



# Genetic correlations between harvest weight and secondary traits in a silver carp (*Hypophthalmichthys molitrix*) genetic improvement program

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## Abstract

In 2017, the base population of a family-based silver carp (*Hypophthalmichthys molitrix*) genetic improvement program was spawned in Bangladesh. This program aims to improve the growth rate of silver carp under polyculture production systems, through direct selection on the *primary trait* of harvest-age weight. The objective of this study was to quantify genetic variation in, and genetic correlations between, harvest-age weight (assessed on 8012 fish from 184 families) and a set of *secondary traits* (assessed on 1603 fish from 175 families). Secondary traits examined included feeding and digestive system traits (i.e. gill raker sponginess and gut length as a ratio of standard length), a morphometric trait (i.e. extent of overlap of pectoral and pelvic fins) and health traits (i.e. presence of *Lernaea* and prevalence of red spots — sites of inflammation/haemorrhaging). Despite not being under direct selection, genetic change in secondary traits is possible across generations in closed genetic improvement populations as a result of a correlated response to selection for the primary trait (i.e. indirect selection), adaptation to culture conditions, inbreeding and/or genetic drift. It was found that the additive genetic variance within genetic groups was significantly different from zero for all but the studied health traits. Heritability estimates for harvest-age weight and pectoral/pelvic fin overlap were moderate (0.24 and 0.22, respectively) but were low for gill raker score and relative gut length (0.12 and 0.09, respectively). Genetic correlations between harvest-age weight and secondary traits were not significantly different from zero, indicating that selection for harvest-age weight will not result in a correlated response to selection in the studied secondary traits.

**Keywords** Silver carp · *Hypophthalmichthys molitrix* · *Cyprinidae* · Genetic improvement · Primary trait · Secondary trait

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## Introduction

Silver carp (*Hypophthalmichthys molitrix*) and carp species (family *Cyprinidae*), generally, have not been the focus of genetic study or genetic improvement commensurate with their global significance (Gheyas et al. 2009). Silver carp is ranked second in terms of volume produced from aquaculture globally, with approximately 4.8 Mt of silver carp being produced annually (FAO 2020). In Bangladesh, annual production of silver carp is in the order of 0.2 Mt (DoF 2020), and the species represents an important source of animal protein for poor farmers and consumers (Belton et al. 2014).

In an effort to improve the genetic quality of silver carp available to Bangladeshi farmers, a family-based (i.e. pedigree-based) genetic improvement program, with the objective of improving growth rate in polyculture production systems, is managed by WorldFish (Hamilton et al. 2021), along with comparable programs for catla (*Catla catla*; Hamilton et al. 2019a) and rohu (*Labeo rohita*; Hamilton et al. 2019b). The base population (Generation 0) of the WorldFish Silver Carp Genetic Improvement Program (WFSCGIP) was spawned in 2017 using founders sourced from multiple Bangladeshi hatcheries (Hamilton et al. 2021). Parent selection in each generation involves identifying individuals with high total estimated additive genetic values—the sum of the estimated genetic group effect and estimated breeding value (EBV) (Wolak and Reid, 2017)—for the *primary trait* of total body weight at harvest-age (herein referred to as *harvest-age weight*), with additional constraints applied to avoid the accumulation of average relatedness/coancestry and inbreeding in populations (Hamilton et al. 2022a).

Hybridisation between silver carp and bighead carp (*H. nobilis*) has been documented in Bangladeshi hatcheries, and introgression of bighead genes into silver carp populations has the potential to undermine or alter the recognised niche of silver carp within, and the productivity of, polyculture systems (Rajts 2004). Silver carp is predominantly grown in earthen ponds in polyculture with other Cyprinid, non-Cyprinid and small-indigenous species. Such polyculture systems aim to efficiently utilise different spatial and trophic levels in ponds by stocking complementary filter-feeding, herbivorous and bottom feeding species (Wahab et al. 2011).

Although silver carp is often described as phytoplanktivorous, depending on the composition of available food, the species also ingests a high proportion of zooplankton in its diet (Battonyai et al. 2015; Kolar et al. 2005). Silver carp are capable of efficiently capturing phytoplankton and other food particles as small as 4 µm primarily due to the structure of their gill rakers—gill appendages used to filter food particles from the water—that have a sponge-like appearance. In contrast, the gill rakers of bighead (*H. nobilis*) have a comb-like or filamentous appearance capable of efficiently filtering larger zooplankton, although phytoplankton can also constitute a sizeable component of bighead's diet (Battonyai et al. 2015; Cohen and Hernandez 2018; Kolar et al. 2005; Lu et al. 2020).

