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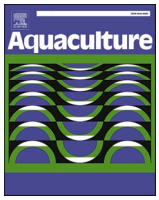

Genotype-by-culture-system interaction in catla and silver carp: Monoculture and biculture

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ABSTRACT

Catla (*Catla catla*) and silver carp (*Hypophthalmichthys molitrix*) are globally significant aquaculture species, primarily grown in polyculture. The objectives of the current study were to i) quantify genetic differences among founder populations (i.e. genetic groups) of family-based genetic improvement programs ii) estimate genetic parameters for harvest weight under different culture systems (i.e. monoculture and biculture) and iii) determine the extent of genotype-by-culture-system interaction – a component of genotype-by-environment-by-management interaction. Founder parents were spawned to generate 188 catla and 184 silver carp base-population full-sibling families. Families were grown out in eight earthen ponds – two monoculture catla, two monoculture silver carp and four biculture – and harvest body weight and survival analysed. Neither interaction (i.e. heterosis) nor main effects among genetic groups were statistically significant in any pond, trait or species. Additive genetic variances were significantly different from zero in all but one pond in each species. Narrow-sense heritability estimates for harvest weight ranged from 0.06 to 0.44 for catla and from 0.18 to 0.51 for silver carp. In contrast to catla, silver carp inter-pond genetic correlations were significantly different from one in multiple cases, indicating the presence of genotype-by-pond interactions. However, these interactions were not entirely explained by genotype-by-culture-system interaction, given the genetic correlation between the monoculture ponds was 0.56 ($P = 0.038$; from one). Additive variances were not statistically significant for survival in either species, with the exception of silver carp in one polyculture pond. Notably catla harvest weight in monoculture ponds was substantially greater than in biculture ponds, indicating the presence of inter-species competition in biculture ponds.

1. Introduction

Catla (*Catla catla*) naturally inhabits freshwater sections of rivers in northern Bangladesh, India, Myanmar and Pakistan (Jhingran, 1968). Silver carp (*Hypophthalmichthys molitrix*) is native to China, Mongolia, Russia and Vietnam (Lu et al., 2020) but is widely cultured outside its natural distribution, including in Bangladesh. Both are cyprinid species and are primarily farmed in Asia in polyculture with other cyprinid and non-cyprinid species. By weight, catla and silver carp are the sixth and second most important finfish aquaculture species, with approximately 3.0 Mt. and 4.8 Mt., respectively, produced globally in 2018 (FAO, 2020).

To improve the genetic quality of catla and silver carp seed supplied to the aquaculture sector in Bangladesh, pedigree-based (i.e. family-based) selective breeding programs have been established by WorldFish. Base populations were spawned from founder parents in 2016–17 (Hamilton et al., 2019a; Hamilton et al., 2021). These programs aim to achieve long-term incremental genetic improvement of growth rate and utilise established and new hatchery, nursery and market systems to disseminate genetically improved seed to farmers adopting homestead, semi-intensive and intensive pond culture (Belton and Azad, 2012).

Carp polyculture systems are adopted to efficiently utilise different spatial and trophic levels in ponds by stocking complimentary filter-feeding, herbivorous and bottom feeding species. Species commonly

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utilised in Bangladesh include catla; silver carp; bighead carp, *Aristichthys nobilis*; grass carp, *Ctenopharyngodon idella*; rohu, *Labeo rohita*; rajputi, *Puntius gonionotus*; mrigal, *Cirrhinus mrigala* and common carp, *Cyprinus carpio*. Carp are also grown in polyculture with non-cyprind species such as pangasius catfish (*Pangasius hypophthalmus*), Nile tilapia (*Oreochromis niloticus*) and small indigenous species (Castine et al., 2017; Kadir et al., 2006; Khan et al., 2009; Rahman et al., 1992; Wahab et al., 2011; Wahab et al., 2019).

While catla predominantly feeds on larger zooplankton, silver carp is capable of filtering phytoplankton from pond water (Wahab et al., 2011). However, both catla and silver carp are considered 'surface feeders' and to some degree are stocked interchangeably in polyculture systems, depending on farmer objectives, availability of quality seed, market demand and price (Rahman et al., 1992).

Historically, low-input carp polyculture systems have been adopted in Bangladesh that primarily rely on natural food production, generally enhanced through the application of organic and/or synthetic fertilisers. However, semi-intensive forms of production, involving supplementary feeding with locally-acquired non-specialised feeds and/or formulated commercial fish feeds are increasingly adopted (Belton and Azad, 2012). Accordingly, in Bangladesh, production systems range from low-input 'homestead' systems – with correspondingly minimal financial risks to low-income small-scale farmers – to semi-intensive or intensive systems, involving regular supplementary feeding – with higher costs, higher yields and reduced dependence on natural feed. Furthermore – although, not fully understood – the propensity of different species to accept and utilise supplementary feed varies in polyculture systems. For example, silver carp is generally not a target species for supplementary feeding in polyculture systems (Chiu et al., 2013; Khan et al., 2009).

Quantifying and understanding genetic variation among and within founder populations, as well as the extent of genotype-by-environment-by-management interaction in traits targeted for improvement are fundamental, if genetic gains are to be optimised through selective breeding (Gjedrem and Baranski, 2009; Li et al., 2017; Quaas, 1988). However, published estimates of genetic variation in important production traits, such as harvest body weight and survival, for catla and silver carp are uncommon in the literature and derived from a relatively small number of parents and progeny (Gheyas et al., 2009; Krishna et al., 2004). The objectives of the current study were to, for harvest weight and survival in catla and silver carp: i) quantify genetic difference among founder populations – sourced from rivers, in the case of catla (Hamilton et al., 2019a), and Bangladeshi hatcheries, in the case of silver carp (Hamilton et al., 2021); ii) estimate genetic parameters under different culture systems (i.e. monoculture and biculture); and iii) determine the extent of genotype-by-culture-system interaction (a component of genotype-by-environment-by-management interaction).

