035220
60. Aslam ML, Carraro R, Bestin A et al (2018) Genetics of resistance to photobacteriosis in gilthead sea bream (Sparus aurata) using 2b-RAD sequencing. BMC Genet 19:43. https://doi.org/10.1186/s12863-018-0631-x
61. Saura M, Carabaño MJ, Fernández A et al (2019) Disentangling genetic variation for resistance and endurance to scuticociliatosis in Turbot using pedigree and genomic information. Front Genet 10:539. https://doi.org/10.3389/fgene.2019.00539
62. Liu Y, Lu S, Liu F et al (2018) Genomic selection using BayesCπ and GBLUP for resistance against Edwardsiella tarda in Japanese flounder (Paralichthys olivaceus). Mar Biotechnol 20:559–565. https://doi.org/10.1007/s10126-018-9839-z
63. Garcia ALS, Bosworth B, Waldbieser G et al (2018) Development of genomic predictions for harvest and carcass weight in channel

catfish. Genet Sel Evol 50:66. https://doi.org/10.1186/s12711-018-0435-5

64. Dong L, Xiao S, Wang Q, Wang Z (2016) Comparative analysis of the GBLUP, emBayesB, and GWAS algorithms to predict genetic values in large yellow croaker (Larimichthys crocea). BMC Genomics 17:460. https://doi.org/10.1186/s12864-016-2756-5
65. Nguyen NH, Premachandra HKA, Kilian A, Knibb W (2018) Genomic prediction using DArT-Seq technology for yellowtail kingfish Seriola lalandi. BMC Genomics 19:107. https://doi.org/10.1186/s12864-018-4493-4
66. Liu G, Dong L, Gu L et al (2019) Evaluation of genomic selection for seven economic traits in yellow drum (Nibea albiflora). Mar Biotechnol 21:806–812. https://doi.org/10.1007/s10126-019-09925-7
67. Wang Q, Yu Y, Yuan J et al (2017) Effects of marker density and population structure on the genomic prediction accuracy for growth trait in Pacific white shrimp Litopenaeus vannamei. BMC Genet 18:45. https://doi.org/10.1186/s12863-017-0507-5
68. Wang Q, Yu Y, Li F et al (2017) Predictive ability of genomic selection models for breeding value estimation on growth traits of Pacific white shrimp Litopenaeus vannamei. Chin J Ocean Limnol 35:1221–1229. https://doi.org/10.1007/s00343-017-6038-0
69. Wang Q, Yu Y, Zhang Q et al (2019) Evaluation on the genomic selection in Litopenaeus vannamei for the resistance against Vibrio parahaemolyticus. Aquaculture 505:212–216
70. Nguyen NH, Phuthaworn C, Knibb W (2020) Genomic prediction for disease resistance to Hepatopancreatic parvovirus and growth, carcass and quality traits in Banana shrimp Fenneropenaeus merguiensis. Genomics 112:2021–2027. https://doi.org/10.1016/j.ygeno.2019.11.014
71. Gutierrez AP, Matika O, Bean TP, Houston RD (2018) Genomic selection for growth traits in Pacific Oyster (Crassostrea gigas): potential of low-density marker panels for breeding value prediction. Front Genet 9:391. https://doi.org/10.3389/fgene.2018.00391
72. Gutierrez AP, Symonds J, King N et al (2020) Potential of genomic selection for improvement of resistance to ostreid herpesvirus in Pacific oyster (Crassostrea gigas). Anim Genet 51:249–257. https://doi.org/10.1111/age.12909
73. Dou J, Li X, Fu Q et al (2016) Evaluation of the 2b-RAD method for genomic selection in scallop breeding. Sci Rep 6:19244. https://doi.org/10.1038/srep19244
74. Wang Y, Sun G, Zeng Q et al (2018) Predicting growth traits with genomic selection methods in Zhikong Scallop (Chlamys farreri). Mar Biotechnol 20:769–779. https://doi.org/10.1007/s10126-018-9847-z
75. Campbell NR, Harmon SA, Narum SR (2015) Genotyping-in-thousands by sequencing (GT-seq): a cost effective SNP genotyping method based on custom amplicon sequencing. Mol Ecol Resour 15:855–867. https://doi.org/10.1111/1755-0998.12357
76. Sun X, Liu D, Zhang X et al (2013) SLAF-seq: an efficient method of large-scale de novo SNP discovery and genotyping using high-throughput sequencing. PLoS One 8:e58700. https://doi.org/10.1371/journal.pone.0058700
77. Tsairidou S, Hamilton A, Robledo D et al (2020) Optimizing low-cost genotyping and imputation strategies for genomic selection in Atlantic salmon. G3 10:581–590. https://doi.org/10.1534/g3.119.400800
78. Tsai H-Y, Matika O, Edwards SM et al (2017) Genotype imputation to improve the cost-efficiency of genomic selection in farmed Atlantic salmon. G3 7:1377–1383. https://doi.org/10.1534/g3.117.040717
79. Yoshida GM, Carvalheiro R, Lhorente JP et al (2018) Accuracy of genotype imputation and genomic predictions in a two-generation farmed Atlantic salmon population using high-density and low-density SNP panels. Aquaculture 491:147–154. https://doi.org/10.1016/j.aquaculture.2018.03.004
80. Sae-Lim P, Gjerde B, Nielsen HM et al (2016) A review of genotype-by-environment interaction and micro-environmental sensitivity in aquaculture species. Rev Aquac 8:369–393. https://doi.org/10.1111/raq.12098
81. Saillant E, Dupont-Nivet M, Haffray P, Chatain B (2006) Estimates of heritability and genotype-environment interactions for body weight in sea bass (Dicentrarchus labrax L.) raised under communal rearing conditions. Aquaculture 254:139–147
82. Smale DA, Wernberg T, Oliver ECJ et al (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nat Clim Chang 9:306–312. https://doi.org/10.1038/s41558-019-0412-1

