

Genetic and non-genetic factors influencing reproductive traits of female *Clarias magur* in a line selected for improved harvest body weight

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ABSTRACT

The Indian catfish species *Clarias magur* is a potential candidate for aquaculture. ICAR-CIFE is implementing a genetic selection programme to harness its production potential by improving harvest body weight. This study estimated genetic parameters and quantified the effects of non-genetic factors on female reproductive traits in selectively bred individuals. Reproductive traits were recorded from 617 individuals across 174 families over three generations during spawning seasons from 2016 to 2021. The spawning age significantly affected all reproductive traits. In contrast, the spawning year, body weight at tagging (TagBW), and pond significantly affected pre-stripping weight (preSW), post-stripping weight (postSW), and spawning success (SS) ($p < 0.05$). Heritability estimates for preSW, postSW, total egg weight (TEW) and egg weight to body weight ratio (EBI) were 0.37 ± 0.10 , 0.35 ± 0.09 , 0.38 ± 0.11 and 0.22 ± 0.12 , respectively. Genetic correlations between reproductive traits ranged from -0.41 to 0.98 . Heritability estimates of reproductive traits suggest potential for genetic improvement. The genetic correlation between the preSW and TEW (0.33 ± 0.15) indicates a moderate association, suggesting that selecting magur for body weight may lead to a favourable correlated response in TEW. The overall SS was 37.60%, with 41.69% in males and 34.85% in females. SS exhibited moderate heritability on the logit (observed) scale (0.42 ± 0.01), indicating genetic variation in this binary trait. Overall, these results indicate that reproductive traits possess additive genetic variance, allowing for direct selection, and correlation with preSW suggests that preSW can be used as a selection criterion to improve reproductive performance in this species.

1. Introduction

Reproductive traits represent complex phenotypes shaped by genetic and environmental factors. In most aquaculture selective breeding programmes, economic traits such as growth rate and disease resistance are the main breeding objectives (Gjedrem, 1983). Efficient propagation of a genetically improved strain largely depends on the selected broodstock's fertility and fecundity (Gjedrem and AKVAFORSK (Norway), 2005). However, while designing the selection objectives, reproductive traits have received limited focus, except in a few species (Srimai et al., 2019). Some important reproductive traits considered for genetic improvement are egg number, egg size, pre-spawning weight, sperm concentration, and sperm motility in salmon, rainbow trout, arctic

charr, tilapia, and *Litopenaeus vannamei* (Charo-Karisa et al., 2007; D'Ambrosio et al., 2020; Gall and Neira, 2004; Kurta et al., 2022; Tan et al., 2017). Understanding the reproductive processes will help design proper management measures for sustainable aquaculture (Mylonas et al., 2010). It is vital to accurately quantify the effect of non-genetic factors, such as pond, sex, batch, and stock, in order to adjust the data for these factors, so that the animal phenotype is a reliable predictor of its genotype. Effective data adjustment for significant non-genetic factors enables the unbiased estimation of genetic parameters and the prediction of breeding values with high accuracy, thereby maximising genetic gain. Knowledge of the non-genetic aspects will influence the objectives of selection and selection methods (Gjedrem et al., 2012). Understanding the effects of non-genetic factors on the trait of interest

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helps to devise better aquaculture practices and optimise reproduction (Dube et al., 2011).

The genetic correlations among reproductive traits and other production traits, such as body weight, can affect the breeding programme designs, which aim to improve the stock's overall net value (Su et al., 2002). The literature suggests that female and male reproductive traits have low heritability (<0.2) in fish species, such as rainbow trout, Nile tilapia, North African catfish, and red tilapia (Charo-Karisa et al., 2007; Gall, 1975; Srimai et al., 2019; Thoa et al., 2017). The genetic and phenotypic correlations between traits affect the performance of related traits when selection targets a specific trait. Previous studies have suggested inconsistent genetic correlations between growth traits and female reproductive traits such as egg size, egg number, egg volume, and post-spawning weight (Charo-Karisa et al., 2007; Su et al., 2002; Thoa et al., 2017). Since the heritability of reproductive traits is low, the expected genetic gain will also be low, which in turn affects the overall improvement of the animal. Recording reproductive traits with a statistically sufficient sample size poses challenges; therefore, incorporating these traits into the selection objective must be considered carefully.

Clarias magur (Hamilton, 1822), commonly known as magur, is an air-breathing catfish with potential as a candidate for aquaculture (Jousy et al., 2018). Despite the feasibility of induced breeding in magur, obtaining sufficient seed for commercial aquaculture remains challenging, primarily due to low reproductive rates, low hatchability, and survival rates during various early life stages. ICAR-Central Institute of Fisheries Education (ICAR-CIFE), Mumbai, India, has implemented a genetic selection programme to improve magur's harvest body weight since 2014. A notable direct response in harvest body weight (the main selection criterion) was observed after three generations of selection (the interval between each generation is two years). Although the selection was practised solely for body weight at harvest, correlated responses were observed in other body measurements, including length and width (unpublished results). However, genetic changes in reproductive traits resulting indirectly from short-term selection for improved growth have yet to be quantified.

In the current study, we hypothesised that genetic selection of the magur population from 2014 to 2021 had no significant impact on the performance of reproductive traits. Furthermore, we investigated quantitative genetic variation in reproductive traits. This study aimed to estimate genetic parameters and quantify the effect of non-genetic factors on key reproductive traits in individuals involved in an ongoing genetic selection programme to improve harvest body weight in magur.

2. Materials and methods

2.1. Ethics statement

This study was carried out as part of a research project authorised by the Institute Research Council (IRC) of ICAR-CIFE, Mumbai, India (Project codes: CIFE-2012/7 and CIFE-2017/2). The experimental procedures adhered to the guidelines notified by the IRC.