2. Methods

2.1. Spawning

At the time of spawning, 312 catla and 219 silver carp parents were selected, at random from a pool of 'candidate founders' in a state of readiness to spawn, to generate 188 and 184 full-sibling families, respectively (Tables 1 and 2). Each parent contributed to not more than two full-sibling 'base-population' (i.e. 'Generation 0') families. In the case of catla, candidate founders were sourced as fertilised spawn from the Halda, Jamuna and Padma (i.e. lower Ganges) rivers (Hamilton et al., 2019a). In the case of silver carp, candidate founders were sourced as adults from 21 Bangladeshi hatcheries (Hamilton et al., 2021). Silver carp founders were assigned to one of six genetic groups based on analysis of single nucleotide polymorphism (SNP) data (Hamilton et al., 2021): (1) Sagor-Mukteshary-Jashore, (2) BRAC, (3) Joyda, (4) Raipur, (5) Akram-Puthia, and (6) Rajshahi-Parbatipur-Nimgachi. For the purpose of analysis, the Sagor-Mukteshary-Jashore and BRAC genetic groups were merged, due to the small number of founders from the BRAC genetic group – one sire and three dams contributing to four full-sibling families – and SNP genetic marker affinity between these groups (Hamilton et al., 2021). Based on mating records and sibship assignment among founders (Hamilton et al., 2019a; Hamilton et al., 2021), all but three catla families had at least one known related family in the base populations.

Each full-sibling family was initially reared in an upwelling hatching jar with mesh at the top to prevent the loss of eggs. Catla were spawned as six batches over a period of 33 days in May and June 2017. Silver carp were spawned as four batches at each of two hatcheries over a period of 23 days in April 2017. The number of retained families per spawning batch ranged from 15 to 42.

Table 1
Number of catla full-sibling families and the genetic group of their sires and dams. The number of sires and dams from each genetic group is presented in parentheses.

		Sire		
		Halda (69)	Jamuna (44)	Padma (47)
Dam	Halda (43)	8*	20*	19*
	Jamuna (69)	55	9	31
	Padma (40)	22	16	8

* One of these families had no known relatives in the base population.

2.2. Nursing

Fry were transferred from hatching jars to hapas (~0.3 mm mesh) after approximately 30 h. Each family was reared in a separate hapa in the same pond. Fry were transferred from hapas of mesh size 1.4 mm at seven to ten days and subsequently to hapas of mesh size 5 mm after 20 to 30 days. Hapas were cleaned at least once every 15 days.

Fry were fed commercially available feed. On day one they were fed Nutri-Egg (manufactured by ACI Animal Health Limited) – protein content ~46%, carbohydrate ~3%, fat ~42% – at 200% of spawn weight. On days two to four they were fed Tiger Nursery Feed (manufactured by Eon Animal Health Products Limited) – protein content >35%, carbohydrate <24%, fat >8%, ash <16% and moisture <12% – at 200% of spawn weight. For the remaining period of nursing, fish were fed Mega Feed Limited Nursery Powder – protein content >35%, carbohydrate <31%, fat >6%, ash <16% and moisture <12%. Mega Nursery Powder was initially fed at 200% of spawn weight but subsequent to transfer to 1.4-mm hapas was fed at 300% of spawn weight in week one, 400% in week two and then 500%. Once transferred to 5-mm hapas, fish below 5 g were fed 10% of body weight and if above 5 g were fed 5% of body weight. The nursery pond was fertilised at intervals guided by pond water colour and Secchi disc data – 6.2 kg ha^{-1} of urea, 4.9 kg ha^{-1} of triple superphosphate and 6.2 kg ha^{-1} of mustard oil cake.

2.3. Grow out

Catla were tagged, with passive integrated transponder (PIT) tags inserted into the body cavity, between 156 and 169 days (mean of 12.8 g and standard deviation of 10.5 g) and silver carp between 202 and 219 days of age (mean of 18.5 g and standard deviation of 10.4 g). Not all families were successfully reared to tagging. That is, some produced no, or insufficient, viable fry – particularly in early-season spawning batches.

After tagging, families were reared together with individuals from each family randomly allocated to grow-out ponds, in proportion to pond size. Eight earthen grow-out ponds were assigned one of three treatments ('culture systems'): monoculture catla (two ponds – 1700 and 1578 m^2), monoculture silver carp (two ponds – 1700 and 1578 m^2) and biculture (i.e. culture of silver carp and catla together; four ponds – 1659, 2064, 1376 and 2590 m^2). Tagged fish were stocked at 1.2 fish m^{-2} in both monoculture and biculture ponds, with equal numbers of

Table 2
Number of silver carp full-sibling families and the genetic group of their sires and dams. The number of sires and dams from each genetic group is presented in parentheses.

		Sire				
		Sagor-Mukteshary-Jashore-BRAC (29)	Joyda (24)	Raipur (4)	Akram-Puthia (23)	Rajshahi-Parbatipur-Nimgachi (31)
Dam	Sagor-Mukteshary-Jashore-BRAC (16)	0	4	0	2	21
	Joyda (31)	5	4	2	23	15
	Raipur (2)	0	0	0	2	1
	Akram-Puthia (41)	19	28	6	12	7
	Rajshahi-Parbatipur-Nimgachi (18)	21	3	0	2	7

each species in biculture.