83. Stillman JH (2019) Heat waves, the new normal: summertime temperature extremes will impact animals, ecosystems, and human communities. Physiology 34:86–100. https://doi.org/10.1152/physiol.00040.2018
84. Breitburg D, Levin LA, Oschlies A et al (2018) Declining oxygen in the global ocean and coastal waters. Science 359:eaam7240. https://doi.org/10.1126/science.aam7240
85. Altieri AH, Gedan KB (2015) Climate change and dead zones. Glob Chang Biol 21: 1395–1406. https://doi.org/10.1111/gcb.12754
86. Mulder HA (2016) Genomic selection improves response to selection in resilience by exploiting genotype by environment interactions. Front Genet 7:178. https://doi.org/10.3389/fgene.2016.00178
87. Yoshizaki G, Yazawa R (2019) Application of surrogate broodstock technology in aquaculture. Fish Sci 85:429–437. https://doi.org/10.1007/s12562-019-01299-y
88. Okutsu T, Shikina S, Kanno M et al (2007) Production of trout offspring from triploid salmon parents. Science 317:1517. https://doi.org/10.1126/science.1145626
89. Abdelrahman H, ElHady M, Alcivar-Warren A et al (2017) Aquaculture genomics, genetics and breeding in the United States: current status, challenges, and priorities for future research. BMC Genomics 18:191. https://doi.org/10.1186/s12864-017-3557-1
90. Rubinacci S, Ribeiro DM, Hofmeister RJ, Delaneau O (2021) Efficient phasing and imputation of low-coverage sequencing data using large reference panels. Nat Genet 53: 120–126. https://doi.org/10.1038/s41588-020-00756-0
91. Gilly A, Ritchie GR, Southam L et al (2016) Very low-depth sequencing in a founder population identifies a cardioprotective APOC3 signal missed by genome-wide imputation. Hum Mol Genet 25:2360–2365. https://doi.org/10.1093/hmg/ddw088
92. Xiang R, MacLeod IM, Daetwyler HD et al (2021) Genome-wide fine-mapping identifies pleiotropic and functional variants that predict many traits across global cattle populations. Nat Commun 12:860. https://doi.org/10.1038/s41467-021-21001-0
93. Macqueen DJ, Primmer CR, Houston RD et al (2017) Functional annotation of all salmonid genomes (FAASG): an international initiative supporting future salmonid research, conservation and aquaculture. BMC Genomics 18:484. https://doi.org/10.1186/s12864-017-3862-8
94. Robledo D, Taggart JB, Ireland JH et al (2016) Gene expression comparison of resistant and susceptible Atlantic salmon fry challenged with Infectious Pancreatic Necrosis virus reveals a marked contrast in immune response. BMC Genomics 17:279. https://doi.org/10.1186/s12864-016-2600-y
95. Luyer JL, Laporte M, Beacham TD et al (2017) Parallel epigenetic modifications induced by hatchery rearing in a Pacific salmon. PNAS 114:12964–12969. https://doi.org/10.1073/pnas.1711229114
96. Gavery MR, Roberts SB (2017) Epigenetic considerations in aquaculture. PeerJ 5: e4147. https://doi.org/10.7717/peerj.4147
97. Moghadam H, Mørkøre T, Robinson N (2015) Epigenetics—potential for programming fish for aquaculture? J Marine Sci Eng 3:175–192. https://doi.org/10.3390/jmse3020175
98. Jonsson B, Jonsson N (2014) Early environment influences later performance in fishes. J Fish Biol 85:151–188. https://doi.org/10.1111/jfb.12432
99. Geurden I, Borchert P, Balasubramanian MN et al (2013) The positive impact of the early-feeding of a plant-based diet on its future acceptance and utilisation in rainbow trout. PLoS One 8:e83162. https://doi.org/10.1371/journal.pone.0083162
100. Anastasiadi D, Vandeputte M, Sánchez-Baizán N et al (2018) Dynamic epimarks in sex-related genes predict gonad phenotype in the European sea bass, a fish with mixed genetic and environmental sex determination. Epigenetics 13:988–1011
101. Brugman S, Ikeda-Ohtsubo W, Braber S et al (2018) A comparative review on microbiota manipulation: lessons from fish, plants, livestock, and human research. Front Nutr 5:80. https://doi.org/10.3389/fnut.2018.00080
102. Uren Webster TM, Consuegra S, Hitchings M, Garcia de Leaniz C Interpopulation variation in the atlantic salmon microbiome reflects environmental and genetic diversity. Appl Environ Microbiol 84: e00691-18. https://doi.org/10.1128/AEM.00691-18
103. Jenko J, Gorjanc G, Cleveland MA et al (2015) Potential of promotion of alleles by genome editing to improve quantitative traits in livestock breeding programs. Genet Sel Evol 47:55. https://doi.org/10.1186/s12711-015-0135-3
104. Johnsson M, Gaynor RC, Jenko J et al (2019) Removal of alleles by genome editing (RAGE) against deleterious load. Genet Sel