In addition to gill raker structure, variations between and within silver carp and bighead have been observed in (i) fin morphology, the length of the pectoral fin and the extent of overlap with the pelvic fin is an external feature commonly used to distinguish silver carp from bighead (Battonyai et al. 2015; Kolar et al. 2005; Rajts 2004); and (ii) intestine length relative to fish length (i.e. relative gut length), ~5.0 silver carp and ~3.3 for bighead (Kolar et al. 2005). The larger relative gut length of silver carp is in keeping with natural selection for a longer gut to facilitate digestion of a diet with a high proportion of phytoplankton. Longer intestines increase food transit time and the ability to extract nutrients from low energy and/or difficult to digest food sources, such as phytoplankton (Bitterlich and Gnaiger 1984; Ke et al. 2008). Ke et al (2008) identified substantial phenotypic plasticity in gut length in silver carp, noting that silver carp altered the morphology of their digestive system to have a longer gut when their diet was comprised of a greater proportion of phytoplankton.

Although silver carp and other Cyprinids are generally considered robust species when well-managed, parasite and disease outbreaks can occur in aquaculture systems, inevitably imposing unnecessary stress on animals, productivity losses and financial imposts. Anchor worms (*Lernaea* spp.) are ectoparasitic copepods, commonly present in carp aquaculture ponds in Bangladesh (Hossain et al. 2018). Adult females attached to fish are visible to the naked eye and are threadlike in appearance with their head anchored in the flesh of the host. At the site of attachment, inflammation and haemorrhaging—commonly manifesting as unsightly red spots—are normal, as are secondary bacterial or fungal infections. Disfigurement, ill-health and the presence of visible parasites substantially reduce the market value of affected fish. Accordingly, anchor worms represent a threat to fish health and marketability, and the productivity and profitability of carp polyculture systems (Abbas et al. 2014; Hossain et al. 2018).

In genetic improvement programs, secondary traits are those of minor, unknown, intermittent or possible future importance and/or are difficult or expensive to measure. Secondary traits are given no or minimal weighting in selection indices of genetic improvement programs. Common secondary traits include those relating to fish health, feeding and digestive systems, external morphology/appearance, processing ease and flesh/carcass quality (Lhorente et al. 2019; Verbyla et al. 2021; Verdal et al. 2017).

Despite not being under direct selection, secondary traits may change across generations in closed populations as a result of a correlated response to selection for primary traits (i.e. indirect selection), adaptation to culture conditions, inbreeding and/or genetic drift (Dufflocq et al. 2017; López et al. 2021). In some instances, secondary traits are assessed routinely, along with traits under direct selection, to monitor changes in breeding populations over time and/or validate predicted correlated responses (Garber et al. 2019; Lhorente et al. 2019; Verbyla et al. 2021). The status of secondary traits can change over time with changes in the understanding of markets and trait preferences (Mehtar et al. 2021), environments (e.g. climate change) (Lhorente et al. 2019), disease introductions/outbreaks (Barría et al. 2020), management systems (e.g. intensification of production) (Fry et al. 2018), or phenotyping/genomic-selection costs (Sonesson and Meuwissen 2009), among other factors.

For a set of secondary traits—gill raker sponginess, gut length as a ratio of standard length, extent of overlap of pectoral and pelvic fins and health traits—in a silver carp breeding population, this study aimed to determine the magnitude of differences between genetic groups and the extent of additive genetic variation within genetic groups—that is, to determine if a response to selection (direct or indirect) might be expected in these traits. In addition, it aimed to estimate genetic correlations between the primary trait targeted for improvement in the breeding population, harvest-age weight and these secondary traits—that is, to determine if recurrent direct selection for harvest-age weight might be expected to result in a correlated response (favourable or adverse) in secondary traits.

