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MULTI-TRAIT BREEDING VALUE-BASED SELECTION AND PREDICTION OF GENETIC GAIN UNDER ALTERNATIVE BREEDING SCENARIOS IN COMMON CARP (*CYPRINUS CARPIO*)

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ABSTRACT

Cyprinus carpio, popularly known as common carp is the fourth most farmed fish in the world. This fish is an exotic introduction in India with limited founding stock but is now very common in water bodies. Long history of inbreeding and negative selection has negatively impacted its aquaculture production. To revive its population and improve productivity, ICAR-CIFE, Mumbai, India, has initiated a selective breeding program targeted at an inland saline production environment. Barren lands challenged with soil salinity and underground saline water are a potential resource for common carp aquaculture owing to its ability to tolerate low saline conditions. The breeding goal is to develop a fast-growing and resilient strain of common carp suitable for inland saline aquaculture systems. In the present study, the utilised growth data comprised a multi-trait, multi-environment dataset. A multi-trait Best Linear Unbiased Prediction (BLUP) approach was employed. Fish reared under low salinity (LS; 2–4 PSU) exhibited superior growth performance, with mean body weight (BW), standard length (SL), and body depth (BH) being higher by 156 g, 1.3 cm, and 0.6 cm, respectively, than those cultured under high salinity (HS; 6–8 PSU) conditions. The growth traits exhibited high heritability (0.36–0.57) and displayed positive between-salinity genetic correlations between 0.76 and 0.97, indicating a low genotype-by-environment interaction. The full-sib effect correlation was moderate to high across traits, indicating a low full-sib by salinity interaction. The between-trait pond effect correlation within each salinity was found to be high (0.80-1.00). A relatively high accuracy (0.72) of multi-trait BLUP (aggregate genotype) was estimated, indicating that a reliable multi-trait selection can be achieved. The theoretical response to aggregate genotype selection was +4.25 index units. Further, a stochastic simulation was performed to delineate the most effective breeding. Specifically, four alternative breeding scenarios, varying in the number of families produced and selected in each generation, were simulated for 10 generations with 10 replicates each. The true breeding values (TBV), BLUP, accuracy, and genetic gain for multi-traits were predicted. Breeding scenario 2 was selected and included 125 families produced by nested mating and 20 fish evaluated per family (5000 total) per generation, followed by selection (maximum four per family) with 200 top males and 250 females selected and mated to produce the next generation. This scenario yielded a higher trend for TBV, accuracy, genetic gain, and a lower rate of inbreeding (0.5 %) than the alternative scenarios. The results of the present study will aid in multi-trait selection and the adoption of an effective breeding strategy for the breeding of common carp in India.

Keywords: Common carp (*Cyprinus carpio*), selective breeding, inland saline aquaculture, multi-trait BLUP, genetic gain and inbreeding management, India.

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1 INTRODUCTION

1.1 General introduction and context

The global population is projected to increase to 9.7 billion by 2050 (Gu, Andreev, & Dupre, 2021). The food and nutrition needs of the population continue to grow which directly puts pressure on the existing food-producing sectors. Globally, fish represent more than 16.6 % of the animal protein supply and 6.5 % of all protein for human consumption (World Bank, 2013). Capture fisheries have reached a plateau in the last five decades, and fish needs are increasingly met by aquaculture (60 % of total fish produced globally) which exhibits a growth rate of more than 7 % (World Bank, 2013). Aquaculture growth is determined by five major components: 1. availability of breeds (selected stocks), 2. availability of quality seeds, 3. feed and nutrition, and 4. health. The breed which may or may not be developed through a breeding program, is a domesticated population at a given evolutionary time whose performance is known and responds to human interventions, such as readily accepting feed, exhibiting expected growth, and responding to captive maturation and reproduction. Currently, global aquaculture is supported by less than 10 % of the breeds developed through breeding programs (Olesen, Bentsen, Phillips, & Ponzoni, 2015). The high dependence of aquaculture on unselected stocks is a challenge that must be addressed. Breeds are a reliable source of known performance (fish with desired traits) and high-quality seeds (non-inbred) which enhance the long-term productivity of aquaculture systems, minimise the cost of production, and reduce the dependency on wild capture. Thus, it is imperative to develop fish breeds to achieve sustainability in aquaculture.

India is one of the largest countries in the world, supporting ~18 % of the global population with only 2.4 % of the land area and 4 % of the freshwater resources (Jain, Sharma, & Kumar, 2004). It is also one of the largest fish-producing countries in the world (ranked second overall and third in aquaculture production) (FAO, 2024). Following the global trend, marine capture fisheries in India have reached a plateau, and only aquaculture can support the growing food and nutrition demand of the growing population. Aquaculture in India is heavily dependent on unselected fish stocks which raises concerns about long-term sustainability. There are only a handful of public funded fish breeding programs in India supported by the Department of Fisheries, Ministry of Fisheries, Government of India and Indian Council of Agricultural Research (ICAR), Fisheries Division through their specialised fisheries research institutes viz., *Labeo rohita* (Jayanthi rohu), *Clarias magur* (Maha magur), *Macrobrachium rosenbergii*, *Labeo catla* (Amrit catla), *Cyprinus carpio* (Saline carp) and *Penaeus indicus*. Each breeding program is unique, and its success depends on correct breeding decisions which are determined through rigorous analysis of breeding data. An important breeding decision is the selection of fish individuals as parents to produce the next generation based on their genetic merit, which in turn determines the quantum of genetic gain in future generations and, thereby, the overall long-term success of the breeding program. The present project analysed the data records of an ongoing breeding program for common carp in India that was initiated in 2019 with funding support from the World Bank and ICAR, and later by the Department of Fisheries, Government of India. A genetic model for the prediction of multi-trait breeding values was optimised, an aggregate genotype index for selection was developed, and the genetic response through stochastic simulations in common carp was predicted. The outcome of this study will aid in

genetic selection and the adoption of an optimal breeding strategy (number of families and family size for genetic evaluation with a controlled rate of inbreeding) and thus contribute to the sustainable long-term breeding of common carp in India.

1.2 Research problem

Cyprinus carpio, popularly known as common carp, is the fourth most widely farmed fish species in the world, with an annual production of 4.18 million tonnes (FAO, 2024). China is the major producer of common carp, followed by other Southeast Asian countries and Europe. Common carp production in India remains highly unstable compared to the global increasing trend (Figure *1*). It is an exotic species with a limited introduction history but is now ubiquitously found in water bodies across the country. The major challenges for sustainable aquaculture production of common carp in India are, among others, i) non-availability of quality seeds owing to inbreeding, ii) negative selection, and iii) hatcheries functioning as closed units, which has led to lower productivity and loss of income (Nagaraja et al., 2026). To boost aquaculture production, ICAR-CIFE has initiated a breeding programme for common carp under the Pradhan Mantri Matsya Sampada Yojana (PMMSY) scheme of the Government of India. The Indian production environment primarily comprises inland saline waters, where common carp demonstrate tolerance and satisfactory growth performance under low-salinity conditions (Raghul et al., 2026), (Nagaraja et al., 2026), (Raghul et al., 2026), and (Lalramnunsanga et al., 2024).

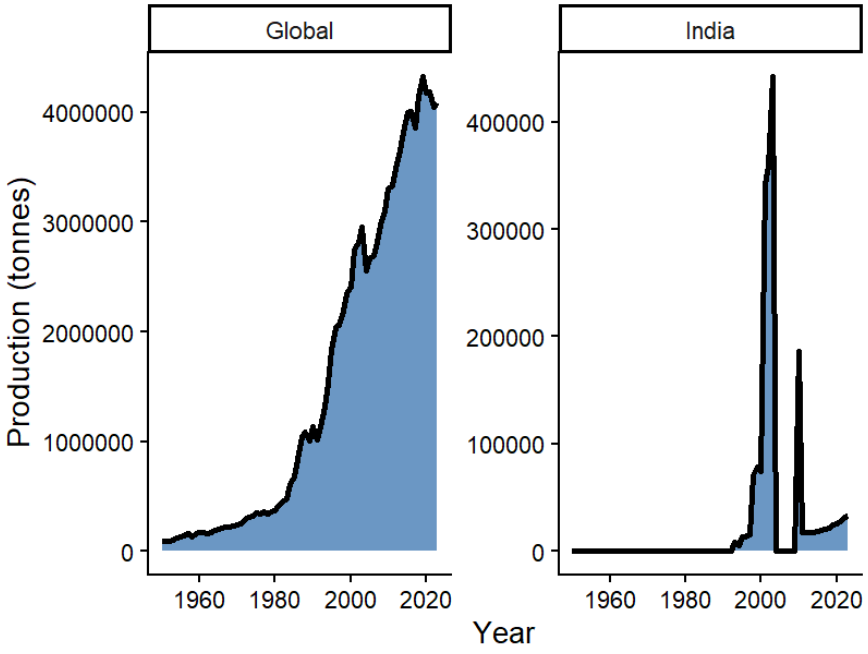

Figure 1. Production trend of common carp, Global and India

In the era of global climate change, soil salinisation is occurring at an alarming rate. It is estimated that 20 % of total cultivated and 33% of irrigated global agricultural lands have been afflicted by salinity (Kraamwinkel, Beaulieu, Dias, & Howison, 2021). In India, 6.74 million

hectares of land are salt-affected (Kumar & K, 2020). These soils are barren and are inundated by underground saline water which is suboptimal for agricultural crops but can be an excellent resource for inland saline aquaculture of salt-tolerant and brackish water species. Common carp is a candidate species for low saline aquaculture (< 8 ppt salinity) and can withstand the adverse temperature conditions of dryland saline ecosystems (surface water temperatures range between 5 and 35^0 C). Thus, owing to the salinity and temperature tolerance abilities of common carp, the production system defined for a breeding programme is an inland saline environment.