Evol 51:14. https://doi.org/10.1186/s12711-019-0456-8

105. Gratacap RL, Wargelius A, Edvardsen RB, Houston RD (2019) Potential of genome editing to improve aquaculture breeding and production. Trends Genet 35:672–684. https://doi.org/10.1016/j.tig.2019.06.006
106. Houston RD, Haley CS, Hamilton A et al (2008) Major quantitative trait loci affect resistance to infectious pancreatic necrosis in Atlantic salmon (Salmo salar). Genetics 178:1109–1115. https://doi.org/10.1534/genetics.107.082974
107. Saberioon M, Gholizadeh A, Cisar P et al (2017) Application of machine vision systems in aquaculture with emphasis on fish: state-of-the-art and key issues. Rev Aquac 9:369–387. https://doi.org/10.1111/raq.12143
108. Føre M, Frank K, Norton T et al (2018) Precision fish farming: a new framework to improve production in aquaculture. Biosyst Eng 173:176–193. https://doi.org/10.1016/j.biosystemseng.2017.10.014
109. Yagiz Y, Balaban MO, Kristinsson HG et al (2009) Comparison of Minolta colorimeter and machine vision system in measuring colour of irradiated Atlantic salmon. J Sci Food Agric 89:728–730. https://doi.org/10.1002/jsfa.3467
110. Martos-Sitcha JA, Sosa J, Ramos-Valido D et al (2019) Ultra-low power sensor devices for monitoring physical activity and respiratory frequency in farmed fish. Front Physiol 10:667. https://doi.org/10.3389/fphys.2019.00667
111. Houle D, Govindaraju DR, Omholt S (2010) Phenomics: the next challenge. Nat Rev Genet 11:855–866. https://doi.org/10.1038/nrg2897
112. Rincent R, Charpentier J-P, Faivre-Rampant P et al (2018) Phenomic selection is a low-cost and high-throughput method based on indirect predictions: proof of concept on wheat and poplar. G3 8:3961–3972. https://doi.org/10.1534/g3.118.200760