## Materials and methods

### Fish management

Details of the studied fish and their management up to the time of harvest-age weight measurement are provided in Hamilton et al. (2022b). In brief, the study was undertaken on fish from the base population (i.e. Generation 0) of the WorldFish Silver Carp Genetic Improvement Program (WFSCGIP). Founders of the WFSCGIP population were sourced as adults from 17 Bangladeshi hatcheries. Only founders that exhibited a ‘pure’ silver carp external phenotype—that is, fish with gill rakers fused to form a sponge-like structure and non-overlapping

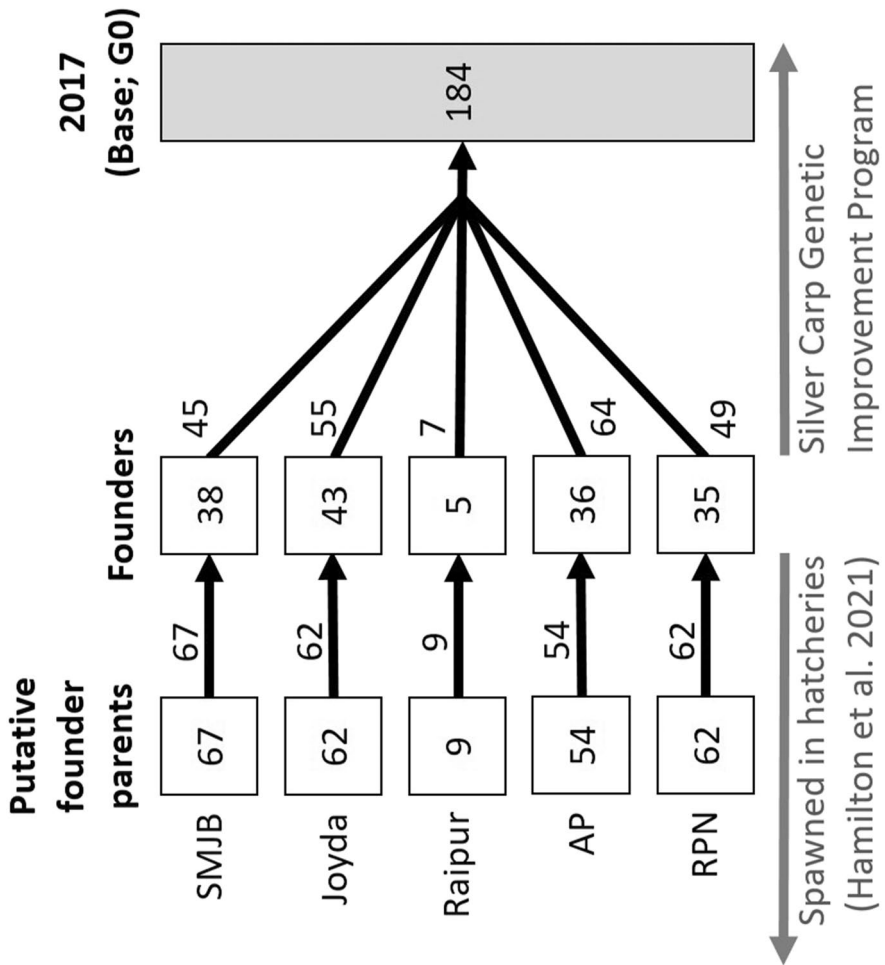
pectoral and pelvic fins (Battonyai et al. 2015; Kolar et al. 2005; Rajts 2004)—were used as parents of the base population. Founders were assigned to one of six genetic groups based on hatchery-identified origins and analysis of single nucleotide polymorphism (SNP) data (2007 SNPs; Hamilton et al. 2021): (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 (Hamilton et al. 2022b).

To generate the base population, 219 silver carp population founders were strip spawned to produce 184 full-sibling families. Mate allocation at the time of spawning occurred at random (i.e. no consideration was given to the hatchery origin or genetic group of the founders). Fish were spawned as four batches at each of two hatcheries over a period of 23 days in April 2017, with 15 to 42 families per spawning batch retained. No founder contributed to more than two base-population families, but all families were putatively related to at least one other family based on analysis of SNP data (Fig. 1; Hamilton et al. 2021).

Hatchlings were transferred from hatching jars to hapas (i.e. nets) after approximately 30 h. Each family was reared in a separate hapa in the same pond and was fed commercially available feed. Fish were tagged, with passive integrated transponder (PIT) tags inserted into the body cavity at between 202 and 219 days of age (mean of 18.5 g and standard deviation of 10.4 g). After tagging 50 individuals per family, where available ( $N=8935$ ), were reared together, with individuals from each family randomly allocated to grow-out ponds. Six earthen grow-out ponds were assigned one of two treatments (i.e. culture systems): monoculture silver carp (two ponds—1700 and 1578 m<sup>2</sup>) and biculture with catla (four ponds—1659, 2064, 1376 and 2590 m<sup>2</sup>). Tagged fish were stocked at 1.2 fish m<sup>-2</sup> in both monoculture and biculture ponds, with equal numbers of each species in biculture. To ensure the availability of natural feed, fertiliser was applied to ponds weekly and lime (calcium carbonate) was applied every four months. To supplement natural feed, fish were fed a commercially available diet during grow out. The harvest-age weight of all surviving fish ( $N=8012$ ) was measured prior to sexual maturity at between 563 and 616 days of age (Hamilton et al. 2022b).