The breeding goal is to develop a fast-growing and resilient strain of common carp adapted to existing inland saline aquaculture systems. The breeding objective for growth can be formulated based on the estimates of quantitative genetic parameters. Growth traits are quantitative (complex) traits, that is, they are influenced by multiple genetic and environmental sources of variation. Multi-trait genetic evaluation allows phenotypic variation to be partitioned into additive genetic effects, full-sib effects (which combine early common environment, dominance, and maternal genetic effects), pond effects (rearing environment), and residual effects. This framework will enable the estimation of genetic parameters, such as heritability and genetic correlations between traits and salinity environments. These estimates will form a basis for selection criteria, predict genetic gain and aid in optimisation of selection strategies in the breeding programme

In common carp breeding programs, as in other fish breeding programs, parents with a high genetic potential for growth must be selected to ensure high-performing future generations. These selection decisions are determined using genetic models. Genetic models represent the genetic architecture of traits in fish populations and use information on observed phenotypes to predict the genetic value of an individual by utilising information about relatedness, for example, a pedigree (estimated breeding value- EBVs). EBVs are central to modern fish breeding programs, enabling the accurate selection of genetically superior individuals and the achievement of targeted genetic improvement over generations (Hutu, Oldenbroek, & Van derWaaji, 2020). Best Linear Unbiased Prediction (BLUP) is a widely used method for predicting EBVs for commercially important traits. BLUP utilises information from all genetically related animals, incorporates correlated traits, and accounts for fixed effects to provide unbiased and accurate EBV estimates (Henderson, 1985), (Lynch & Walsh, 1998), (van der Werf, 2009).

In the present study, phenotypic records for body weight (BW), standard length (SL), and body depth (BH) of common carp reared under “low” salinity and “high” salinity conditions were used. Although both salinity levels are rather brackish water levels and thus not at seawater salinity, they are referred to as low saline (LS: 2-4 ‰) and high saline (HS: 6-8 ‰). Thus, the breeding data constitute a multi-trait, multi-environment dataset. Such datasets allow the simultaneous evaluation of multiple correlated traits while accounting for genotype-by-environment interactions. Therefore, a multi-trait BLUP approach needs to be employed to estimate breeding values by utilising information from correlated traits, genetically related individuals, and environmental effects, thereby improving the accuracy of genetic evaluation and selection decisions. Furthermore, the Nucleus Breeding Centre (NBC) for common carp in India has an evaluation capacity of approximately 5000 fish per year class. For effective breeding, it is desirable to employ stochastic simulation to assess alternative breeding scenarios to choose the optimal breeding strategy limited by the total number of individuals but varying the number of families and number of individuals per family that maximises the long-term

genetic response. The breeding program aims to achieve the highest genetic response while maintaining high genetic variability and controlling the rate of inbreeding. Simulations of alternative breeding scenarios will provide an optimal strategy that maximises genetic gain while maintaining acceptable levels of inbreeding in the NBC.

With this background, the present study was performed with the following objectives.

1.3 Objectives

- To estimate additive genetic, full-sib, pond, and residual variance components for growth traits of common carp reared under two varying salinities.
- To predict multi-trait EBVs and their accuracy using a multi-trait BLUP model.
- To predict the genetic response to selection under alternative breeding scenarios using stochastic simulations.

2 METHODOLOGY

2.1 Details of Data

The data comprised phenotypic records of growth performance at two salinity levels and a pedigree of an ongoing selective breeding program of common carp *Cyprinus carpio* in India (saline car) (Table *1*). BW was measured using a portable digital weighing balance (weighed to the nearest 0.01 g), SL (horizontal distance from the snout to the base of the caudal fin, measured using a ruler to the nearest mm), and BD (vertical distance between the anterior origin of the dorsal fin and the anterior origin of the pelvic fin, measured using a ruler to the nearest mm).

Table 1. Breeding structure of the two-year classes used for data analysis

Generation	Year class	Sires	Dams	Families	Progeny per family	Total progeny
Second	2023	77	96	96	24	2291
	2024	277	326	326	12	4010
Total	2	354	422	422	15	6301

2.2 Estimation of (co)variance components

The breeding data of the present study comprised growth records of second-generation common carp consisting of two year classes. They are based on three founding stocks, viz., those originating from North, Central, and South India. The breeding nucleus was kept open for the first two generations; hence, there was an introduction of fresh founders in both generations. Second-generation families consisting of two year classes were also produced partially by selective breeding based on the estimated breeding value for the BW of their parents, which were fish belonging to the first generation. Therefore, the population for genetic analysis in the present study was an admixture of progeny obtained from the selective breeding of both parents (based on single trait EBV for BW), selected single parent (EBV for BW), single parent of unselected founders, and both parents of unselected founders. The first step of the current analysis involved reconstructing the pedigree so that the inverse relationship matrix (A^{-1}) incorporated all founding individuals and stocks as genetic groups. Thus, all the founders were explicitly included in the pedigree file, as were potential genetic differences due to differences between founding stocks. This follows the method to estimate the inverse relationship matrix directly from the pedigree, as previously reported (Meuwissen & Luo, 1992), and adjusts for differences in mean genetic breeding values among founding stocks.

Phenotypic data were analysed using a multi-trait linear mixed model implemented in ASReml-R (v 4.2) (Butler, Cullis, Gilmour, Gogel, & Thompson, 2023) to estimate (co)variance components and various fixed effects. The focal traits expressed in the two salinity environments were treated as distinct but genetically correlated traits, enabling the estimation of environment-specific genetic parameters (such as EBVs and heritability) and evaluation of

genotype re-ranking across environments. A low genetic correlation between salinity environments would indicate a strong genotype × environment interaction, resulting in the re-ranking of individuals. Consequently, selection based on performance at one salinity level will not lead to optimal genetic improvement at another salinity level, suggesting the need for salinity-specific genetic evaluation and selection strategies. Conversely, a high genetic correlation between salinity environments would indicate limited genotype × environment interaction, suggesting that genotypes perform consistently across salinity conditions and that selection in one environment would result in comparable genetic improvements in the other environment. Heritability is the proportion of total phenotypic variance that can be attributed to additive genetic variance. It determines the extent to which phenotypic differences reflect differences in breeding values (additive genetic merit), thereby influencing the efficiency of selection and the expected response to the genetic improvement of a trait.

The statistical model used was as follows:

$$\boldsymbol{y} = \mathbf{Xb} + \boldsymbol{Z_{as}a_s} + \boldsymbol{Z_{fs}f_s} + \boldsymbol{Z_{ps}p_s} + \mathbf{e}$$

where:

- **y** is the vector of phenotypic observations
- **b** is the vector of fixed effects
- $\mathbf{a}_s$ represents additive genetic effects interacting with salinity environments
- $\mathbf{f}_s$ denotes full-sib-by-salinity interaction effects (the full-sib effect includes maternal genetic effects, common early rearing environment effects and non-additive genetic effects)
- $\mathbf{p}_s$ represents pond effects conditional on salinity environments
- **e** is the vector of residual effects
- **X**, $\mathbf{Z}_{as}$, $\mathbf{Zf}_s$, and $\mathbf{Z}_{ps}$ are incidence matrices that relate observations to their respective effects.

2.2.1 Fixed Effects

The fixed component included the full interaction of year class, salinity, and sex:

Year_Class × Salinity × Sex

to account for management differences among production cycles, systematic environmental variations, and sex-specific performance in each salinity environment.

2.2.2 Random Effects

2.2.2.1 Additive Genetic Effects

The additive genetic effects interacting with salinity were assumed to follow:

$$\mathbf{a}_s \sim N(0, \mathbf{G}_{as} \otimes \mathbf{A})$$

where **A** is the inverse of the numerator relationship matrix derived from pedigree information and $\mathbf{G}_{as}$ is the 2x2 additive genetic covariance matrix for the two salinity environments. This formulation models the performance between salinity environments as genetically correlated traits.

2.2.2.2 Full-sib effects

The full-sib by salinity interaction effects were fitted to account for common full-sib environmental influences and non-additive genetic effects, which may vary between the two salinity environments:

$$\mathbf{f}_s \sim N(0, \mathbf{I}_f \otimes \mathbf{F}_s)$$

where **I_f** is an identity matrix for families and $\mathbf{F}_s$ represents the covariance matrix for the two salinity environments.

2.2.2.3 Pond effects

The ponds were restricted to individual salinity environments; therefore, pond effects were modelled as effects conditional on salinity without covariance between environments ((because every pond represented only one salinity environment) with heterogeneous variances):

$$\mathbf{p}_s \sim N(0, \mathbf{I}_{p(s)}\sigma^2_{P(s)})$$

where $I_{p(s)}$is an identity matrix for ponds within each salinity environment and $\sigma^2_{P(s)}$denotes salinity-specific pond variances.

2.2.2.4 Residual Effects

The residual effects were assumed to be independent between salinity environments (because every fish was kept only in one salinity environment) with heterogeneous variances:

$$\mathbf{e} \sim N(0, \mathbf{I} \otimes \mathbf{R}_s)$$

where **R** is a diagonal residual covariance matrix that allows salinity environment-specific residual variances and no residual covariance between salinity environments.

2.2.3 Estimation of Genetic Parameters

The variance components were estimated using restricted maximum likelihood (REML) under the implementation of the average information algorithm in ASReml-R (v 4.2) (Butler, Cullis, Gilmour, Gogel, & Thompson, 2023), and EBVs were predicted via BLUP (Henderson, 1975). Environment-specific heritability was calculated as follows:

$$\boldsymbol{h}^2_{\boldsymbol{s}} = \frac{\boldsymbol{\sigma}^2_{\boldsymbol{A,s}}}{\boldsymbol{\sigma}^2_{\boldsymbol{A,s}} + \boldsymbol{\sigma}^2_{\boldsymbol{F,s}} + \boldsymbol{\sigma}^2_{\boldsymbol{P,s}} + \boldsymbol{\sigma}^2_{\boldsymbol{E,s}}}$$

where, specific to a salinity environment s:

- $\sigma^2_{A,s}$= additive genetic variance

- $\sigma^2_{F,s}$= among-family variance
- $\sigma^2_{P,s}$= among-pond variance
- $\sigma^2_{E,s}$= residual variance s.