2.2. Fish population

Data were collected from the magur population subjected to three generations of selection for improved harvest body weight at the breeding nucleus located at the Fresh Water Fish Farm (FWFF) of ICAR-CIFE, Balabhadrapuram, Kakinada, Andhra Pradesh, India. Detailed information on the population, mating design, selection procedure, and animal management is provided by Jousy et al. (2018) and Rameez et al. (2020). In brief, the base population was established by collecting magur stocks from the states of Andhra Pradesh, Assam, and West Bengal in India during 2014 and 2015 (in two-year batches) to establish the base population. For the production of first and subsequent generations the fish were selected based on high estimated breeding values

(EBVs) for body weight at harvest (One year pond-age) by using a linear mixed model that included Batch, Sex, and Pond as fixed effects, Body weight at stocking as a covariate, and animal as a random effect, with the additive genetic relationship matrix and full-sib effect incorporated to estimate breeding values. Combined selection was carried out, assigning different weights to breeding values from both between- and within-family selection (0.70 and 0.30, respectively). While the selection was based on breeding values, constraints on the number of individuals selected as parents from each family were imposed to minimise inbreeding. Full and half-sib matings were avoided, and single pair and nested mating designs (2 dams nested within a sire) were used to produce full-sibs and sire half-sibs. Over six spawning years (2016–2021), comprising generations G1, G2, and G3, 617 breeding females (offspring from 174 families) were used to produce progeny, and data from these females were analysed in this study.

2.3. Family production, rearing to harvest

Breeding occurred annually from July to October. Induced breeding and tagging of magur followed the methods described by Jousy et al. (2018) and Rameez et al. (2020). Hatching occurs 24–28 h post-fertilisation, and yolk absorption is completed by 72 h post-hatching. The spawns were fed with zooplankton *ad libitum*. Fifteen days after hatching, the fry were transferred to an indoor nursery and fed Artemia flakes. The fry were reared in full-sib families in rectangular Fibre-reinforced plastic (FRP) tanks measuring $3.0 \times 0.6 \times 0.45$ m, housed in the fry-rearing indoor unit. During the nursery phase, the fry were fed zooplankton harvested from the pond as well as crumbled starter feed containing 35% protein and artemia flakes. Uneaten food and debris were removed daily before feeding. After 30 days in the indoor nursery, families were transferred to separate cement tanks measuring $4.0 \times 1.5 \times 1.0$ m, with a maximum of 200 fish per tank. Families were reared until PIT-tagged at about 10–15 g of body weight. Tagging was done to identify the individuals by inserting sterilised PIT tags into the fish's abdominal cavity. A minimum of 10 and a maximum of 30 fish from each full-sib family were randomly selected for tagging, further rearing, and analysis. Families with fewer than ten offspring were not selected for tagging and further rearing, and tagged fish were observed in FRP tubs for two days; any observed mortalities were compensated for by tagging additional fish from the same family. Table 1 summarises the timeline of breeding and tagging across years, including the spawning window, tagging dates, tag age, and culture period. Growth traits were measured on the third day after tagging before releasing the fish into earthen ponds for communal rearing.

The fish were fed twice daily with commercially available feed containing 30% protein at 5% of their body weight (2% in the morning and 3% in the evening). The feed quantity was adjusted based on the average body weight estimated through random sampling every 15 days. Water quality parameters were maintained at optimal levels, and water was exchanged as needed. These management procedures were

Table 1

Timeline of breeding and tagging in magur across years, showing spawning period, tagging dates, tag age, and culture period.

Spawning year	Birth year	Spawning period	Month and year of tagging	Age at tagging (days)	Culture period (days)
2016	2014	July–October	March 2015	175–240	360
2017	2015	August–September	August 2016	325–360	360
2018	2016	August–September	April 2017	212–240	360
2019	2017	August–September	May 2018	266–293	360
2020	2018	August–September	May 2019	240–266	360
2021	2019	August–September	February 2020	158–189	360

consistently practised across all generations throughout the selection programme, from stocking to harvest.

After one year of aquaculture, fish were measured for growth traits (body weight, standard length, body depth, and head length). Breeding values for body weight at harvest were predicted for all individuals in the pedigree, and fish were ranked accordingly; highly ranked individuals were selected as parents for the next generation. Reproductive traits were measured each breeding season, and the same procedures for family production, genetic evaluation, and selection were consistently applied across subsequent generations. Table 2 summarises the number of families and tagged individuals across generations.

G0 is the base generation created using wild stocks; consequently, the number of sires and dams of these G0 breeders are unknown, and G0 individuals are not included in this analysis.

2.4. Measurement of reproductive traits

Reproductive traits were measured during family production. Females' body weight pre stripping (preSW) and post stripping (postSW) were recorded as live weights before fertilisation. Total egg weight (TEW) was recorded using a digital balance to weigh the entire egg mass. The egg weight-to-body weight ratio (EBI) trait was derived from the ratio of TEW to preSW, indicating the relationship between egg weight and female body weight (Fig. 1). Spawning success (SS), indicating the ability of parents to produce offspring for the next generation, was assessed. Individuals who successfully spawned were assigned a value of "1", while those who did not were assigned "0".

2.5. Statistical analysis

2.5.1. Basic statistics

Data were checked for normal distribution using Proc Univariate in SAS®, where deviations from the normal distribution were identified. Appropriate transformations or removal of outliers, or both, were applied to normalise the data. Descriptive statistics were computed on the entire dataset before normality testing employing the *proc MEANS* procedure in SAS 9.4.

2.5.2. Non-genetic factors

In this study, the spawning year (2016–2021), the spawning age (the age at which fish spawned), body weight at tagging (TagBW), the tank (rearing environment before tagging), and the effects of ponds were considered non-genetic factors. The spawning year accounts for annual variation related to the monsoon season, as magur breeding coincides with the monsoon. Spawning age can influence reproductive performance. TagBW accounts for initial variation due to the common

environment, while tank accounts for the common rearing environment. Pond effects capture environmental differences. All factors were initially included in the analysis; however, tank effects were found to be non-significant ($p > 0.05$) and were therefore excluded from the final model. The impact of the remaining non-genetic factors on reproductive traits was quantified by adopting a generalised linear model (GLM), with an identity link function, where spawning age (covariate), TagBW (covariate), year, and pond were treated as fixed effects. The model was fitted using *proc glm* in SAS 9.4 to test the significance of these factors on reproductive traits. The least-squares means derived after fitting the model were used to quantify the effect of these non-genetic factors. Multiple comparisons between different levels of each non-genetic factor were conducted using the Tukey-Kramer test. All possible interaction terms were initially included in the model, and non-significant interaction effects were subsequently removed from the analysis.

