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Improving commercial body weight in turbot using records from fish measured under production conditions: A simulation study

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Introduction

Turbot (*Scophthalmus maximus*) breeding programs are well established, with growth being the primary breeding objective. Traditionally, selection has been based on body weight measured in candidates reared under controlled nucleus conditions (NW). However, the ultimate goal of the industry is to improve performance under commercial farming conditions, particularly commercial body weight (CW). This distinction is especially relevant when genotype-by-environment (GxE) interactions exist, as environmental differences can alter genotype ranking and reduce the efficiency of selection based solely on nucleus phenotypes (Falconer and Mackay, 1996). Several studies have reported G×E in aquaculture species (reviewed by Houston *et al*., 2020). In turbot, preliminary research from our group indicate a moderate genetic correlation (~0.5) between NW and CW, suggesting that selection exclusively on NW may substantially limit genetic progress for CW.

To enhance the selection response for CW, it is therefore necessary to incorporate CW records from sibs of nucleus candidates reared under commercial conditions. However, the minimum number of commercial sibs per family required to obtain accurate CW evaluations remains unknown. The objective of this study was to evaluate, using stochastic simulations, the impact of increasing the number of measured sibs reared under commercial conditions on the genetic gain for CW. Both BLUP and genomic evaluation methods were considered.

Materials & Methods

Genome structure. A genome of ~600 Mb was simulated, consisting of 22 chromosomes to reflect the structure of the turbot genome. Genotypes were simulated for ~5,000 biallelic loci corresponding to SNPs included on a commercially available low-density 5K Affymetrix chip. These loci were distributed across the genome according to the most recent turbot genetic map (Maroso *et al.*, 2018). All simulations were performed using an in-house program written in Fortran.

Generation of the base population. The simulation was designed to replicate the structure of a turbot breeding program, in which full-sib families split into nucleus and commercial production environments. An initial population of 5,620 fish (50% males and 50% females) was generated using real 5K SNP-chip genotypes from Nueva Pescanova's breeding population. Missing genotypes and haplotype phases were imputed using BEAGLE 5.4 (Browning *et al*., 2021). Recombination was simulated by modeling Poisson-distributed crossover events along each chromosome. The population was expanded through one generation of random mating, with each individual mated to eight partners and producing one offspring per mating. This process yielded 22,480 fish, which served as the source pool for 100 independent simulation replicates. Each replicate was initiated with 100 males and 100 females, generating 100 full-sib families, with offspring allocated to either nucleus or commercial rearing conditions.

Traits simulated. Genotype-by-environment interaction was modelled by simulating performance in the two different environments (nucleus and commercial) as two genetically

correlated traits. Sensitivity analyses were conducted by evaluating the genetic correlation between these traits (ρ_a) using the estimate for turbot (i.e., 0.5) as well as one lower and one higher alternative value (ρ_a = 0.2, 0.5 and 0.8). Both traits (NW and CW) were controlled by 200 QTLs that were randomly chosen at t = 0 from the ~5,000 simulated loci. These 200 QTLs affected simultaneously both traits but with trait-specific effects, thereby enabling the simulation of different levels of genetic correlation. QTL effects were sampled from a bivariate normal distribution with mean 0 and variance 1 for each trait, with the specified genetic correlations. The initial phenotypic variance was set to 1 and heritability to 0.3 for both traits (Xu *et al*., 2015).

Genetic evaluation. Traditional BLUP and genomic evaluations were conducted to obtain estimates of breeding values. Genomic evaluations were performed using the GBLUP method (Hayes *et al*., 2009). In both cases, a bivariate animal model was assumed. Evaluations included data from the current generation and the three preceding generations and were performed using the BLUPf90 software (Misztal *et al*., 2015).

Selection scenarios. Each generation, the 100 males and 100 females with the highest estimated breeding values for CW were selected from the pool of 2,000 candidates. These selected individuals were randomly paired, creating 100 full-sib families per generation. Each mating produced 20 offspring to be reared as selection candidates in the nucleus and a number of offspring to be reared under commercial production conditions (ranging from 10 to 60 per family). A benchmark scenario without commercial sibs was also simulated. Selection was conducted over five discrete generations. Schemes were compared in terms of cumulative genetic gain for CW and genealogical inbreeding, assuming unrelated and non-inbred founders at t = 0. Results shown are averages across 100 replicates.

Results

When selection relied exclusively on NW records (0 sibs), genetic gain increased markedly with rising ρ_a (Table 1). The relative increase in genetic gain was substantially greater when ρ_a rose from 0.2 to 0.5 (~150%) than when it increased from 0.5 to 0.8 (~60%), indicating diminishing returns at higher values of ρ_a. Across all scenarios, GBLUP consistently outperformed BLUP; however, the magnitude of this advantage was smaller than the gains attributable to increasing ρ_a.

Compared to scenarios without commercial sib data, genetic gain increased substantially when CW phenotypes were used, with the largest effects observed at low ρ_a values. For example, when ρ_a = 0.2, recording phenotypes for only 10 sibs per family increased genetic gain by more than 300% under both BLUP and GBLUP relative to selection based solely on NW records. In contrast, at ρ_a = 0.8, the same increase in sib data resulted in only a ~20% improvement. Consequently, the benefit of including commercial sib data diminished as ρ_a increased. For a given number of sibs, GBLUP consistently achieved higher genetic gain than BLUP. Notably, GBLUP with only 10 sibs achieved a level of genetic gain comparable to that obtained by BLUP with 60 sibs.