The genetic correlations between salinity environments were estimated as:

$$\boldsymbol{r_g = \frac{\sigma_{A,ij}}{\sqrt{\sigma^2_{A,i}\sigma^2_{A,j}}}}$$

where $\sigma_{A,ij}$is the additive genetic covariance between salinity environments $i$and j, and $\sigma^2_{A,i}$and $\sigma^2_{A,j}$are the corresponding salinity-specific additive genetic variances (Falconer, Introduction to quantitative genetics., 1981).

2.3 Construction of Multi-trait Selection Index

The EBVs obtained from the multi-trait BLUP analysis were combined into a linear selection index to rank the selection candidates across traits and salinity environments. The selection index is a linear combination of EBVs for multiple traits weighted by their relative economic weights into a single value for an individual. Individuals can be further compared or ranked based on this index value (overall genetic merit). The selection index (Hazel, 1943) for each animal was defined as:

$$I = \sum_{i=1}^{m} w_i \ \hat{A}_i$$

where:

- $I$is the selection index value,
- $\hat{A}_i$is the estimated breeding value for trait i,
- $w_i$is the economic weight assigned to trait i,
- $m$is the number of traits included in the breeding objective.

The EBVs were derived from the multi-trait BLUP evaluation (Henderson, Applications of linear models in animal breeding, 1984). It accounts for pedigree relationships, genetic correlations among traits, genotype-by-salinity interaction effects, and heterogeneous environmental variances.

2.3.1 Trait Scaling and Economic Weights

The phenotypic traits were standardised prior to genetic analysis; consequently, EBVs were expressed on comparable scales and were not further standardised. Because reliable economic values were unavailable at this time, equal economic weights were assumed for all traits:

$$w_1 = w_2 = \cdots = w_m$$

Under this assumption, the selection index reduces to the unweighted sum of EBVs:

$$I = \sum_{i=1}^{m} \hat{A}_i$$

representing equal genetic emphasis across all traits and salinity environments.

2.3.2 Accuracy of the multi-trait BLUP

The accuracy of the multi-trait was approximated using prediction error variances (PEV) obtained from the BLUP evaluation. The PEV reflects the uncertainty associated with EBVs. The reliability of the index was calculated as follows:

$$\text{Rel}_I = 1 - \frac{PEV_I}{\sigma^2_{A,I}}$$

where $PEV_I$is the prediction error variance of the index, obtained via the predict function of the ASReml-R (v 4.2) and $\sigma^2_{A,I}$is the additive genetic variance of the aggregate breeding objective obtained via multi-trait analysis (equation in 3.2).

The accuracy, which represents the correlation between the estimated multi-trait BLUP and the true aggregate breeding value, was calculated as follows:

$$r_{IH} = \sqrt{\text{Rel}_I}$$

2.3.3 Prediction of Genetic Response

The expected genetic gain was predicted using the breeder's equation:

$$\boldsymbol{\Delta G = i \times r_{IH} \times \sigma_{A,H}}$$

where:

- $i$is selection intensity,
- $r_{IH}$is index accuracy,
- $\sigma_{A,H}$is additive genetic standard deviation of the aggregate genotype.

A selection intensity of $i = 1.76$ was assumed, corresponding approximately to selection of the top 10% of candidates under truncation selection. The predicted response follows the standard quantitative genetic theory for selection of an aggregate breeding objective (Falconer & Mackay, 1996; Lynch & Walsh, 1998).

2.4 Stochastic Simulation Framework

A stochastic simulation was conducted to evaluate the effects of breeding design on genetic improvement. The simulation represented a closed nucleus breeding population undergoing selection based on EBVs from a multi-trait BLUP model. The generation-wise trends were used to compare differences among breeding scenarios

2.4.1 Simulation Structure

A base population was generated using a pedigree structure that was consistent with the empirical dataset. Subsequent generations were simulated under different scenarios varying in

the number of families per generation, number of progenies per family (family size), and selection intensity, while keeping the total population size similar at approximately 5000 individuals (matching the breeding program capacity for each year class). Each scenario was evaluated over ten discrete generations with ten independent stochastic replicates to account for random variations in Mendelian segregation, sampling, and mating (Table *2*). The Bulmer effect was simulated for the first three generations. Simulations were performed using R software (version R. 4.5.2) and various source codes. The objective of the simulations was to determine the optimum combination for family number and family size for a known mating design which yields the highest and most consistent genetic gain across ten generations.

Table 2 Scenarios simulated

Scenarios/Parameters	**1**	**2**	**3**	**4**
No of families/generation	250	125	85	65
Mating	2	2	2	2
Within family	10	20	30	40
Total offspring	5000	5000	5100	5200
Selected from family (max)	4	4	4	4
Generation	10	10	10	10
Replication	10	10	10	10
Top males	400	200	136	105
Top females	500	250	170	130

2.4.2 Genetic Model

The true breeding values (TBVs) were simulated under an infinitesimal additive genetic model as follows:

$$\mathbf{a} \sim N(0, \mathbf{A}\sigma_A^2)$$

The phenotypes were generated using a simple model that ignores putative additional effects, such as pond and full-sib effects, as follows:

$$\mathbf{y} = \mathbf{a} + \mathbf{e}, \mathbf{e} \sim N(0, \mathbf{I}\sigma_E^2)$$

Heritability was fixed based on empirical estimates from the BLUP analysis.

2.4.3 Genetic Evaluation in Simulation

For each generation and replicate, the TBVs were obtained directly from simulated genetic values, the EBVs were predicted using the same multi-trait BLUP framework as the empirical analysis (but omitting the full-sib and pond effect), and selection was performed based on the selection index.

Prediction accuracy (r) was calculated as the correlation between TBV and EBV, and averaged across replicates

$$r = \text{cor(TBV,EBV)}$$

2.4.4 Realised Genetic Gain

Genetic improvement was quantified as the realised true genetic gain per generation:

$$\Delta G_t = T\bar{B}V_{selected,t} - T\bar{B}V_{base,t}$$

where $T\bar{B}V_{selected,t}$ is the mean TBV of selected individuals in generation t, and $T\bar{B}V_{base,t}$ is the mean TBV of the base population in the same generation.

2.4.5 Inbreeding Estimation

The inbreeding coefficients were computed from the pedigree relationship matrix:

$$F_i = 1 - A_{ii}$$

where A_{ii} is the diagonal element of the numerator relationship matrix. The rate of inbreeding per generation was calculated using t as an index of generation:

$$\Delta F_t = \frac{F_t - F_{t-1}}{1 - F_{t-1}}$$

3 RESULTS

3.1 Descriptive statistics

The descriptive statistics, viz., number of observations, mean, standard deviation, coefficient of variation (%), and minimum and maximum values for the growth traits were estimated (Table 3). The common carp grown in LS exhibited higher mean values for the growth traits (percentage of difference; BW: 18 %, SL: 4.5 %, and BH: 5.4 %) when compared to HS fish, whereas the HS common carp exhibited higher coefficient of variation (13.5–35 %) when compared to LS fish (11.5–31.8 %) across traits. Among the traits, BW expressed a higher CV (31.8–35 %) than SL and BH (10.4–13.5 %).

Table 3. Descriptive statistics of growth traits at each salinity

Salinity		**LS**			**HS**	
Traits	**BW(g)**	**SL(cm)**	**BH(cm)**	**BW(g)**	**SL(cm)**	**BH(cm)**
Mean	998.1	30	11.7	842.8	28.7	11.1
SD	317.4	3.1	1.3	295.2	3.1	1.5
CV (%)	31.8	10.4	11.5	35	10.8	13.5
Min	306	20.2	8.1	136	14.5	5.7
Max	2748	45.1	17.5	2725	42.3	17.2
N	2639	2639	2637	2373	2373	2372

The visualised relationships among growth traits demonstrated strong associations among growth traits and revealed variations across salinity levels and sex (Figure *2* and 3).