To ensure the availability of natural feed, fertiliser was applied to ponds weekly – 6.2 kg ha^{-1} of urea, 4.9 kg ha^{-1} of triple superphosphate and 6.2 kg ha^{-1} of mustard oil cake – and lime (calcium carbonate) was applied every four months at a rate of 62 kg ha^{-1}. Secchi disk depth measurements were monitored but not used to adjust fertilisation rates. To supplement natural feed, from 18 April 2018 until measurement (11 November 2018–11 December 2018), fish were fed a commercially available diet – Mega Feed Limited Pre Starter with a protein >33%, carbohydrate <30%, fat >8%, ash <18% and moisture <12% – at ~0.1% of body weight per day.

2.4. Measurement and analysis

The harvest-age body weight (herein referred to as harvest weight) of all surviving fish was measured prior to sexual maturity – between 510 and 573 days of age, for catla, and 563 and 616 days of age, for silver carp. All data collection, and fish husbandry, reported in this study was undertaken as part of the routine operations of the WorldFish Carp Genetic Improvement Program in accordance with the Guiding Principles of the Animal Care, Welfare and Ethics Policy of the WorldFish Center (WorldFish, 2004).

Prior to data analysis, putatively erroneous records were excluded. Specifically: i) data for 26 catla and 135 silver carp records were removed on the basis that their pond at harvest did not match their recorded pond at input; ii) for the analysis of survival three catla and two silver carp individuals were excluded as their PIT tag identifiers were erroneously recorded at the time of stocking; and iii) data for three catla families were removed on the basis that they had no relatives in the trial.

Data were analysed separately for each species and pond using ASReml (Gilmour et al., 2014) with the following univariate mixed model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$$

where $\mathbf{y}$ is the vector of trait observations, $\mathbf{b}$ is a vector of fixed effects with its design matrix $\mathbf{X}$, $\mathbf{u}$ is a vector of random effects with its design matrix $\mathbf{Z}$, and $\mathbf{e}$ is the vector of random residual terms. The model included as fixed effects in $\mathbf{b}$ the overall mean, genetic group and spawning batch. In addition, in the case of harvest weight only, age at tagging (days), age at harvest (days) and the count of surviving fish per family at tagging were included as covariates in $\mathbf{b}$. These covariates were standardised to have a mean of zero and standard deviation of one, as recommended in Gilmour et al. (2014). Genetic group effects were modelled by fitting the proportional contribution of each genetic group to each individual's genome as fixed covariates – synonymous to fitting a 'genetic groups model' (Quaas, 1988; Wolak and Reid, 2017). Genetic group means were then estimated separately using the predict function of ASReml (Gilmour et al., 2014) – where the proportional contribution of the genetic group in question was specified as one, and the proportional contributions of the other genetic groups were specified as zero. The significance of the genetic group effect was then gauged by fitting genetic group as a random effect (Quaas, 1988; Swan et al., 2015) – fitted in ASReml using the '!G' qualifier to read the proportional contribution of each of the three genetic groups to the genome of each individual (Gilmour et al., 2014; Wolak and Reid, 2017) – and undertaking a one-tailed likelihood ratio test.

The random effects in $\mathbf{u}$ were the genetic group interaction – fitted in ASReml using the '!G' qualifier (Gilmour et al., 2014) to read the proportional contribution of each possible combination of two parental genetic groups to the genome of each individual – hapa (i.e. common nursing environment) and the additive genetic component. It was assumed that the joint distribution of the random terms was multivariate normal, with the following means and (co)variances:

$$\begin{bmatrix}\mathbf{u}\\ \mathbf{e}\end{bmatrix} \sim N\left(\begin{bmatrix}\mathbf{0}\\ \mathbf{0}\end{bmatrix}, \begin{bmatrix}\mathbf{G} & \mathbf{0}\\ \mathbf{0} & \mathbf{R}\end{bmatrix}\right)$$

where $\mathbf{G}$ is a (co)variance matrix corresponding to $\mathbf{u}$, $\mathbf{R}$ is a (co)variance matrix corresponding to $\mathbf{e}$, and $\mathbf{0}$ is a null matrix. The (co)variance matrix $\mathbf{G}$ was defined as $\mathbf{G_{gs}} \oplus \mathbf{G_h} \oplus \mathbf{G_a}$, where $\mathbf{G_{gs}} = \sigma^2_{gs}\mathbf{I}$, $\mathbf{G_h} = \sigma^2_h\mathbf{I}$, $\mathbf{G_a} = \sigma^2_a\mathbf{A}$, and $\oplus$ is the direct sum operation. Furthermore, $\mathbf{R} = \sigma^2_e\mathbf{I}$, σ^2_{gs} is the genetic group interaction variance, σ^2_h is the hapa variance, σ^2_a is the additive genetic variance, σ^2_e is the residual variance, $\mathbf{I}$ is an identity matrix and $\mathbf{A}$ is the additive (i.e. numerator) relationship matrix accounting for putative sibship among founders identified in Hamilton et al. (2019a) and Hamilton et al. (2021). The significance of σ^2_{gs}, σ^2_h, σ^2_a from zero was tested with a one-tailed likelihood ratio test separately for each pond and trait (Gilmour et al., 2014).

Preliminary analyses of harvest weight data revealed evidence of heteroscedastic residuals. Accordingly harvest weight data were square root transformed prior to final analyses (Hamzah et al., 2014). Furthermore, genetic group interaction variance (i.e. genetic group heterosis) was found to be small in magnitude and not significantly different from zero in any pond or trait and was removed from models used in final analyses.