Increasing the number of sibs led to higher genetic gain, but the marginal benefit progressively declined as the number of sibs increased for both BLUP and GBLUP. For BLUP, genetic gain increased on average by about 3 - 5% when the number of sibs increased from 10 to 20, followed by smaller increments by 2 - 4% from 20 to 30, 1 - 2% from 30 to 40 and from 40 to 50, and less than 1% beyond 50 sibs. A similar trend was observed for GBLUP: genetic gain increased by approximately 4 - 8% when increasing sibs from 10 to 20, about 2 - 3% from 20 to 30, 1 - 2% from 30 to 40, and around 1% from 40 to 50 and from 50 to 60. Note that the incremental benefit of adding more sibs was smaller when ρ_a = 0.8.

Under BLUP, the lowest inbreeding coefficients were observed when no sib data were included in the evaluations (Table 1). Incorporating data from only 10 sibs led to a substantial increase in inbreeding, particularly at low ρ_a. However, as the number of sibs increased, inbreeding levels declined (with no change observed for $\rho_a = 0.8$). In contrast, GBLUP maintained consistently low inbreeding levels across all scenarios.

Table 1. Cumulative genetic gain for commercial body weight, measured as the mean true breeding value, and inbreeding coefficients at generation 5 from BLUP and GBLUP selection, for different genetic correlations between commercial and nucleus body weight (ρ_a), and varying numbers of sibs per family recorded under commercial conditions (n_{sibs}).

		$r_a = 0.2$		$r_a = 0.5$		$r_a = 0.8$	
	n_{sibs}	BLUP	GBLUP	BLUP	GBLUP	BLUP	GBLUP
Genetic gain	0	0.50	0.58	1.25	1.43	2.00	2.31
	10	2.05	2.59	2.14	2.65	2.34	2.78
	20	2.15	2.79	2.25	2.82	2.41	2.89
	30	2.24	2.88	2.32	2.91	2.46	2.96
	40	2.29	2.94	2.34	2.96	2.45	2.99
	50	2.31	2.97	2.38	3.00	2.49	3.02
	60	2.33	3.00	2.41	3.03	2.48	3.04
Inbreeding	0	0.08	0.05	0.08	0.05	0.08	0.05
	10	0.16	0.06	0.13	0.06	0.10	0.06
	20	0.14	0.06	0.13	0.05	0.10	0.05
	30	0.14	0.05	0.12	0.05	0.10	0.05
	40	0.14	0.05	0.12	0.05	0.10	0.05
	50	0.13	0.05	0.11	0.05	0.10	0.05
	60	0.13	0.04	0.11	0.05	0.10	0.05

Standard errors were $\leq 3 \times 10^{-2}$ for genetic gain and $\leq 2 \times 10^{-2}$ for inbreeding coefficients.

Discussion

Under low ρ_a, which reflects the strong GxE interaction commonly observed in aquaculture (Houston *et al*., 2020), the inclusion of data from sibs reared under commercial conditions becomes essential to achieve meaningful genetic improvement in CW.

Incorporating commercial sib data provides additional genetic gains but also entails additional costs, so an optimal balance is needed to ensure that the expected gains justify the investment under realistic scenarios. In BLUP evaluations, incorporating sib data requires family-level tagging and individual weighing of commercial fish, both of which demand substantial personnel effort and expenses. Additionally, in GBLUP evaluations, costs also arise from genotyping. It is important to note that our study relied on genotypic data corresponding to a recently developed low-density SNP array for turbot. Despite the limited marker density, substantial genetic gain was achieved even under a low ρ_a, highlighting the efficiency of genomic selection with reduced-density panels. This finding is consistent with Kriaridou *et al*. (2020), who reported that low- and medium-density SNP arrays are generally sufficient to reach accuracies close to the maximum attainable in aquaculture populations. Moreover, SNP genotypes used for genetic evaluations can accurately estimate coancestry and inbreeding, thereby eliminating the need for family tagging in the commercial

population. Genotyping costs are also expected to continue decreasing with ongoing technological advances (Robledo *et al*., 2018).
In any case, the additional genetic gain obtained by recording more than 50 fish per family was minimal for both BLUP and GBLUP, indicating that measuring and genotyping (in the case of GBLUP) very large numbers of commercial fish is unnecessary. Nevertheless, uncontrollable factors under commercial conditions (e.g. survival or missing records) may require transferring a larger number of fish from the nucleus in order to ensure that a sufficient number are effectively measured.

Conclusions

Using data from sibs reared under commercial conditions markedly increased the genetic gain for CW, particularly when ρ_a was low. Although gain continued to rise with the inclusion of additional sibs, the rate of improvement declined progressively. Overall, our results suggest that increasing the number of sibs beyond 50 in both BLUP and GBLUP provides only marginal improvements in genetic gain, with no further reduction in inbreeding.

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