2.5.3. Estimation of heritability

Reproductive traits, variance components, and heritability estimates were derived using the Residual Maximum Likelihood (REML) method in ASReml-R Version 4 (Butler et al., 2017) with the standard linear mixed model (LMM). The full model (A + M + C), including additive, maternal and family effects, was specified as:

$$y = X\beta + Z_1u + Z_2m + Z_3c + e \quad (1)$$

Reduced models were also fitted, including additive + maternal (A + M), additive + family (common environment) (A + C), and additive only (A) models, to assess the contribution of each variance component to the traits. All models converged successfully.

Here, y is the vector of phenotypic trait observations, β is the vector for fixed effects including the overall mean, spawning age (covariate), TagBW (covariate), pond, and spawning year. u is the vector for the random animal genetic effects, m and c represent maternal and family (common environmental) effects, respectively, and e is the vector of random residual effects. The design matrix X relates each observation in y to the corresponding fixed effects (including both categorical effects and covariates), while Z_1 , Z_2 , and Z_3 map observations to the respective random effects.

It was assumed that random effects (u , m , c and e) are normally distributed;

- $u \sim N(0, A\sigma_a^2)$, where σ_a^2 is the additive genetic variance, and A is the additive genetic relationship matrix derived from the pedigree.
- $m \sim N(0, A\sigma_m^2)$, where σ_m^2 is the maternal genetic variance, and A is the additive genetic relationship matrix derived from the pedigree.
- $c \sim N(0, I\sigma_c^2)$, where σ_c^2 is the family (common environmental) variance, and I is the identity matrix.

Table 2

Summary of families, tagged individuals, and the number of female and male breeders, including their sires and dams, across generations and spawning years.

Generation	No. of Families (Half-sib/Full-sib)	No. of Tagged Individuals	Spawning year	Sex	Breeders	Sires	Dams
G0	78 (0/78)	2328	2014	F	39	–	–
				M	39	–	–
			2015	F	39	–	–
				M	39	–	–
G1	46 (8/38)	1333	2016	F	62	27	28
				M	61	28	29
			2017	F	99	31	33
				M	44	20	21
G2	82 (14/68)	1371	2018	F	96	36	36
				M	70	33	33
			2019	F	99	49	54
				M	59	27	31
G3	75 (22/53)	1735	2020	F	100	64	67
				M	74	46	49
			2021	F	161	56	54
				M	107	45	45
Total	281	6767			1188	257	266