For each species and treatment, the narrow-sense heritability (h^2) was estimated from univariate analyses as follows:

$$\widehat{h}^2 = \frac{\widehat{\sigma}^2_a}{\widehat{\sigma}^2_h + \widehat{\sigma}^2_a + \widehat{\sigma}^2_e}$$

Genetic correlations between ponds were estimated separately for each species with models that extended the univariate model, with (co) variance matrices $\mathbf{G_h}$, $\mathbf{G_a}$ and $\mathbf{R}$ defined as follows ($\mathbf{G_{gs}}$ was excluded):

$$\mathbf{G_h} = \begin{bmatrix}\sigma^2_{h_1}\mathbf{I} & \cdots & \sigma_{h_{1,n}}\mathbf{I}\\ \vdots & \ddots & \vdots\\ \sigma_{h_{n,1}}\mathbf{I} & \cdots & \sigma^2_{h_n}\mathbf{I}\end{bmatrix} \mathbf{G_a} = \begin{bmatrix}\sigma^2_{a_1}\mathbf{A} & \cdots & \sigma_{a_{1,n}}\mathbf{A}\\ \vdots & \ddots & \vdots\\ \sigma_{a_{n,1}}\mathbf{A} & \cdots & \sigma^2_{a_n}\mathbf{A}\end{bmatrix} \mathbf{R} = \begin{bmatrix}\sigma^2_{e_1}\mathbf{I} & \cdots & \mathbf{0}\\ \vdots & \ddots & \vdots\\ \mathbf{0} & \cdots & \sigma^2_{e_n}\mathbf{I}\end{bmatrix}$$

where the subscripts refer to ponds 1 to n (n is the number of ponds), $\sigma_h$denotes the hapa covariance, $\sigma_a$denotes the additive genetic covariance and all other terms are as previously described. In the case of catla, difficulties with convergence did not allow full multivariate analyses to be undertaken. Accordingly, only pairwise inter-pond genetic correlations (r_a) were estimated. In the case of silver carp, for which a

multivariate (i.e. six-pond) model could be fitted, 'common genetic correlations' between monoculture and polyculture ponds (i.e. eight pairwise correlations) and between different biculture ponds (i.e. six pairwise correlations) were estimated, by constraining pairwise correlations to be equal (refer to Section 7.1.1 of Gilmour et al., 2014). Standard errors of parameters were estimated from the average information matrix, using a standard truncated Taylor series approximation (Gilmour et al., 2014).

3. Results

Secchi disk depth measurements indicated notably high water transparency in Biculture 1 and notably low transparency in Biculture 2 over the grow out period (Fig. 1). Catla harvest weight in monoculture ponds was substantially greater than in biculture ponds (Fig. 2) and for silver carp, harvest weight in Biculture 2 was notably greater than that in other ponds (Fig. 3).

For catla, the Jamuna genetic group grew more rapidly than Padma and Halda in all ponds except Biculture 1. Survival was greatest in the Jamuna genetic group. For silver carp, harvest weight was greatest for the Raipur genetic group in most ponds and survival was greatest for the Akram-Puthia genetic group across all ponds (Fig. 3). However, differences among genetic groups were not statically significant in any pond, trait or species (Figs. 2 and 3).

For harvest weight, additive variances were statistically significant in all ponds except Biculture 3 in the case of catla (Table 3) and Biculture 1 in the case of silver carp (Table 4), conceivably due to low statistical power resulting from the relatively small number of individuals of each species in these ponds. For all ponds and both species, the additive variance was greater than that for the common rearing environment (i.e. hapa). Heritability estimates for harvest weight in catla ranged from 0.06 (Biculture 3) to 0.44 (Biculture 4), with estimates in biculture ponds on average greater than those for monoculture ponds (Table 3). For silver carp, heritability estimates ranged from 0.18 (Biculture 1) to 0.51 (Biculture 4) but no tendency towards greater heritability biculture ponds was evident – indeed the average heritability in monoculture ponds was marginally greater (Table 4). Additive variances were not statistically significant for survival in either species, with the exception of silver carp in Biculture 2 (Tables 3 and 4).

In a high proportion of bivariate analyses, the additive genetic correlation between ponds hit the boundary of the parameter space for correlations (i.e. at one). For catla, only the genetic correlation between Biculture 1 and Biculture 2 was significantly different from one ($r_g = 0.69$; $P < 0.01$; Table 5). However, for silver carp, an inter-pond genetic correlation significantly different from one was evident between the two monoculture ponds ($r_g = 0.74$; $P < 0.05$); Monoculture 1 with Biculture 4 ($\hat{r}_g = 0.48$; $P < 0.05$); and Monoculture 2 with Biculture 2 and Biculture 4 ($\hat{r}_g = 0.26$; $P < 0.01$ and $\hat{r}_g = 0.45$; $P < 0.05$; respectively) (Table 5). For silver carp, the 'common genetic correlation' between monoculture and biculture ponds was 0.48 (SE = 0.15), between biculture ponds was 0.94 (SE = 0.09; $P = 0.286$) and between monoculture ponds was 0.56 (SE = 0.18), with correlations between monoculture and biculture ponds and between monoculture ponds significantly different from one ($P = 0.044$ and $P = 0.038$, respectively). Genetic correlations for survival were not computed, given the lack of additive genetic variation expressed in this trait.

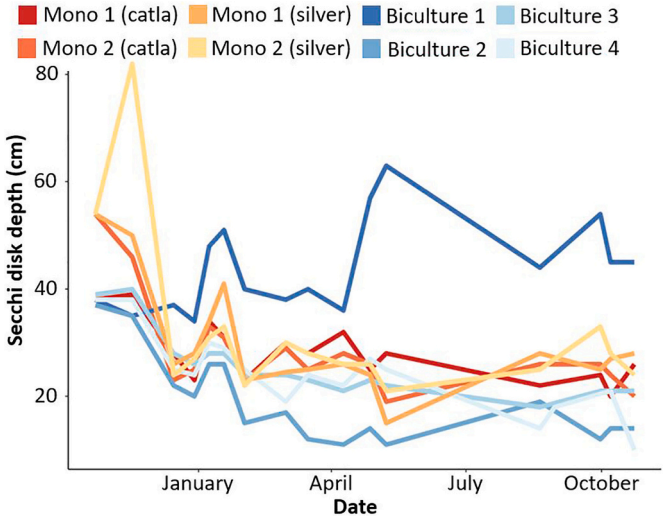

Fig. 1. Secchi disc depth over time by pond.