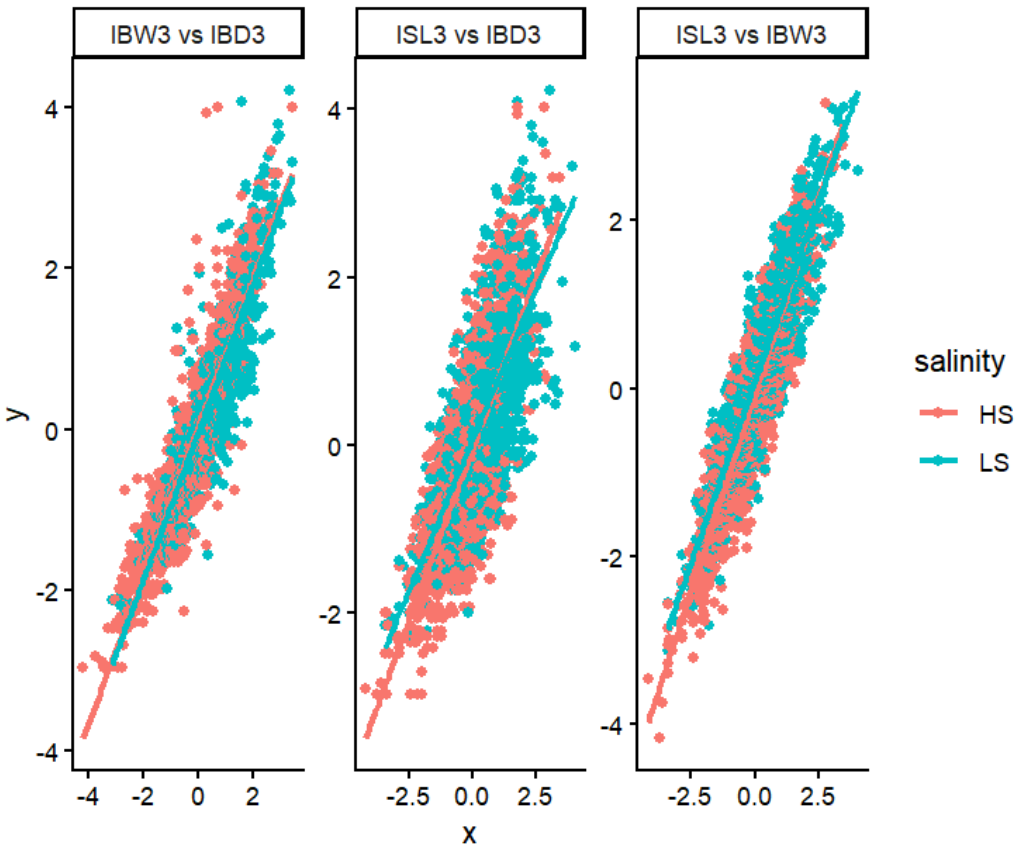

Figure 2. Relationship of growth traits vs salinity

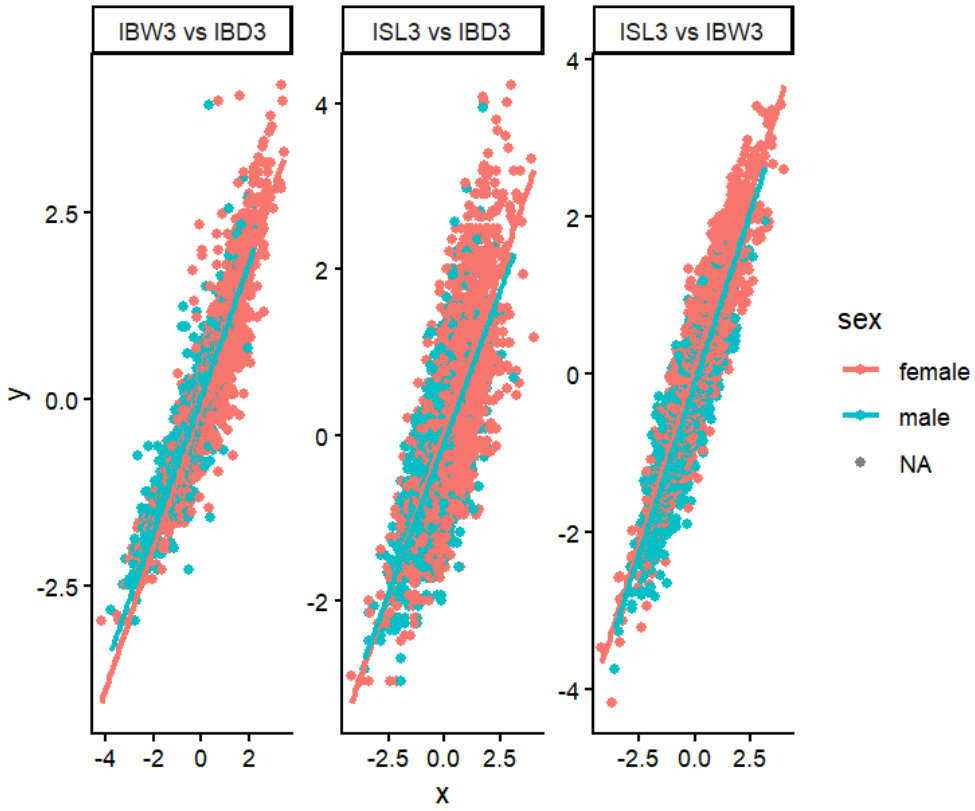

Figure 3. Relationship of growth traits vs sex

3.2 Fixed effects

The fixed factors, viz., year class, sex, salinity, and their interactions, had a significant effect on BW, SL, and BH, except for the year class*sex interaction (**Error! Not a valid bookmark self-reference.**). This indicates that temporal environmental conditions influenced growth traits, and the significant interactions reflected variations in trait responses across factors.

Table 4. Wald tests for fixed effects

Effect	BW		SL		BH	
	denDF	Fvalue	denDF	Fvalue	denDF	Fvalue
year class	20377	61.71*	20377	29.18*	20377	139.3*
sex	425.4	1168*	422.7	99.22*	421.2	946*
year class *sex	4615.2	0.56	7414	2.6	2045.7	0.02
year class*salinity	20377	10.66*	20377	12.58*	20377	21.91*
sex*salinity	370.2	42.94*	399.9	39.48*	418.5	40.61*
year class*sex*salinity	20377	5.68**	20377	8.06*	11295	4.11**

Signif. codes: 0 ‘*’ 0.05 ‘**

3.3 Random effects

3.3.1 Full-sib effects

The full-sib effect correlation matrix revealed positive association for growth traits across salinity environments (correlation range: 0.62-0.94). The full-sib effect which includes maternal genetic effects, common early rearing environment effects, and non-additive genetic effects, was moderate to high across traits. This indicates a minimum full-sib effect by salinity interactions, except between SL_LS and BH_HS, where a low correlation was detected (0.34), indicating a strong full-sib-effect-by-salinity interaction (Table 5).

Table 5. Full-sib effect correlation matrix of growth traits

	BW_HS	**SL_HS**	**BH_HS**	**BW_LS**	**SL_LS**	**BH_LS**
BW_HS	1.00	0.93	0.94	0.77	0.62	0.82
SL_HS	0.93	1.00	0.76	0.82	0.80	0.73
BH_HS	0.94	0.76	1.00	0.57	0.34	0.74
BW_LS	0.77	0.82	0.57	1.00	0.93	0.93
SL_LS	0.62	0.80	0.34	0.93	1.00	0.73
BH_LS	0.82	0.73	0.74	0.93	0.73	1.00

3.3.2 Common environment (pond) effects

The pond effect correlation matrix revealed a strong positive association between traits within each salinity environment. For HS, the correlation ranged between 0.80 and 1.00, and for LS, from 0.93 to 0.99, indicating consistent pond-related influences on all growth traits (**Error! Not a valid bookmark self-reference.**).

Table 6. Pond effect correlation matrix of growth traits

	BW_HS	**SL_HS**	**BH_HS**	**BW_LS**	**SL_LS**	**BH_LS**
BW_HS	1.00	1.00	0.81	NA	NA	NA
SL_HS	1.00	1.00	0.80	NA	NA	NA
BH_HS	0.81	0.80	1.00	NA	NA	NA
BW_LS	NA	NA	NA	1.00	0.96	0.99
SL_LS	NA	NA	NA	0.96	1.00	0.93
BH_LS	NA	NA	NA	0.99	0.93	1.00

3.3.3 Additive genetic effects

The additive genetic correlation matrix revealed a strong positive association between traits (Table 7). The growth traits showed strong and positive genetic correlations ranging between 0.76 and 0.97, except between SL_HS and BH_LS which demonstrated a moderate genetic correlation (0.69). Overall, the results indicate a low re-ranking of families across salinities and thus a low genotype-by-environment interaction, which is advantageous for common and effective selective breeding in both salinity environments.

Table 7. Additive genetic correlation matrix of growth traits

	BW_HS	SL_HS	BH_HS	BW_LS	SL_LS	BH_LS
BW_HS	1.00	0.89	0.96	0.97	0.88	0.91
SL_HS	0.89	1.00	0.81	0.81	0.95	0.69
BH_HS	0.96	0.81	1.00	0.96	0.82	0.96
BW_LS	0.97	0.81	0.96	1.00	0.87	0.97
SL_LS	0.88	0.95	0.82	0.87	1.00	0.76
BH_LS	0.91	0.69	0.96	0.97	0.76	1.00

3.3.4 Residual effects

The residual effect correlation matrix revealed strong positive associations between the traits within each salinity environment. The residual correlation among traits ranged between 0.76 and 0.92 in HS and between 0.82 and 0.90 for traits in LS, indicating consistent random environmental influence (and measurement error) on growth traits within each salinity (Table *8*).

Table 8. Residual correlation matrix of growth traits

	BW_HS	SL_HS	BH_HS	BW_LS	SL_LS	BH_LS
BW_HS	1.00	0.92	0.85	NA	NA	NA
SL_HS	0.92	1.00	0.76	NA	NA	NA
BH_HS	0.85	0.76	1.00	NA	NA	NA
BW_LS	NA	NA	NA	1.00	0.89	0.82
SL_LS	NA	NA	NA	0.90	1.00	0.70
BH_LS	NA	NA	NA	0.82	0.70	1.00

3.3.5 Phenotypic correlations

The resulting phenotypic correlation matrix displayed strong positive associations between traits within each salinity environment (Table 9). The phenotypic correlation ranged between 0.77 and 0.91 for traits in HS and between 0.74 and 0.92 in LS.

Table 9. Phenotypic correlation matrix of growth traits

	BW_HS	SL_HS	BH_HS	BW_LS	SL_LS	BH_LS
BW_HS	1.00	0.91	0.90	NA	NA	NA
SL_HS	0.91	1.00	0.77	NA	NA	NA
BH_HS	0.90	0.77	1.00	NA	NA	NA
BW_LS	NA	NA	NA	1.00	0.89	0.92
SL_LS	NA	NA	NA	0.89	1.00	0.74
BH_LS	NA	NA	NA	0.92	0.74	1.00

3.3.6 Estimates of heritability (h^2), pond variance (c^2), full-sib effect (f^2) and residual variances (r^2) for growth traits

Based on the estimates, the traits expressed high heritability, moderate full-sib effects, but low pond effects (Table *10*). The heritability generally ranged from 0.36 to 0.57. Among traits,

BH_LS had the highest heritability (0.57), whereas BW_HS had the lowest (0.38). The heritability estimates for growth traits were higher in LS (0.52 – 0.57) than in HS (0.36 – 0.44). The pond variance was higher in LS (0.04 – 0.09) than in HS (0.007–0.02), whereas the full-sib effect variance was higher in HS (0.09 – 0.14) than in LS (0.07 – 0.09), and the residual variance was also higher in HS (0.43 – 0.47) than in LS (0.29 – 0.31).