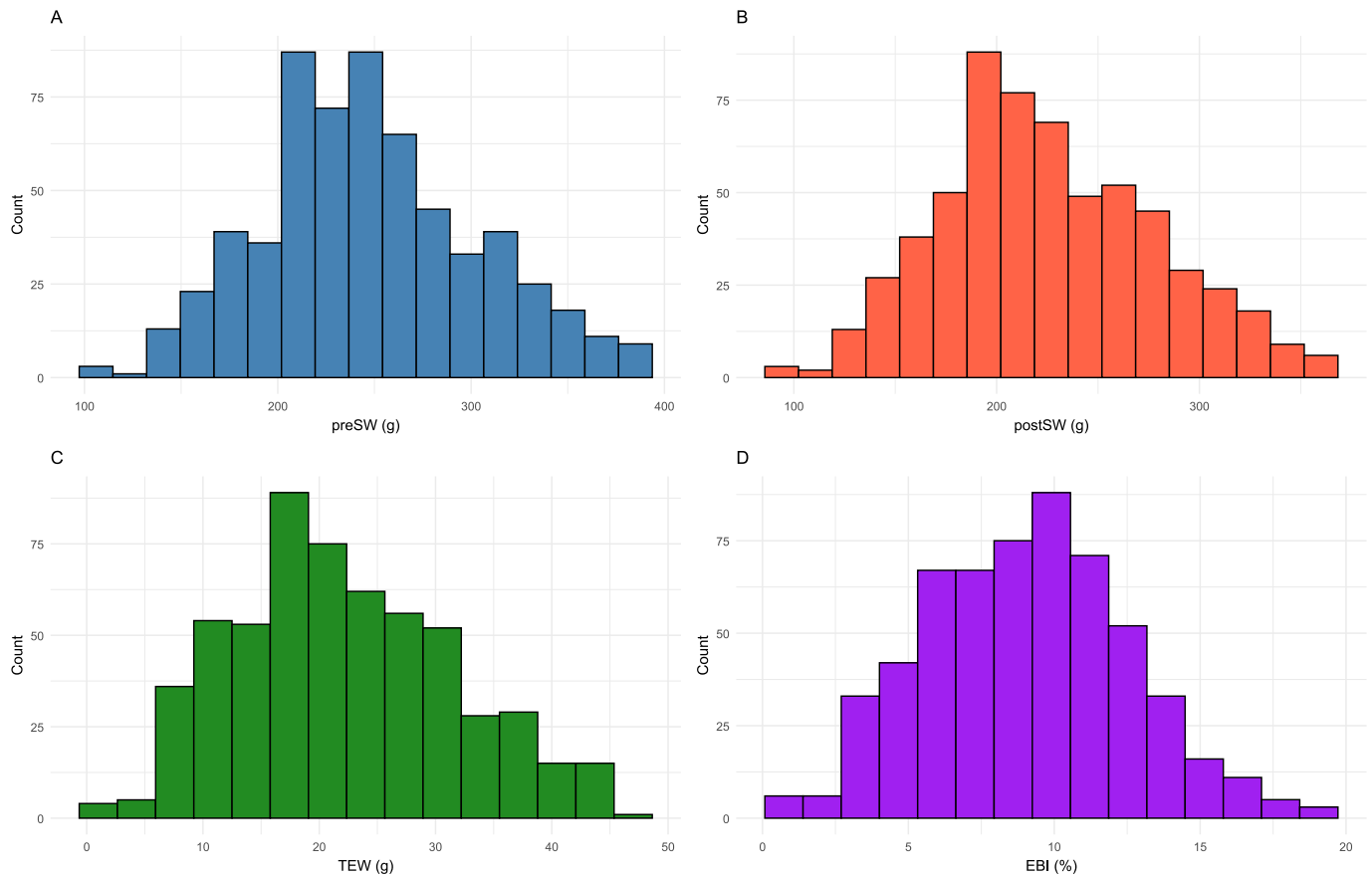


Fig. 1. Distribution of reproductive traits in the magur population: pre-stripping body weight (preSW), post-stripping body weight (postSW), total egg weight (TEW), and egg-to-body weight ratio (EBI).

- $e \sim N(0, I\sigma_e^2)$, where σ_e^2 is the residual variance, and I is the identity matrix.

The estimated variance components were expressed relative to the total phenotypic variance σ_p^2 :

- Additive heritability (h^2) = σ_a^2 / σ_p^2
- Maternal ratio (m^2) = σ_m^2 / σ_p^2
- Family/Common environmental ratio (c^2) = σ_c^2 / σ_p^2

The total phenotypic variance was calculated as the sum of all components: $\sigma_p^2 = \sigma_a^2 + \sigma_m^2 + \sigma_c^2 + \sigma_e^2$

For the binary trait Spawning Success (SS), the analyses were performed using both a linear mixed model and a generalised linear mixed model (GLMM) with a logit link function. Let p be the vector of SS observations (0 = failure, 1 = success):

$$\text{logit}(p) = X\beta + Z_1u + Z_2c + e \quad (2)$$

All model terms and distributional assumptions remained as described for the LMM (Model 1), with sex additionally included as a fixed effect. The residual variance on the logit scale was fixed to $\pi^2/3$. For Model 2, only the additive (A) and additive + family (common environment) (A + C) models successfully converged; models with maternal effects did not converge and were excluded from further analysis of this specific trait.

For the SS, the heritability estimated on the liability (logit) scale was transformed to the observed (0/1) scale using the formula (Robertson and Lerner, 1949):

$$h_0^2 = h_L^2 \left(\frac{z^2}{p(1-p)} \right)$$

where h_0^2 is the heritability on the observed scale, h_L^2 is the estimated heritability on the liability (logit) scale, p is the proportion of spawning success in the data, and z is the height of the standard normal density at the truncation point corresponding to p .

2.5.4. Estimation of genetic and phenotypic correlations

The genetic and phenotypic correlations of reproductive and Body weight at harvest were estimated by fitting the bivariate linear mixed model as in model (1), with additive effects only (A), since inclusion of maternal and common environment effects in the models prevented convergence, in ASReml-R Version 4 (Butler et al., 2017). The same fixed effects described above in model 1 were employed.

The genetic correlation is estimated using the following formula:

$$r_g = \frac{\sigma_{a_i a_j}}{\sqrt{\sigma_{a_i}^2 \times \sigma_{a_j}^2}}$$

where, $\sigma_{a_i a_j}$ is the additive genetic covariance between the two traits and $\sigma_{a_i}^2, \sigma_{a_j}^2$ are the corresponding additive genetic variances of two traits.

The phenotypic correlation is estimated using the following formula:

$$r_p = \frac{\sigma_{p_i p_j}}{\sqrt{\sigma_{p_i}^2 \times \sigma_{p_j}^2}}$$

where, $\sigma_{p_i p_j}$ is phenotypic covariance between the two traits and $\sigma_{p_i}^2, \sigma_{p_j}^2$ are the corresponding phenotypic variances of two traits.

3. Results

3.1. Preliminary analysis

The study analysed 617 breeding females (offspring of 257 sires and 266 dams) with recorded reproductive performance data from 2016 to 2021 (Table 2). Table 3 presents the descriptive statistics for the reproductive traits, including the mean, coefficient of variation, and minimum and maximum values. The coefficient of variation for TEW was high, potentially due to inherent variability in TEW or other unaccounted factors.

3.2. Non-genetic factors

Spawning age significantly affected all reproductive traits, including preSW, postSW, TEW, EBI, and SS (Table 4). The pond and spawning years affected only the preSW, postSW and SS. TagBW had a significant effect on preSW, postSW, and SS, but not on TEW or EBI. There was no significant difference in the mean TEW between the spawning years and ponds, and there was also no difference in EBI in different ponds and spawning years.

The number of animals attempted for breeding and the number successfully spawned from 2016 to 2021 are presented in Supplementary Table S1. A total of 1032 fish were used for breeding, of which 415 were males, and 617 were females. Out of 415 males, 173 spawned successfully, while 215 females out of 617 spawned. The fish used for breeding were from 174 full-sib families, with males and females derived from 144 and 157 families, respectively. The spawning success across the years and months is presented in Supplementary Table S2. Overall, magur's spawning success was 37.60%. Males had an overall success rate of 41.69%, whereas females had an overall success rate of 34.85%. The highest spawning success was recorded in 2018, whereas the lowest was in 2021.

3.3. Heritability estimates

Heritability for reproductive traits was estimated by adopting linear mixed models and a logit model, and the results are presented in Table 5. The heritabilities of the reproductive traits were found to be moderate to high, with estimates ranging from 0.22 to 0.42. For the full model (A + M + C), preSW, postSW, and TEW were moderately heritable (0.37 ± 0.10 , 0.35 ± 0.09 , and 0.38 ± 0.11 , respectively). EBI also showed moderate heritability (0.22 ± 0.12), although this estimate had a large standard error. Maternal effects were generally low, particularly for postSW ($m^2 = 0.18 \pm 0.07$), while common family effects were negligible across traits. Under reduced models, heritability estimates for growth-related traits increased. In the additive-only model (A), preSW and postSW showed higher heritabilities (0.46 ± 0.07 and 0.52 ± 0.06), suggesting that part of the variance originally attributed to maternal or common environmental effects may have been absorbed into the additive genetic component when these effects were removed. For spawning success (SS), the logit model produced a heritability of 0.42 ± 0.01 on the observed scale under the A + C model and 0.44 ± 0.01 under the A model, corresponding to 0.69 ± 0.03 and 0.72 ± 0.02 on the liability scale, respectively. Family variance for SS was close to zero, and the residual variance was fixed at $\pi^2/3$ in the threshold models. In contrast, the linear mixed model heritability estimate was zero.