4. Discussion

The slower growth of catla in biculture with silver carp is in keeping with the findings of Wahab et al. (2011), Kadir et al. (2006, 2007) and Milstein et al. (2008), who noted that catla growth was adversely impacted by competition from silver carp when stocked at high densities in carp polyculture systems. Silver carp is a highly efficient filter feeder capable of grazing on phytoplankton, as well as larger zooplankton and other suspended particles (Wahab et al., 2011). Accordingly, the 1:1 catla:silver carp stocking ratio in our biculture ponds likely impacted on catla food availability – although there was no clear evidence of a difference in water transparency (i.e. Secchi disc depth) between monoculture and biculture ponds.

Among biculture ponds, the relatively rapid growth of silver carp in Biculture 2, and lack of correspondingly rapid growth in catla, was notable. These relative differences in growth conceivably resulted from an abundance of feed accessible to silver carp that was not accessible to catla (e.g. phytoplankton). It is notable that Biculture 2 exhibited greater average turbidity – an indicator of high phytoplankton biomass – than other ponds over the grow-out period (Fig. 1). Although, reasons for the high turbidity of Biculture 2 are uncertain – as management, fertiliser and feed regimes applied were the same across ponds over the trial period – differences in the composition of natural food resources among ponds may have resulted from variation in nutrient availability due to differences in historical pond use and management, and stochastic differences in pond dynamics.

The lack of significant genetic group (Hamilton et al., 2019a; Hamilton et al., 2021), main or interaction (i.e. group-level heterotic) effects in either harvest weight or survival (Nielsen et al., 2010) indicates that the breeding population of each of these species can be managed as a single 'composite' population (Mahapatra et al., 2018), with no need to preference or target any one genetic group over others. However, this does not preclude the introduction of additional founders from populations not currently represented in the WorldFish Carp Genetic Improvement Program breeding populations to further diversify the genetic foundations of breeding populations – such as recent or additional introductions of silver carp to Bangladesh (Hamilton et al., 2021). The lack of significant differences among genetic groups in catla is in contrast with a study by Khan et al. (2018), which found Halda river fish sourced as spawn exhibited a significantly greater harvest weight (with a mean of 1168 g) to spawn sourced from the Padma and Jamuna rivers (1100 g and 1105 g, respectively).

It was not possible to accurately partition the hapa variance into common nursery environment and genetic dominance variance components in our study (Ninh et al., 2011). However, the hapa variance was, in most cases, substantially less than the additive genetic variance (Tables 3 and 4), indicating that genetic variation observed in harvest weight was primarily additive in both species. Furthermore, the significant additive genetic variance for harvest weight observed in most ponds indicated that growth rate can be improved in the studied breeding populations through recurrent selection – genetic gains in growth rate in excess of 10% per generation have been achieved over