Table 10. Estimates of heritability (h2), pond variance (c2), full-sib effect (f2) and residual variances (r2) for growth traits

Parameters	BW_HS	SL_HS	BH_HS	BW_LS	SL_LS	BH_LS
h^2	0.38 ± 0.11	0.44 ± 0.11	0.36 ± 0.11	0.52 ± 0.11	0.52 ± 0.1	0.57 ± 0.1
c^2	0.02 ± 0.02	0.02 ± 0.02	0.01 ± 0.01	0.09 ± 0.07	0.06 ± 0.04	0.04 ± 0.03
f^2	0.12 ± 0.05	0.09 ± 0.04	0.14 ± 0.05	0.08 ± 0.04	0.09 ± 0.04	0.07 ± 0.04
r^2	0.45 ± 0.07	0.43 ± 0.07	0.47 ± 0.07	0.29 ± 0.06	0.31 ± 0.06	0.30 ± 0.06

3.3.7 EBVs and G x E interaction

The genetic correlation estimates of EBVs for growth traits BW, SL, and BH across salinities were 0.96 ± 0.07, 0.95 ± 0.06, and 0.95 ± 0.08, respectively, indicating low reranking of genotypes between salinity environments for all three growth traits. The plots for EBVs reflected this low G × E (Figure *4*, 5, and 6).

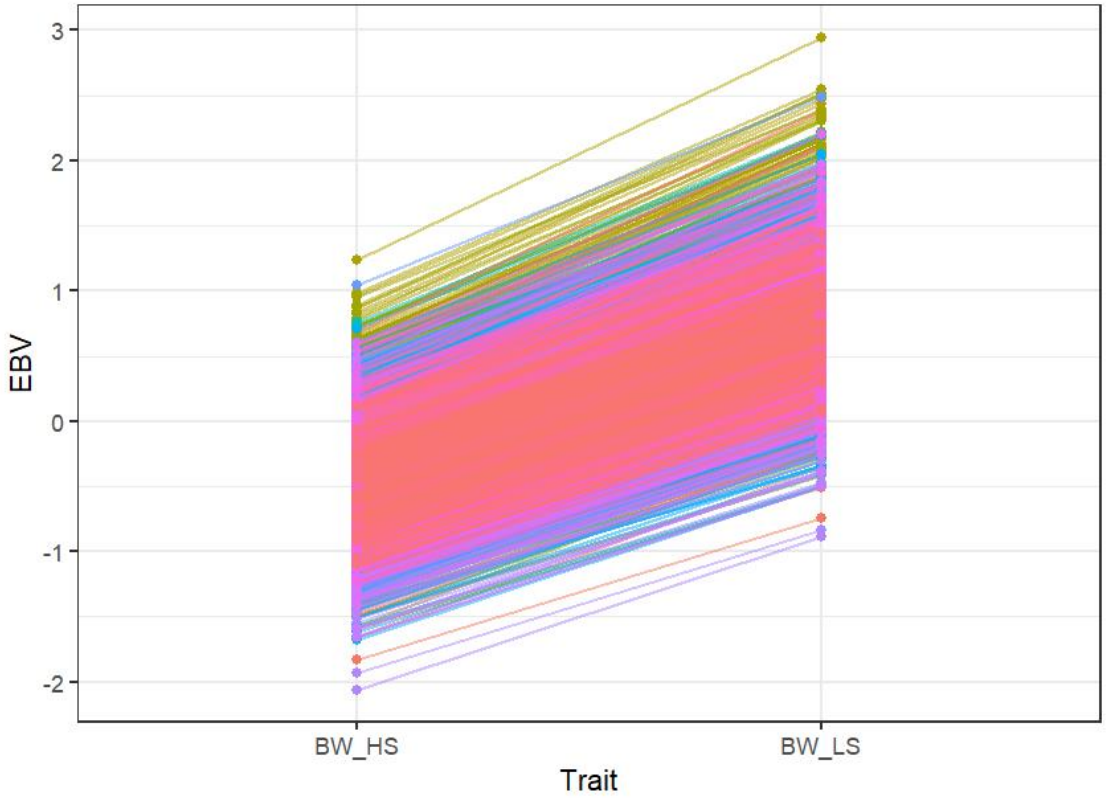

Figure 4. EBVs for BW across salinities

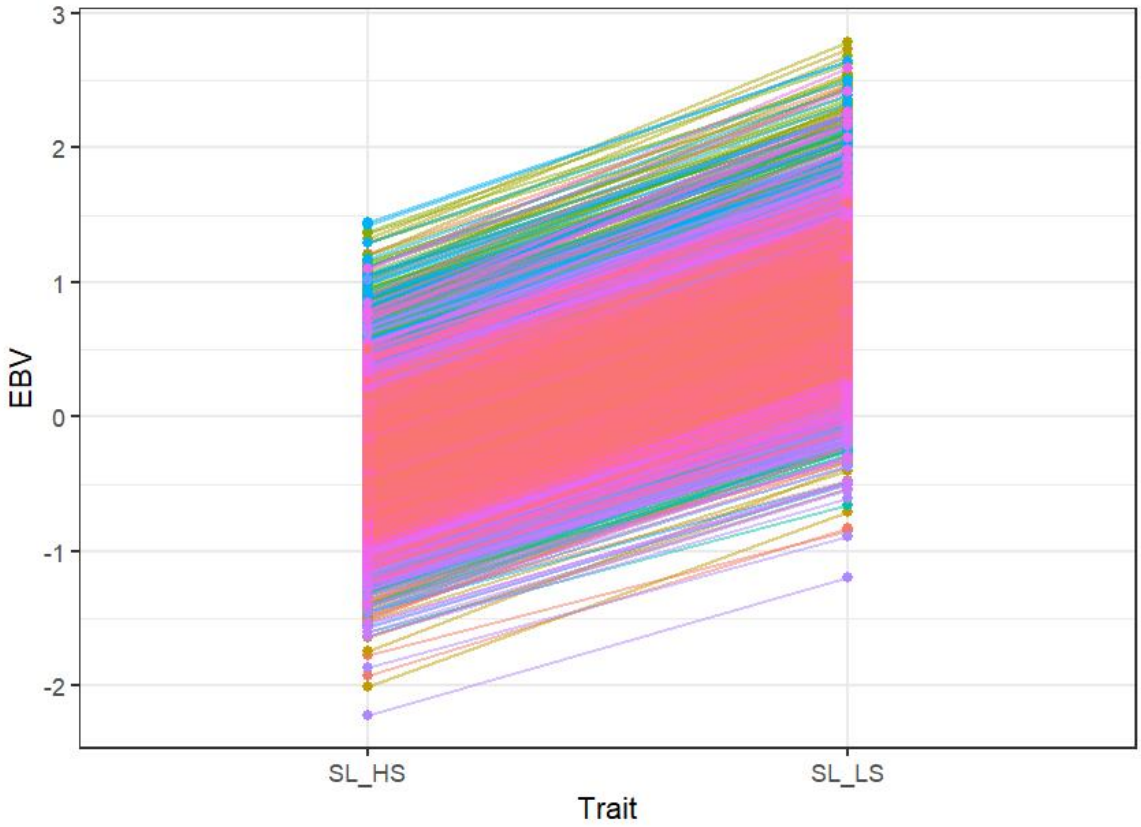

Figure 5. EBVs for SL across salinities

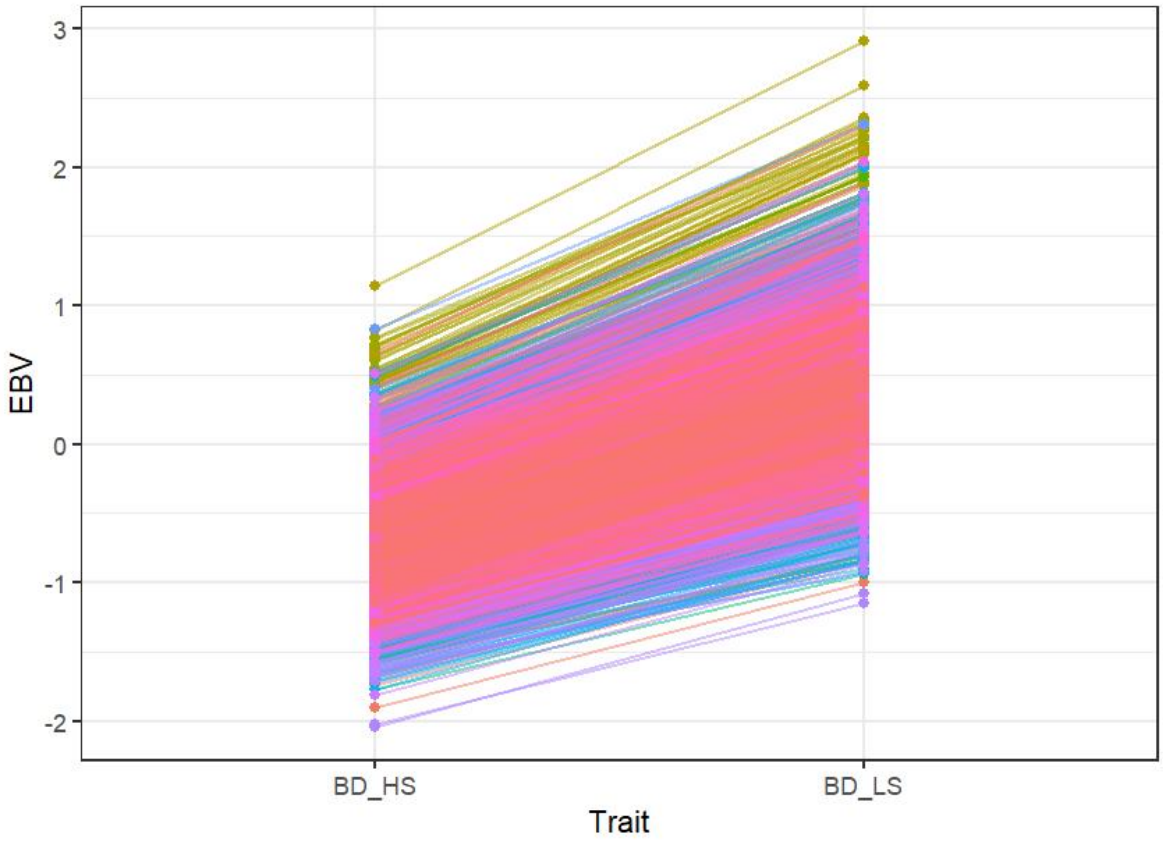

Figure 6. EBVs for BH across salinities

3.3.8 Accuracy of multi-trait BLUP and prediction of genetic response

The frequency distribution of the multi-trait BLUP aggregate genotype estimates revealed clear variation among individuals, reflecting the genetic variability available for selection (Figure 7). The prediction error variance (PEV) of multi-trait BLUP for all growth traits ranged between 0.12 and 0.22 (Table 11).