Table 3
Basic statistics of reproductive traits of female magur.

Traits	Number of observations (N)	Minimum	Maximum	Mean $\pm$ SE	CV (%)
preSW (g)	606	106	385	246.97 $\pm$ 2.25	22.41
postSW (g)	599	94	360	225.00 $\pm$ 2.15	23.36
TEW (g)	574	1	47	22.15 $\pm$ 0.40	42.90
EBI (%)	575	0.74	19.07	9.05 $\pm$ 0.15	38.45

3.4. Genetic and phenotypic correlations

The genetic and phenotypic correlations between the reproductive traits and body weight at harvest (BWHarvest) are presented in Table 6. All correlations were estimated using bivariate linear mixed models with additive effects only (A), as models including maternal and family effects (A + M, A + C and A + M + C) did not converge. The genetic correlations varied from -0.41 to 0.98 . The genetic correlation between PreSW and PostSW was positive and high (0.98 ± 0.005). Likewise, TEW and EBI also showed a strong genetic correlation (0.82 ± 0.05). TEW had moderate genetic correlations with preSW (0.33 ± 0.15) and postSW (0.25 ± 0.14), although the relatively large standard errors suggest caution in interpreting these as definitive. In contrast, EBI was negatively genetically correlated with both preSW (-0.30 ± 0.18) and postSW (-0.41 ± 0.16); however, the large standard errors indicate that these estimates are less precise. The phenotypic correlation between preSW and the postSW was strong and positive (0.97 ± 0.002), while that between preSW and EBI was negligible (0.0009 ± 0.04). A moderate positive phenotypic correlation was observed between preSW and TEW (0.42 ± 0.04), and between postSW and TEW (0.24 ± 0.04). PostSW and EBI showed a negative phenotypic correlation (-0.19 ± 0.04), whereas TEW and EBI were highly positively correlated (0.88 ± 0.01). Importantly, BWHarvest showed moderate to high positive genetic correlations with preSW (0.85 ± 0.04) and TEW (0.38 ± 0.10). Phenotypically, correlations with reproductive traits ranged from -0.08 to 0.69 . Additionally, a positive linear relationship was observed between TEW and preSW, with a slope of 0.073 ± 0.007 ($p < 0.001$), indicating that heavier females produced more eggs.

4. Discussion

Magur possesses all the essential qualities to be a viable candidate species for aquaculture. It adapts to diverse climatic conditions, can survive in low dissolved oxygen levels, and can be cultured in high stocking densities (Ferosekhan et al., 2021; Sahoo et al., 2019). Despite these qualities, magur aquaculture remains limited and small in scale, with farmers typically relying on natural seeds or the seeds from the brooders collected from their natural habitat for magur culture (Majhi and Kumar, 2017). Although magur can mature in pond conditions and induced breeding is possible, it remains a challenging breeder, characterised by low fecundity, reduced fertilisation rates, and poor survival of fry and fingerlings. Assessing the effects of genetic and non-genetic factors on the key economic traits is essential for maximising aquaculture production and implementing the selective breeding programme.

Genetic parameter estimation for reproductive traits has been studied in various fish species, including Nile tilapia (Charo-Karisa et al., 2007; Thoa et al., 2017; Trøng et al., 2013), Coho salmon (Gall and Neira, 2004), Russian sturgeon (Song et al., 2022), Arctic charr (Kurta et al., 2022), and Rainbow trout (D'Ambrosio et al., 2020). In Thailand, a genetic selection programme aimed at improving the body weight of African catfish was implemented, and genetic parameters for reproductive traits were estimated to assess the impact of selection for growth on reproductive traits from a quantitative perspective (Srimai et al., 2019).

Table 4Mean sum of squares from the analysis of variance and R^2 values of the model for reproductive traits.

Source	preSW		postSW		TEW		EBI		SS	
	DF	MSS	DF	MSS	DF	MSS	DF	MSS	DF	MSS
Pond	20	4405.36*	20	4156.85*	19	89.21	19	8.79	20	0.22*
Spawning age	130	3519.24*	130	3023.88*	130	104.01*	129	15.55*	154	0.33*
Spawning year	4	15,154.24*	4	12,898.81*	4	68.40	4	5.46	4	0.29*
TagBW	105	1605.10*	105	1345.53*	103	74.77	103	8.64	135	0.18*
Sex	–	–	–	–	–	–	–	–	1	0.50
Error	315	1431.72	307	1203.08	285	68.52	287	8.72	679	0.19
R^2 (%)		74.8		76.8		61.2		62.6		43.7

* (p-value <0.05).

Table 5Estimates ($\pm$ SE) of variance components and ratios for reproductive traits.