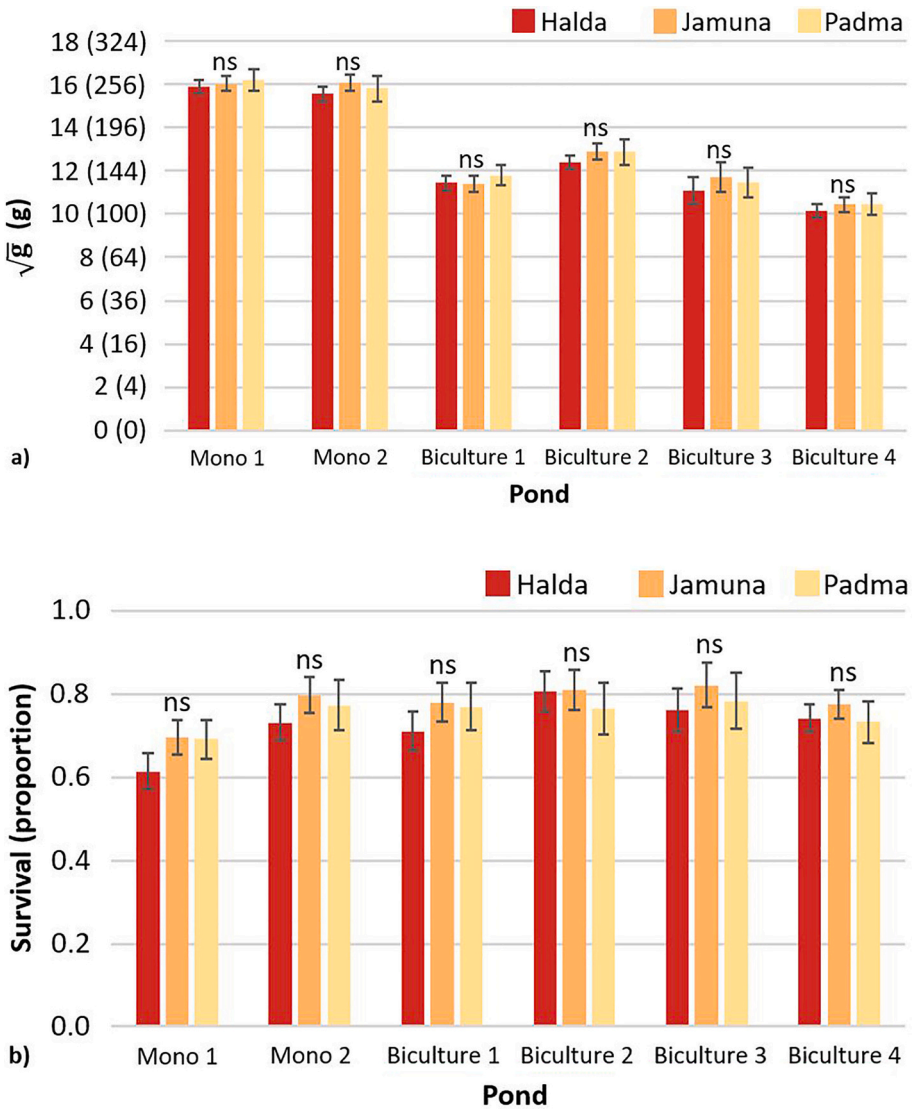

Fig. 2. Mean harvest weight (a) and survival (b) of catla by pond and genetic group. Differences among genetic groups within ponds were not statistically significant (ns).

multiple generations in numerous other finfish species (reviewed by Gjedrem and Rye, 2018).

Comparison of our estimates of narrow-sense heritability ($\hat{h}^2$) for growth in catla and silver carp with previous studies was of limited value given their scarcity, highly variable results and the fact that published estimates of narrow-sense heritability for these species are derived from studies of small numbers of parents and progeny – three sires, three dams and an unspecified number of catla progeny assessed for growth at age eight weeks in the case of Krishna et al. (2004) ($\hat{h}^2 = 0.06$ to 0.10 for body weight and $\hat{h}^2 = 0.85$ to 0.88 for length); and 36 sires, 36 dams and 319 silver carp progeny assessed for size at age six months in the case of Gheyas et al. (2009) ($\hat{h}^2 = 0.67$ for body weight and $\hat{h}^2 = 0.51$). However, our estimates of heritability for body weight are comparable to estimates in other cyprinid species assessed at greater than one year of age: common carp (*Cyprinus carpio*) – 0.17 (Dong et al., 2015), 0.70 (Kocour et al., 2007), 0.50 (Nielsen et al., 2010), 0.25 to 0.32 (Ninh et al., 2011), 0.51 and 0.63 (Prchal et al., 2018) and 0.49 (Spasić et al., 2010), 0.31 to 0.44 (Vandeputte et al., 2008) – and rohu (*Labeo rohita*) – 0.00 to 0.64 (Gjerde et al., 2019).

For catla, despite a substantial difference in harvest weight between monoculture and biculture ponds, there was no evidence of genotype-by-culture-system interaction. The only estimated genetic correlation significantly different from one – indicating the presence of genotype-by-pond-environment interaction – was that between Biculture 1 and Biculture 2. The possibility that this lower genetic correlation was driven by differences in natural feed availability between ponds – given the consistently different turbity in these ponds (Fig. 1) – warrants further investigation.

For silver carp, significant genotype-by-culture-system interaction was evident – the combined genetic correlation between monoculture and biculture ponds was 0.48 and significantly different from one (Li et al., 2017). However, the genetic correlation between the two monoculture ponds was also significantly different from one – suggesting that the weak combined genetic correlation between monoculture and biculture ponds may have been due, in part at least, to environmental differences (and genotype-by-environment interaction) between the two monoculture ponds. Indeed, when common genetic correlations between monoculture and biculture ponds were estimated separately for Monoculture 1 (four pairwise correlations) and Monoculture 2 (four pairwise correlations) the common correlation with Monoculture 1 was moderately strong ($\hat{r}_g = 0.67$; SE = 0.17) and not significantly different from one ($P = 0.076$), whereas the common correlation with Monoculture 2 was weak ($\hat{r}_g = 0.35$; SE = 0.17) and significantly different