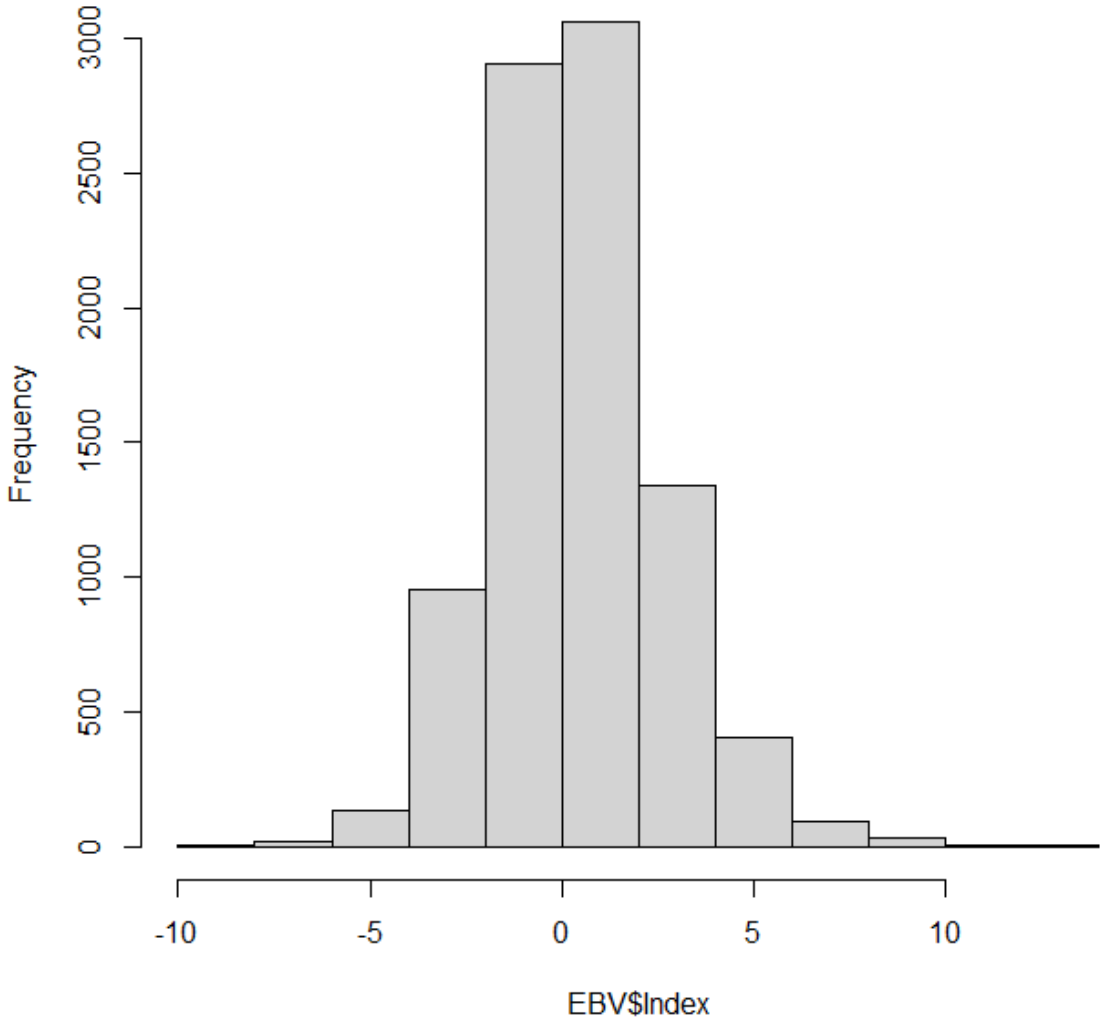

Figure 7. Distribution of multi-trait BLUP index

Table 11. PEV of multi-trait BLUP

	BW_HS	BW_LS	SL_HS	SL_LS	BH_HS	BH_LS
BW_HS	0.16	0.15	0.15	0.14	0.14	0.15
BW_LS	0.15	0.21	0.14	0.19	0.14	0.20
SL_HS	0.15	0.14	0.19	0.17	0.13	0.13
SL_LS	0.14	0.19	0.17	0.22	0.12	0.17
BH_HS	0.14	0.14	0.13	0.12	0.13	0.15
BH_LS	0.15	0.20	0.13	0.17	0.15	0.22

Based on the PEV and having defined selection intensity as1.76, the accuracy of multi-trait BLUP was estimated as 0.72. The aggregate response to selection was estimated to be +4.25 index units. All six traits (three growth traits in two salinity environments) exhibited a positive response to aggregate genotype selection (Table 12). The growth traits in LS yielded a higher response to selection (0.74 – 0.81) than those in HS (0.64 – 0.74). The trait SL yielded a high and consistent response to selection at both salinities (0.74 – 0.79) compared to other traits.

Table 12. Response to multi-trait selection

	BW_HS	BW_LS	SL_HS	SL_LS	BH_HS	BH_LS
Response	0.67	0.74	0.74	0.79	0.64	0.81

3.4 Simulation for alternative breeding scenarios

The stochastic simulation for four alternative breeding scenarios (Table 2) resulted in trend lines for TBVs, BLUP, accuracy, and genetic gain for multi-traits across 10 generations.

The traits in LS compared to HS exhibited a higher trend line for TBV (Figure *8*). Further, the breeding strategy in Scenario 2 demonstrated higher and more consistent TBVs across generations than the other scenarios.

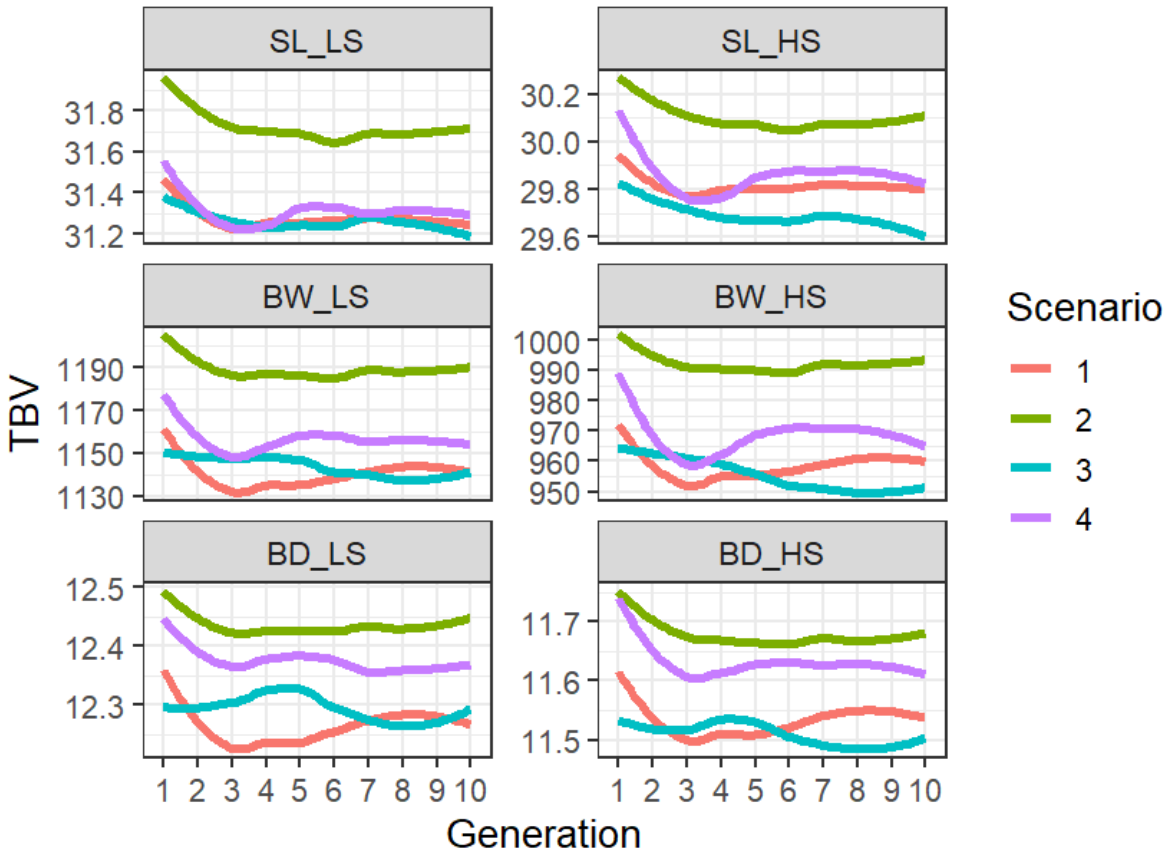

Figure 8. True Breeding Value trend for the three traits in the two salinities across the four simulated different breeding scenarios

The breeding strategy in scenario 1 demonstrated higher BLUP across generations, closely followed by scenario 2, whereas scenario 4 had the lowest trend for BLUP values across the ten simulated generations (Figure *9*). Here, the BLUP was standardised with a mean = 100 and SD = 10.

The traits in LS exhibited higher selection accuracy than those in HS. The traits SL and BD expressed a higher accuracy trend than BW. Furthermore, Scenario 2 demonstrated higher and more consistent multi-trait accuracy across the ten generations (Figure *10*).