Trait	Model	Variance parameters					Ratios				
		A (additive)	M (maternal)	C (family)	E (residual)	P (phenotypic)	h ² (additive)	m ² (maternal)	c ² (family)	e ² (residual)	
preSW	A + M + C	820.60 $\pm$ 248.28	159.47 $\pm$ 155.43	1.30 $\pm$ 2.65	1180.69 $\pm$ 138.88	2162.07 $\pm$ 156.51	0.37 $\pm$ 0.10	0.07 $\pm$ 0.07	0.0006 $\pm$ 0.001	0.54 $\pm$ 0.07	
	A + M	824.92 $\pm$ 249.20	169.99 $\pm$ 156.52	–	1181.18 $\pm$ 139.24	2176.10 $\pm$ 157.80	0.37 $\pm$ 0.10	0.07 $\pm$ 0.07	–	0.54 $\pm$ 0.07	
	A + C	791.49 $\pm$ 230.32	–	203.34 $\pm$ 130.77	1169.70 $\pm$ 135.43	2164.54 $\pm$ 154.10	0.36 $\pm$ 0.09	–	0.09 $\pm$ 0.05	0.54 $\pm$ 0.07	
	A	988.38 $\pm$ 200.66	–	–	1155.91 $\pm$ 132.44	2144.29 $\pm$ 148.72	0.46 $\pm$ 0.07	–	–	0.53 $\pm$ 0.07	
postSW	A + M + C	703.19 $\pm$ 212.31	362.14 $\pm$ 165.21	1.22 $\pm$ 2.50	928.36 $\pm$ 113.45	1994.93 $\pm$ 158.95	0.35 $\pm$ 0.09	0.18 $\pm$ 0.07	0.0006 $\pm$ 0.001	0.46 $\pm$ 0.06	
	A + M	702.31 $\pm$ 213.29	375.27 $\pm$ 166.40	–	930.73 $\pm$ 114.05	2008.32 $\pm$ 160.38	0.34 $\pm$ 0.09	0.18 $\pm$ 0.07	–	0.46 $\pm$ 0.06	
	A + C	704.53 $\pm$ 197.80	–	351.20 $\pm$ 136.97	907.80 $\pm$ 109.35	1963.53 $\pm$ 149.09	0.35 $\pm$ 0.09	–	0.17 $\pm$ 0.06	0.46 $\pm$ 0.06	
	A	992.81 $\pm$ 178.09	–	–	913.07 $\pm$ 108.36	1905.88 $\pm$ 135.18	0.52 $\pm$ 0.06	–	–	0.47 $\pm$ 0.06	
TEW	A + M + C	33.62 $\pm$ 11.16	0.34 $\pm$ 6.04	0	52.71 $\pm$ 6.42	86.69 $\pm$ 6.13	0.38 $\pm$ 0.11	0.004 $\pm$ 0.06	0	0.60 $\pm$ 0.08	
	A + M	33.63 $\pm$ 11.16	0.34 $\pm$ 6.04	–	52.71 $\pm$ 6.42	86.69 $\pm$ 6.13	0.38 $\pm$ 0.11	0.004 $\pm$ 0.06	–	0.60 $\pm$ 0.08	
	A + C	31.89 $\pm$ 10.19	–	1.96 $\pm$ 5.07	52.91 $\pm$ 6.26	86.76 $\pm$ 6.12	0.36 $\pm$ 0.10	–	0.02 $\pm$ 0.05	0.60 $\pm$ 0.08	
	A	34.04 $\pm$ 8.64	–	–	52.61 $\pm$ 6.18	86.65 $\pm$ 6.09	0.39 $\pm$ 0.08	–	–	0.60 $\pm$ 0.08	
EBI	A + M + C	2.56 $\pm$ 1.43	0.41 $\pm$ 0.86	0	8.54 $\pm$ 0.90	11.53 $\pm$ 0.76	0.22 $\pm$ 0.12	0.03 $\pm$ 0.07	0	0.74 $\pm$ 0.08	
	A + M	2.56 $\pm$ 1.43	0.41 $\pm$ 0.86	–	8.54 $\pm$ 0.90	11.53 $\pm$ 0.76	0.22 $\pm$ 0.12	0.03 $\pm$ 0.07	–	0.74 $\pm$ 0.08	
	A + C	2.71 $\pm$ 1.22	–	0.37 $\pm$ 0.69	8.44 $\pm$ 0.85	11.52 $\pm$ 0.76	0.23 $\pm$ 0.10	–	0.03 $\pm$ 0.06	0.73 $\pm$ 0.07	
	A	3.08 $\pm$ 0.99	–	–	8.41 $\pm$ 0.85	11.49 $\pm$ 1.30	0.26 $\pm$ 0.07	–	–	0.73 $\pm$ 0.07	
SS ^a	A + C	8.11 $\pm$ 0.98	–	0.29 $\pm$ 0.21	$\pi^2/3$	11.67 $\pm$ 0.96	0.69 $\pm$ 0.03 ^L	–	0.02 $\pm$ 0.01	–	
							0.42 $\pm$ 0.01 ^O	–			
	A	8.85 $\pm$ 0.99	–	–	$\pi^2/3$	12.14 $\pm$ 0.99	0.72 $\pm$ 0.02 ^L	–	–	–	
							0.44 $\pm$ 0.01 ^O	–			

h², m², c², and e² represent the proportion of phenotypic variance (σ_p^2) attributed to additive genetic, maternal genetic, family, and residual effects, respectively. A + M + C indicates the full model, which includes random animal, dam, and family effects, respectively, as well as random residual effects.

^a For the binary trait Spawning Success (SS), heritabilities are reported on both the liability (L) and observed (O) scales. Models with maternal genetic effects failed to converge for SS.

4.1. Non-genetic factors

Non-genetic factors highly influence growth and reproductive traits, especially the latter. Jousy et al. (2018) and Rameez et al. (2020) have reported the significant effect of non-genetic factors on the growth traits of magur. As indicated in the results, spawning age had a significant effect on all measured reproductive traits. Magur spawning spreads from July to October, coinciding with the monsoon period. Variation in spawning age influenced the reproductive traits (Table 4); therefore, spawning age was included as a covariate in the model for estimating variance components of these traits, with 138 levels considered. The distribution of spawning ages suggests that environmental factors preceding the spawning season significantly influence the age at which males and females attain sexual maturity each year. The average spawning age of magur was two years in the present study. This is mainly because the magur were PIT tagged at about 6–9 months and then cultured for one year. Typically, magur will mature at one year, with an average spawning age of 1–2 years (Ferosekhan et al., 2021; Majhi et al., 2020).