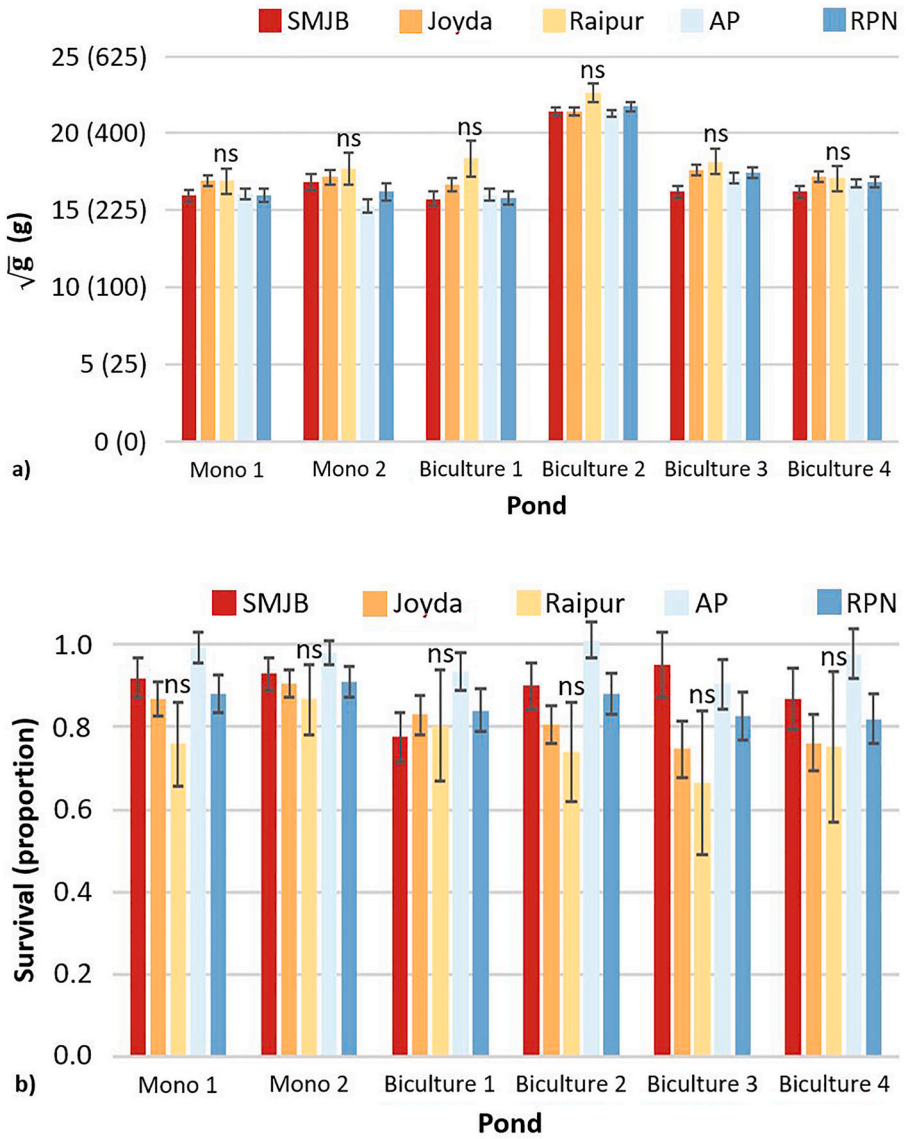

Fig. 3. Harvest weight (a) and survival (b) of silver carp by pond and genetic group. SMJB refers to Sagor-Mukteshary-Jashore-BRAC, AP to Akram-Puthia and RPN to Rajshahi-Parbatipur-Nimgachi. Differences among genetic groups within ponds were not statistically significant (ns).

Table 3
Variance component estimates for catla harvest weight and survival with standard errors in parentheses.

	N	Trait	Mean	Hapa Variance	Additive Variance	Residual Variance	Phenotypic Variance	Narrow-sense heritability[a]
Monoculture 1	1384	Weight	16.01 (0.19)	0.970 (0.335)***	1.047 (0.743)*	2.563 (0.391)	4.58 (0.251)	0.23 (0.16)
		Survival	0.666 (0.017)	0.028 (0.005)***	0 (0)[ns]	0.174 (0.006)	0.202 (0.007)	0 (0)
Monoculture 2	1509	Weight	15.82 (0.21)	0.585 (0.382)*	1.689 (0.918)**	6.983 (0.555)	9.256 (0.392)	0.18 (0.10)
		Survival	0.769 (0.021)	0.020 (0.007)***	0.014 (0.014)[ns]	0.128 (0.008)	0.163 (0.006)	0.08 (0.09)
Biculture 1	774	Weight	11.52 (0.30)	0.176 (0.238)[ns]	1.182 (0.603)***	1.569 (0.326)	2.927 (0.185)	0.40 (0.19)
		Survival	0.755 (0.022)	0.027 (0.011)**	0.009 (0.021)[ns]	0.128 (0.012)	0.164 (0.008)	0.05 (0.13)
Biculture 2	1026	Weight	12.70 (0.22)	0 (0)[ns]	2.523 (0.55)*	4.087 (0.41)	6.610 (0.339)	0.38 (0.07)
		Survival	0.798 (0.023)	0.034 (0.01) ***	0.013 (0.018)[ns]	0.104 (0.01)	0.151 (0.007)	0.08 (0.12)
Biculture 3	685	Weight	11.42 (0.60)	0.435 (0.248)*	0.251 (0.449)[ns]	3.495 (0.311)	4.181 (0.241)	0.06 (0.11)
		Survival	0.791 (0.026)	0.028 (0.013)*	0.018 (0.027)[ns]	0.095 (0.015)	0.141 (0.008)	0.12 (0.19)
Biculture 4	1289	Weight	10.35 (0.26)	0.079 (0.283)ns	1.592 (0.781)*	1.959 (0.406)	3.63 (0.212)	0.44 (0.20)
		Survival	0.754 (0.018)	0.019 (0.005)***	0.011 (0.01)[ns]	0.132 (0.006)	0.162 (0.004)	0.07 (0.06)

[ns] not significant; * $P < 0.05$; ** $P < 0.01$; ** $P < 0.001$; [a] narrow-sense heritability for survival is expressed on the observed scale (Robertson and Lerner, 1949).

from one ($P = 0.015$).

To maximise genetic gains in pedigree-based genetic improvement programs in the presence of genotype-by-environment-by-management interaction, progeny tests should be undertaken in agro-climatic conditions, pond environments and culture/management systems comparable to those in targeted grow out systems (Gjedrem and Baranski, 2009; Li et al., 2017). However, in the context of genetic improvement of fish species grown in polyculture, biosecurity protocols and capacity

Table 4
Variance component estimates for silver carp harvest weight and survival with standard errors in parentheses.