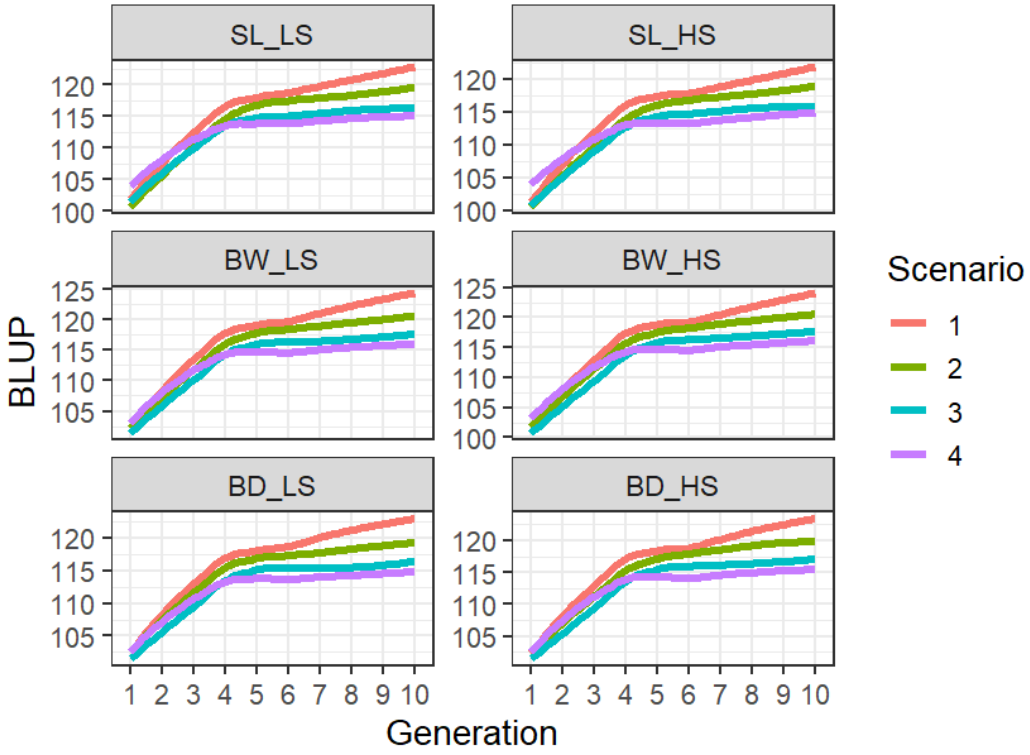

Figure 9. BLUP trend for the three traits in the two salinities across the four simulated different breeding scenarios

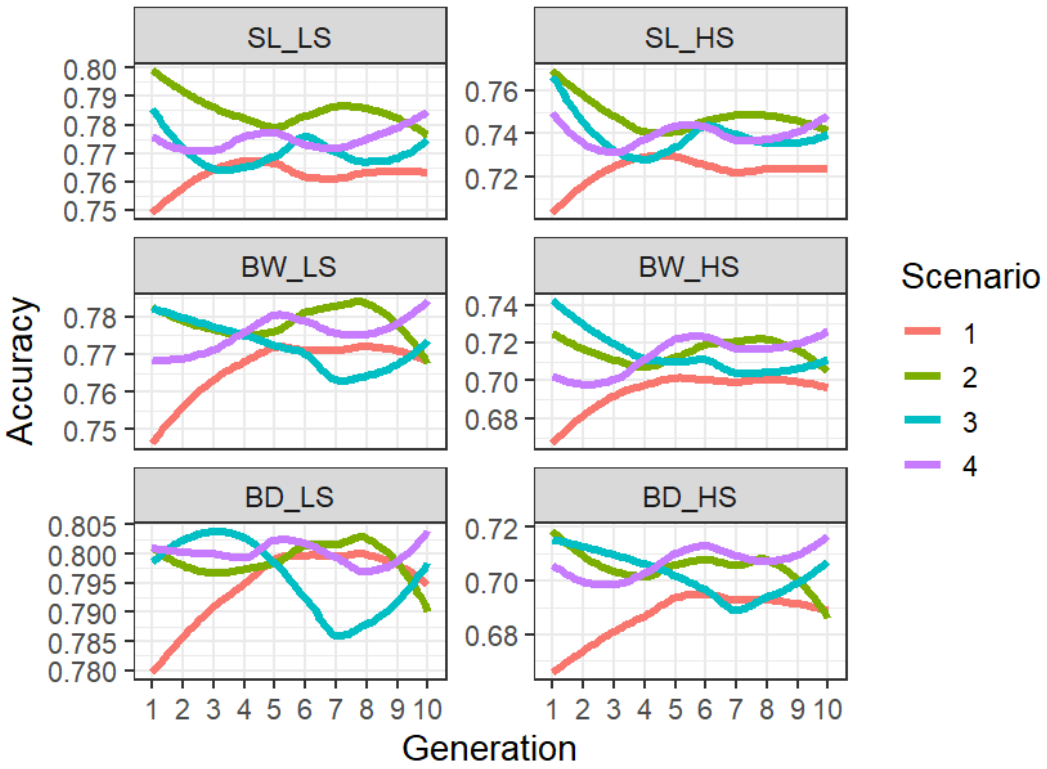

Figure 10. Accuracy trend for the three traits in the two salinities across the four simulated different breeding scenarios

The traits in LS exhibited a higher genetic gain than those in HS. Breeding scenario 2 exhibited higher and more consistent genetic gains in SL and BW across ten generations. However, a distinct trend towards genetic gain in BD was not observed in any of the four scenarios (Figure *11*).

Breeding scenario 1 yielded the lowest inbreeding rate (F= ranging from 0 to 0.5) across the ten generations (**Error! Reference source not found.**). Breeding scenario 2 was the second best in controlling the rate of inbreeding, and the maximum inbreeding rate observed at generation 10 was 0.5 % (**Error! Reference source not found.**). The breeding scenarios 4 yielded higher inbreeding rate ranging between 1 and 1.5 % whereas scenario 3 resulted in inconsistent rate of inbreeding (Figure *12*)

Overall, breeding scenario 2 is the most effective breeding scenario that can be adopted at NBC owing to the higher TBV, accuracy, and genetic gain across the ten generations and a low rate of inbreeding.

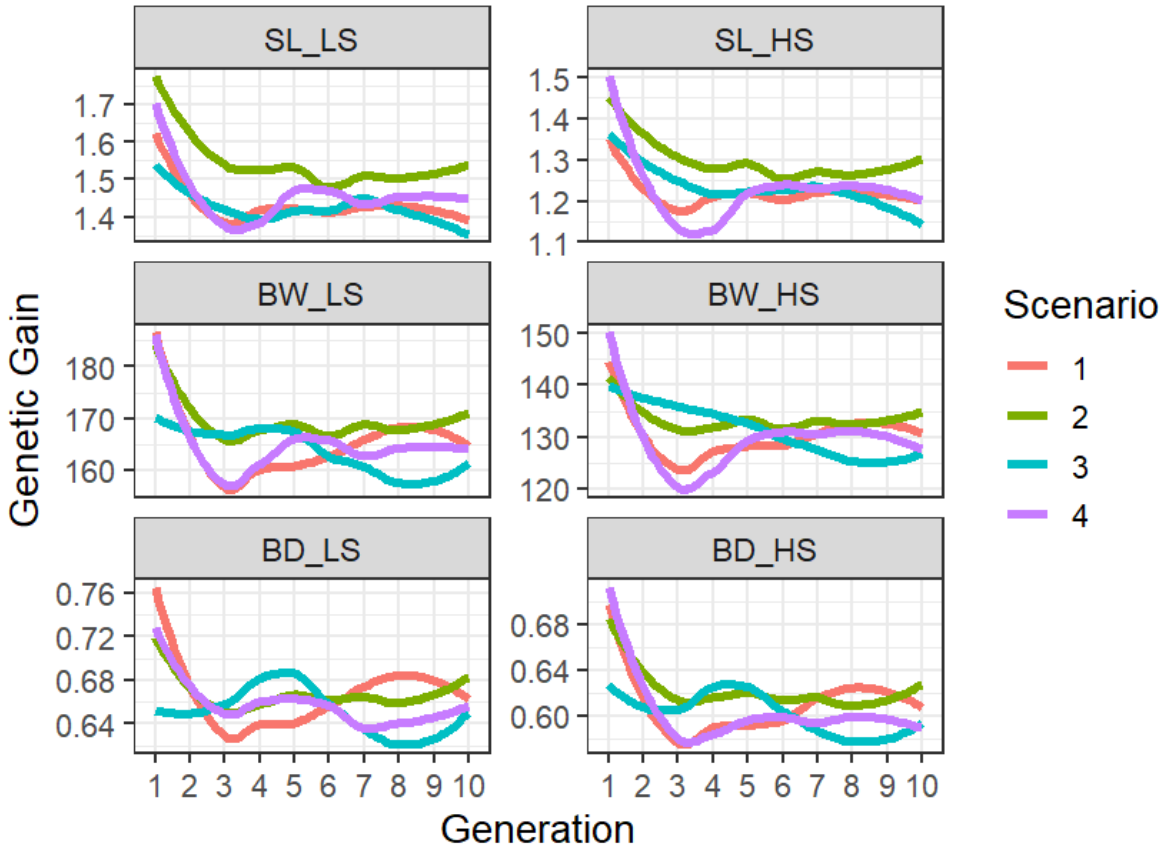

Figure 11. Genetic gain trend for the three traits in the two salinities across the four simulated different breeding scenarios