TagBW significantly influenced preSW and postSW. This effect reflects the initial variation in body weight resulting from differences in age at tagging and the common rearing environment prior to communal culture, including the stocking density in that environment, indicating that initial body condition strongly affects growth during the reproductive period. This effect is also consistent with previous studies, where

TagBW significantly influenced magur harvest weight (Rameez et al., 2020); Hence, it was included in the model as a covariate.

The spawning year significantly affected the preSW and postSW (Table 4), likely due to an increase in the average body weight of female individuals from the genetic improvement programme, which is also documented in the GIFT strain (Hamzah et al., 2016). However, the spawning year did not affect the TEW or EBI in magur. This lack of variation in TEW and EBI may be due to the use of some older females across years, which compensated for variation; age tends to influence egg production, as observed in this study, with older females generally producing more eggs. Females of varying ages used for breeding may have balanced the TEW across years. Additionally, consistent environmental and management conditions helped minimise year-to-year differences in these traits. While variation in reproductive traits from year to year is normal, an increase in egg weight over the years has been observed in coho salmon (Gall and Neira, 2004). Furthermore, Parra Bracamonte et al. (2017) reported that the sampling month had a significant effect on egg mass weight in Channel catfish.

The pond significantly affected the preSW and postSW of female magur, likely due to the dynamic conditions in aquaculture ponds that led to weight variation in magur. The differences in stocking density, which may have arisen over time due to mortality, may also significantly affect the preSW and postSW. However, it did not affect the TEW or EBI, as magur is a seasonal breeder whose reproductive cycle is more influenced by seasonal cues such as monsoon and temperature shifts

Table 6

Genetic (below diagonal) and phenotypic (above diagonal) correlations between reproductive traits (preSW: Pre stripping weight, postSW: Post stripping weight, TEW: Total egg weight, and EBI: Egg weight to body weight ratio) and body weight at harvest (BWHarvest).

	preSW	postSW	TEW	EBI	BWHarvest
preSW		0.97 ± 0.002	0.42 ± 0.04	0.0009 ± 0.04	0.69 ± 0.03
postSW	0.98 ± 0.005		0.24 ± 0.04	−0.19 ± 0.04	0.68 ± 0.03
TEW	0.33 ± 0.15	0.25 ± 0.14		0.88 ± 0.01	0.24 ± 0.06
EBI	−0.30 ± 0.18	−0.41 ± 0.16	0.82 ± 0.05		−0.08 ± 0.06
BWHarvest	0.85 ± 0.04	0.82 ± 0.04	0.38 ± 0.10	−0.13 ± 0.11	

(Ferosekhan et al., 2021). Thus, pond differences had minimal effect on these traits. The female reproductive system develops primarily in response to physiological and environmental stimuli, which, in this case, diminished the pond's impact. In contrast, the tank environment was found to significantly affect the reproductive traits of African catfish (Srimai et al., 2019).

The ability of parents to produce offspring for the next generation is known as spawning success. Successful spawning increases magur production, making reproductive efficiency critical for animal farming systems (Davis and White, 2020). For genetic improvement programmes, achieving high reproduction rates is essential (D'Ambrosio et al., 2020). Spawning success depends on environmental parameters (Walsh et al., 2013), and the spawning season for magur extends from July to October. During this period, environmental factors vary and influence spawning outcomes, with multiple factors contributing to spawning success. Based on data from 1032 animals, it was concluded that the success rate was higher for males (41.69%) compared to females (34.85%), with an overall success rate of 37.60% in magur. However, a chi-squared test revealed that the difference in spawning success between male and female magur is not significant (p -value > 0.05). Nevertheless, there was a significant difference in spawning success across the years (p -value < 0.05), likely due to environmental conditions and timing of breeding attempts, which led to seasonal variations. These variations may lead to physiological and hormonal differences affecting induced breeding. These results are consistent with findings in Channel catfish (Bosworth et al., 2020; Kelly, 2004). Spawning success was higher in August (47.93%) compared to other months in the breeding season since the rainy season in Andhra Pradesh coincides with the southwest monsoon, and the maximum rainfall occurs in August.

4.2. Heritability estimates

Heritability estimates indicate the proportion of additive genetic variation contributing to phenotypic variation. Understanding the heritability of economic traits is crucial for designing breeding programmes. Using linear mixed models (A + M + C, A + M, A + C, and A), this study estimated heritability for preSW, postSW, TEW, EBI, and spawning success. The logit model was applied exclusively to estimate heritability for spawning success. Additive, maternal, and common environmental effects were examined in the models to assess their impact on reproductive traits, as these factors can influence the expression of traits.

The estimated heritability values from the full model (A + M + C), which included additive, maternal, and common environmental effects, for preSW, postSW, and TEW, ranged between 0.35 and 0.38. At the same time, EBI showed a heritability of 0.22 ± 0.12 , consistent with ranges reported for the Rainbow trout (D'Ambrosio et al., 2020). Maternal effects were low ($m^2 < 0.18$), and common environmental effects were negligible across all traits. The long period between birth and spawning, standardised aquaculture practices, and *ad libitum* feeding may have helped overcome the maternal and common environmental effects that the fish may have experienced in the early stage of their life. These findings are consistent with reports in other aquaculture species, including European seabass, black bream, and Nile Tilapia, during the later stages of culture (Doupe and Lymbery, 2005; Garcia De

Leon et al., 1998; Nguyen et al., 2007; Ponzone et al., 2010). When only the additive (A) model was fitted, heritability estimates increased to 0.39–0.52 for preSW, postSW, and TEW and to 0.26 for EBI (Table 6). This indicates that even though maternal and common environmental effects are low or negligible, accounting for them in the model slightly reduces the proportion of phenotypic variance attributed to additive genetic effects compared with the additive-only model, as also observed in Atlantic cod (Tosh et al., 2010). However, because the number of half-sibs in the analysis is small, the reliability of maternal effect estimates is limited and warrants caution. Even so, accounting for these effects, however minor, is important for obtaining more accurate and unbiased heritability estimates. For comparison, heritability values for the spawning weight traits in tilapia ranged from 0.25 to 0.68 (Hamzah et al., 2016; Trøng et al., 2013); In Rainbow trout, heritability was 0.34 (Paul et al., 2022). Su et al. (1997) reported low heritabilities for post-spawning weight, with values ranging from 0.09 for the control line to 0.26 for the line selected for egg size in Rainbow trout. The heritability values for preSW and postSW in this study are relatively low compared with those reported for harvest body weight analysis (Rameez et al., 2022), likely due to the inclusion of maternal and common environmental effects, also be due to the number of families, and the number per family is less, as well as the fact that records encompass individuals from three generations and reflect selection effects.