	N	Trait	Mean	Hapa Variance	Additive Variance	Residual Variance	Phenotypic Variance	Narrow-sense heritability[a]
Monoculture 1	1867	Weight	16.28 (0.19)	0.308 (0.155)*	1.330 (0.430)**	1.986 (0.234)	3.624 (0.178)	0.37 (0.11)
		Survival	0.920 (0.015)	0.012 (0.004)***	0.010 (0.008)^{ns}	0.052 (0.004)	0.075 (0.003)	0.14 (0.10)
Monoculture 2	1822	Weight	16.26 (0.24)	0.117 (0.234)^{ns}	2.211 (0.720)**	5.677 (0.433)	8.005 (0.329)	0.28 (0.08)
		Survival	0.935 (0.011)	0.013 (0.003)***	0.001 (0.005)^{ns}	0.048 (0.003)	0.062 (0.003)	0.01 (0.08)
Biculture 1	897	Weight	16.13 (0.16)	0.727 (0.355)**	1.021 (0.762)^{ns}	4.036 (0.448)	5.784 (0.318)	0.18 (0.13)
		Survival	0.850 (0.015)	0.022 (0.004)***	0 (0)^{ns}	0.104 (0.005)	0.126 (0.006)	0 (0)
Biculture 2	1145	Weight	21.48 (0.11)	0.141 (0.077)*	0.58 (0.201)***	0.855 (0.113)	1.576 (0.086)	0.37 (0.12)
		Survival	0.903 (0.017)	0.011 (0.005)***	0.021 (0.01)*	0.049 (0.006)	0.081 (0.004)	0.26 (0.12)
Biculture 3	741	Weight	17.14 (0.20)	0.012 (0.101)^{ns}	0.796 (0.286)**	1.351 (0.174)	2.159 (0.134)	0.37 (0.12)
		Survival	0.850 (0.02)	0.035 (0.006)***	0 (0)^{ns}	0.091 (0.005)	0.126 (0.008)	0 (0)
Biculture 4	1405	Weight	16.75 (0.14)	0.037 (0.06)^{ns}	0.966 (0.247)***	0.893 (0.135)	1.897 (0.113)	0.51 (0.11)
		Survival	0.856 (0.021)	0.025 (0.009)***	0.013 (0.017)^{ns}	0.083 (0.009)	0.121 (0.006)	0.11 (0.14)

^{ns} not significant; * $P < 0.05$; ** $P < 0.01$; ** $P < 0.001$; [a] narrow-sense heritability for survival is expressed on the observed scale (Robertson and Lerner, 1949).

Table 5
Bivariate genetic correlation estimates ($\hat{r}_g$) for catla (below diagonal) and silver carp (above diagonal) with standard errors in parentheses. Correlations of 1.00 indicate that the estimate hit the boundary of the parameter space. The significance of differences from one are indicated.

	Monoculture 1	Monoculture 2	Biculture 1	Biculture 2	Biculture 3	Biculture 4
Monoculture 1		0.74 (0.12)*	0.58 (0.23)^{ns}	1.00^{ns}	0.95 (0.20)^{ns}	0.48 (0.20)*
Monoculture 2	1.00^{ns}		0.54 (0.29)^{ns}	0.26 (0.21)**	0.67 (0.15)^{ns}	0.45 (0.20)*
Biculture 1	0.96 (0.30)^{ns}	1.00^{ns}		1.00^{ns}	0.47 (0.30)^{ns}	0.58 (0.24)^{ns}
Biculture 2	0.96 (0.20)^{ns}	0.90 (0.14)^{ns}	0.69 (0.24)**		1.00^{ns}	1.00^{ns}
Biculture 3	1.00^{ns}	1.00^{ns}	1.00^{ns}	1.00^{ns}		1.00^{ns}
Biculture 4	1.00^{ns}	1.00^{ns}	1.00^{ns}	1.00^{ns}	1.00^{ns}	

^{ns} not significant; * $P < 0.05$; ** $P < 0.01$.

constraints can make 'on-station' progeny testing (i.e. testing within dedicated genetic improvement facilities comprised of hatchery, nursery and grow out ponds) using conventional species ratios and stocking rates unrealistic. These issues are applicable to the WorldFish Carp Genetic Improvement Program which includes three – catla, silver carp and rohu (*Labeo rohita*) (Hamilton et al., 2019a; Hamilton et al., 2019b; Hamilton et al., 2021) – but not all, carp species stocked in conventional Bangladeshi polyculture systems (Wahab et al., 2011). However, such issues do not preclude the adoption of routine 'off-station' or 'on-farm' progeny testing – that is, testing under agro-climatic conditions, pond environments and culture/management systems comparable to those in targeted carp polyculture systems in Bangladesh (Belton and Azad, 2012; Wahab et al., 2011) – to further quantify and understand genotype-by-environment-by-management interaction and improve the accuracy of estimated breeding values for parental candidates (Kube et al., 2012). Regular on-farm performance testing of genetically improved fish against control lines and or commercial strains may also be adopted to validate and quantify genetic gains (Hamzah et al., 2014; Ibrahim et al., 2019).

5. Conclusion

This study revealed no evidence of heterosis or differences between genetic groups for harvest weight or survival in either catla or silver carp. However, significant additive genetic variation was evident for harvest weight in both species. In silver carp, the presence of genotype-by-pond interaction was indicated by multiple inter-pond genetic correlations being significantly different from one. However, these inter-pond interactions were not entirely explained by genotype-by-culture-system interaction – the genetic correlation between the two monoculture ponds was 0.56 and significantly different from one. Despite suppression of growth when grown in biculture with sliver carp, genotype-by-pond interaction was generally not significantly different from one in the case on catla. Additive variances were not statistically significant for survival in either species, with the exception of silver carp in one polyculture pond.

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CRediT authorship contribution statement

Matthew G. Hamilton: Methodology, Formal analysis, Data curation, Writing – original draft, Visualization. **Wagdy Mekkawy:** Conceptualization, Investigation, Data curation, Writing – review & editing, Supervision, Project administration. **Md. Badrul Alam:** Investigation, Resources, Data curation, Writing – review & editing, Supervision, Project administration. **Benoy K. Barman:** Writing – review & editing, Supervision, Project administration. **Manjurul Karim:** Writing – review & editing, Supervision, Project administration. **John A.H. Benzie:** Conceptualization, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare no conflicts of interest.

Data availability

The data that has been used is confidential.

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