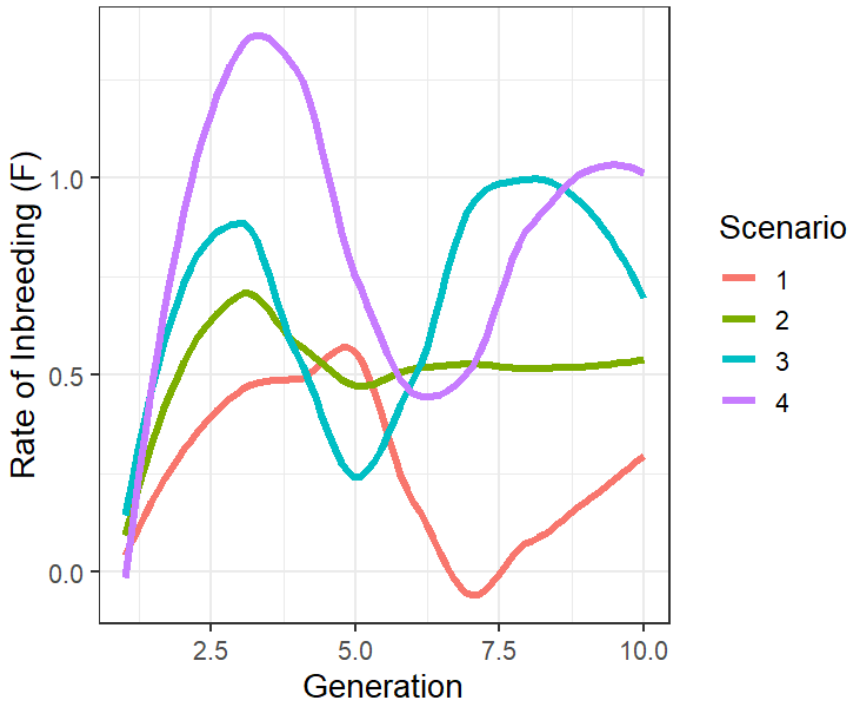

Figure 12. Rate of inbreeding across the four simulated scenarios

4 DISCUSSION

The prediction of breeding value is a fundamental component of breeding programs for genetic improvement (Mrode & Thompson, 2005). The present study deals with the breeding data generated in a genetic improvement program for common carp in India. An analysis was performed to predict the breeding values through an optimum genetic model and identify an effective breeding strategy for sustainable breeding at the NBC of common carp.

The growth traits in the present study exhibited high genetic correlations; hence, genetic evaluation of growth based on multi-trait BLUP was adopted, as it is expected to result in lower mean bias than single trait BLUP (Mrode & Pocrnic, 2023) (Viana, Sobreira, De Resende, & Faria, 2010). Further, one growth trait in two environments with different salinities can be considered as the performance of two traits with a genetic between-environment correlation. If the genetic correlation significantly deviates from unity, it indicates a genotype-by-environment interaction (Falconer, 1960). Thus, a multi-trait multi-environment modelling approach was employed in the present analysis. The phenotypic information combined with pedigree information allowed the estimation of BLUP EBV for all fish and all traits. The multi-trait BLUP EBV is a procedure that optimally combines information on animals and their relatives to simultaneously estimate EBVs for several traits. The BLUP methodology thus resulted in a set of EBVs per animal, one for each trait (Schneeberger, Barwick, Crow, & Hammond, 1992) (van der Werf, 2009). The EBVs were then combined in a selection criterion (aggregate genotype) under equal economic weights. An index accuracy of 0.72 was obtained, corresponding to a correlation of 0.72 between estimated and true breeding values, which indicates effective prediction of genetic merit and supports its use for selection decisions.

The fixed effects in the present study had a significant effect on the focal growth traits, except for year class*sex. The year-class effects indicate a significant difference in temporal culture conditions which may be unique for each year class. Temporal culture differences may be due to fluctuations in temperature, length of day, and rainfall across year classes. Regarding the sex effect, sexual dimorphism in common carp is a well-known physiological phenomenon wherein females attain comparatively higher growth relative to males (Dong, Nguyen, & Zhu, 2015).

The growth traits exhibited moderate to high heritability (0.36 – 0.57). These estimates are comparable to previously reported estimates for common carp, but were estimated via univariate analysis (0.37 – 0.59) (Nagaraja, et al., 2026). The estimates agree with earlier wide-ranging findings in common carp by various authors (0.00-0.75) (Vandeputte, 2003) but are comparatively higher than the reported heritability for body weight (0.17) in a selective breeding program of common carp (four generations of selective breeding) in China (Dong, Nguyen, & Zhu, 2015). The relatively high heritability estimates obtained in the present study indicate that a substantive genetic gain in growth traits may be achieved by exploiting additive genetic variation via selection.

As members of a fish family are reared together until they attain a size suitable for individual tagging, they share a common environment, which contributes to the similarity between family members. This gives rise to an additional covariance between members of a family due to this early shared common environment, which increases variation among different families (Mrode & Thompson, 2005). It is essential to estimate these effects and adjust other effects for; otherwise, it may upwardly bias the additive genetic effects. The full-sib effects in the model estimate common environment effects (in addition, it also includes dominance and maternal

genetic effects). The contribution of the full-sib effects on growth traits to phenotypic variance estimated in the present study ranged from 0.07-0.14. This is comparatively lower than the previously reported full-sib effect in common carp which was 0.17 of the total phenotypic variation (Dong, Nguyen, & Zhu, 2015) and full-sib effect between 0.11-0.30 (Ninh, et al., 2011). A longer separate rearing period of families until they reach tagging size is likely to increase the full-sib effect on later-expressed growth traits. Early communal rearing (three days after hatching) likely reduces full-sib effects on later-expressed growth traits, as previously reported in a common carp breeding program in Vietnam (Ninh et al., 2011).

The very high genetic between-salinity correlation estimate (0.95 – 0.96) for the focal traits obtained in the present analysis indicates a low re-ranking of families and a low genotype-by-environment interaction (GxE). The multi-trait genetic correlation is higher and more consistent than the previously reported genetic correlation (0.64 – 0.85) obtained via the bivariate model (Nagaraja et al., 2026). There are no other reports on GxE in common carp for salinity, but a comparable low G × E (r_g = 0.97) has also been obtained for barramundi in Australia which was tested in various growth environments and salinities (freshwater and saline: 25 to 36 PSU) (Domingos, et al., 2013). However, contrasting results have been reported in other fish species, such as a moderate genetic correlation (0.33 – 0.67) in Arctic charr in freshwater and brackish water environments (20 PSU) in Canada (Chiasson, Quinton, Danzmann, & Ferguson, 2013) and a moderate genetic correlation (0.26) in Atlantic salmon reared in freshwater and seawater (35 PSU) in Chile has been reported (Gonzalez, Gallardo-Hidalgo, & Yáñez, 2022).

The Nucleus Breeding Centre (NBC) of common carp in India has the capacity to evaluate approximately 5000 fish per year class. The simulations considered the Bulmer effect for the first three generations, as it is widely reported that the maximum reduction in genetic variance occurs in the first three generations (Seyedsharifi, Azizyan, Boustan, Seifdavati, & Mojtahedin, 2018). The inclusion of Bulmer's effect aids in the accurate prediction of genetic gain, and ignoring Bulmer's effect will introduce a bias in predicting genetic progress per generation, as previously reported (Seyedsharifi, Azizyan, Boustan, Seifdavati, & Mojtahedin, 2018). In the present study, alternative breeding scenarios were simulated to determine an optimum breeding strategy for sustainable breeding. Breeding scenario 2 yielded a higher trend for TBV, BLUP, accuracy, and genetic gain across ten generations and can thus be considered an optimal strategy for sustainable breeding. Specifically, 250 families per generation (250 dams nested within 160 sires) and 20 progenies from each of these families were used, resulting in an anticipated total capacity of 5000 fish. Similar stochastic simulations have been previously reported for various aquaculture species. Assortative mating with large family sizes substantially enhances the response to selection, particularly when family selection methods are applied in aquaculture breeding programs compared to random mating schemes (Saura, Villanueva, Fernández, & Toro, 2017). They reported a comparatively higher genetic gain around 40 and 80% at early generations, and approximately 10 and 60% at later generations, respectively, unlike our present study, wherein we observed lesser but more consistent genetic gain (14 - 17 % for BW and 4 – 6 % for SL and BD) per generation. (Saura, Villanueva, Fernández, & Toro, 2017) also reported that the inbreeding coefficient after ten generations of selection was 300% higher when assortative matings were performed under sib selection. In contrast, our study reported a very low rate of inbreeding (0.5 percent per generation), indicating a sustained genetic gain at an acceptable level of inbreeding accumulation.

At NBC, induced spawning is practiced in a natural setting, and no stripping or in vitro fertilisation is performed owing to the adhesive nature of common carp eggs. Males can be used for repeated spawning in the same generation, but females cannot be used more than once. Thus, various mating designs were not attempted in the simulation for alternative breeding scenarios. It was decided to use only the nested mating design, as it seemed most appropriate and corresponded to the practically feasible mating designs in the NBC. It is well known that various mating designs would differ in terms of long-term genetic variability and genetic response. A previous study reported that for the same selection pressure, designs which created the highest number of families were the most efficient (Dupont-Nivet, Vandeputte, Haffray, & Chevassus, 2006). They reported factorial designs as the most efficient, followed by nested designs, and single-pair designs were the least efficient. The differences between full factorial and partial factorial designs seem to be small. A partial factorial mating design would be a good compromise to achieve high genetic responses while preserving genetic variability (Dupont-Nivet, Vandeputte, Haffray, & Chevassus, 2006). However, Dupont-Nivet, Vandeputte, Haffray, and Chevassus (2006) tested the simulations using an individual-based selection, unlike the index selection used in the present study.

5 CONCLUSION

The genotype by salinity interaction, full-sib-effect-by-salinity interaction, and between-trait pond effect correlation within each salinity were delineated using a multi-trait animal model. The growth traits exhibited high heritability and positive genetic correlation. The EBVs for growth traits displayed a low G × E for salinity. The accuracy of multi-trait EBVs was predicted to be 0.72, indicating the high accuracy and reliability of multi-trait selection. The multi-trait EBV-based index predicted an aggregate genetic gain of +4.25 index units. The stochastic simulations for alternative breeding scenarios suggest that 250 families produced using a ratio of 4:5 (male: female) and 20 progeny per family is the most effective breeding strategy for sustainable breeding at the NBC of common carp in India.

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