The heritability estimate for TEW was medium (0.38 ± 0.11) (Table 5). The analysis involved individuals selected from across families as part of the selection process; however, these numbers are attributed to the smaller family sizes, which may have led to an upward bias in the estimated heritability. This value is lower than the heritability reported for Coho salmon (Gall and Neira, 2004), while in Rainbow trout, heritability ranged from 0.28 to 0.32 (D'Ambrosio et al., 2020; Paul et al., 2022). For the derived trait, EBI, the estimated heritability was medium and lower than the heritability reported for Sturgeon (Bestin et al., 2021). This trait reflects the gonadal development of female magur and indicates the efficiency of female egg production. In the present study, all reproductive traits, except for EBI heritability estimates, were associated with low standard errors, implying the reliability of the values. These estimates indicate the presence of significant additive genetic variance in the reproductive traits, which can be utilised to improve these traits in the current stock.

Heritability for spawning success (SS, a binary trait) was estimated using both linear mixed and logit models. The linear mixed model yielded a heritability of zero. In contrast, the logit model produced a heritability of 0.42 ± 0.01 on the observed scale, indicating the presence of genetic variation for this trait in the current population. The discrepancy between models arises because spawning success is a binary trait. Linear mixed models, which assume continuous data, tend to underestimate variance components for binary outcomes, often yielding near-zero heritability estimates (Casellas et al., 2007; Chen et al., 2016). In contrast, the logit model is more appropriate for binary traits, as it accounts for the underlying liability scale, thereby revealing genetic variation that is masked in the linear framework. In contrast, Ajithkumar (2020) reported a heritability of 0.22 ± 0.11 for spawning success in magur. This discrepancy may be due to differences in sample structure; the previous study included fewer individuals (298) and a single generation, which could have constrained environmental variation and

affected the estimate. The present study likely captured greater batch-to-batch variation. Few studies have examined spawning success and its heritability in aquaculture species, and reproductive traits are rarely included in selection objectives because most aquaculture species have high reproductive rates. Moreover, assigning spawning success to individual males or females is challenging, as breeding outcomes depend on both sexes. Without additional methods, such as assessing milt and egg quality or using a full factorial mating design to evaluate offspring production, identifying the causes of spawning failure is difficult. Consequently, the spawning success rates and heritability reported here may be influenced by the absence of these approaches. To the best of our knowledge, only two reports provide heritability estimates for spawning success in aquatic species: Nile Tilapia (Trøng et al., 2013) and *L. vannamei* (Tan et al., 2017).

4.3. Genetic and phenotypic correlations

A high genetic correlation was observed between preSW and postSW (0.98 ± 0.005), and both traits were also strongly correlated with BWHarvest ($0.82\text{--}0.85$), consistent with observations in Rainbow trout (D'Ambrosio et al., 2020). Previous studies suggest that selection for body weight at any age would cause a correlated response to body weight at other ages, including slaughter weight and age at spawning for females (Crandell and Gall, 1993). Both preSW and postSW had a medium genetic correlation with the TEW. However, the relatively large standard errors reduce the confidence in these estimates, making the magnitude of correlated response uncertain. In contrast, the genetic correlation between BWHarvest and TEW was 0.38 ± 0.10 , indicating that selection for higher body weight at harvest could be utilised to enhance total egg weight. Conversely, preSW and postSW were negatively correlated with EBI, again with large standard errors, suggesting that selection for larger body size may increase egg production but also reduce its efficiency. Similar patterns have been reported in sturgeon (Bestin et al., 2021).

These results imply that increasing body weight through genetic selection could impact reproductive-related traits, although the strength and direction of correlated responses may vary. Similar results have been noted in Rainbow trout (D'Ambrosio et al., 2020). A strong phenotypic correlation was observed between preSW and postSW, while both traits showed moderate phenotypic correlations with the TEW. This indicates that genetic selection for body weight will yield a correlated response in total egg weight, helping to increase total egg weight. Consequently, it is reasonable to assume that genetic improvement programmes aimed at improving body weight will also enhance total egg weight.

5. Conclusion

This study reported the first estimation of genetic parameters for reproduction-related traits in magur. The effects of non-genetic factors, such as spawning age, spawning year, and pond, on reproductive traits were quantified. Given that the spawning season of magur extends from July to October, the spawning age significantly affected all the reproductive traits studied. This suggests that reproduction can be improved in the genetically improved magur by standardising brooders' management aspects.

The heritability for reproductive traits was estimated using linear mixed models and logit models. While estimated heritability indicates the potential for genetic improvement through selection, the positive genetic correlations suggest that selecting for increased body weight may also enhance reproductive performance in magur. In particular, the positive moderate genetic correlation between preSW and TEW implies that such selection may positively impact reproductive traits. Therefore, preSW can be considered suitable for improving overall reproductive performance. As this study is limited to weight-related reproductive traits, a future evaluation of quality and fertility-related traits is

necessary to understand better and improve reproductive traits.

CRedit authorship contribution statement

Kishor B. Gowda: Writing – original draft, Investigation, Formal analysis, Data curation. **Shrinivas Jahageerdar:** Writing – review & editing, Resources, Methodology, Formal analysis, Conceptualization. **Mujahidkhan Pathan:** Writing – review & editing. **Jayasankar Jayaraman:** Validation, Formal analysis.

Declaration of competing interest

The authors declare that they have no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.aquaculture.2026.743690>.

Data availability

Data will be made available on request.

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