After harvest-age assessment, 10 fish, where available ( $N=1718$ ), from each of 175 families, were retained in addition to candidate parents retained for routine genetic improvement activities. These fish represented those in the ~40th to ~60th percentile of total additive genetic value (Hamilton et al. 2022a; Pollak et al. 1984) for harvest-age weight within each family. The study fish continued to be maintained in polyculture with catla in two ponds until January 2021, when it was noted that fish were suffering from an anchor worm (*Lernaea* spp.) infestation and many exhibited skin lesions (red spots) consistent with those caused by *Lernaea* spp. (Hossain et al. 2018). The scale of this infestation was regarded as a risk to fish health and wellbeing by the WorldFish Health Team, and it was determined that the fish should be humanely euthanised.

The presence of *Lernaea* spp. and red lesions on fish provided an opportunity to assess individual fish for these health traits (i.e. presence/absence and red spot score) at the time of euthanasia, aged 1434–1457 days. In addition, fish were assessed for a number of secondary traits post euthanasia: i) feeding and digestive system traits—gill raker score and relative gut length and (ii) morphometric traits—pectoral/pelvic fin overlap. All measurement, animal husbandry and euthanasia procedures reported in this study were undertaken in accordance with WorldFish Carp Genetic Improvement Program Standard Operating Procedures and the Guiding Principles of the Animal Care, Welfare and Ethics Policy of the WorldFish Center (WorldFish 2004).



**Fig. 1** WorldFish Silver Carp Genetic Improvement Program cohorts. Founders were sourced as adult fish from 17 Bangladeshi hatcheries that were assigned to genetic groups—Sagor-Mukteshary-Jashore-BRAC (SMJB); Joyda, Raipur, Akram-Puthia (AP), and Rajshahi-Parbatipur-Nimgachi (RPN). The number of full-sibling families are shown in boxes, and the number of parents used to generate families are shown adjacent to arrows

## Assessment methods

*Gill-raker score* was visually assessed on a 6-point ordinal scale, where one represented a filamentous phenotype typical of bighead carp and six represented a sponge-like fused structure typical of silver carp (Table 1; Supplementary Material 1); gut length was measured from the beginning of the oesophagus to the anus and was expressed as a ratio of the standard length (herein referred to as *gut length ratio*) (Ke et al. 2008; Rajts 2004); and *pectoral/pelvic fin overlap* was recorded as the distance between the tip of the pectoral fin and the base of the pelvic fin, with positive values representing non-overlapping fins (i.e. silver-carp like) (Rajts 2004). To assess the severity of *Lernaea* spp. infestation, *Lernaea* spp. were counted on individual fish. However, despite some individuals experiencing severe infestations—the maximum count on an individual fish was 255—82% of fish had no *Lernaea* spp. attached and, accordingly, this trait was analysed as a binary presence-absence trait (herein referred to as *Lernaea* presence). The severity of red spots was visually assessed according to a 6-point ordinal scale (herein referred to as *red spot score*), with categories defined using the 6-point method outlined in Raymond and Cotterill (1990)—where one represented the least-severely, and six the most-severely, affected categories. All surviving fish ( $N=1603$ ) were assessed for each trait.

## Analyses

Prior to data analysis, 135 harvest-age weight records and 52 records for secondary traits were excluded due to uncertainty relating to pond identifiers. Furthermore, data for all traits except *Lernaea* presence were rescaled to have a mean of zero and phenotypic standard deviation of one within each grow-out pond and, in the case of secondary traits only, post-harvest pond.

For harvest-age weight, variance components and the narrow-sense heritability were estimated using ASReml (Gilmour et al. 2014) according to the following univariate mixed model (Hamilton et al. 2022b):

$$y = X_1b + X_2Qg + Zu + e$$

where  $y$  is the vector of trait observations;  $b$  is a vector of fixed effects with its design matrix  $X_1$ ;  $g$  is a vector of fixed genetic group effects with its design matrix  $X_2$ ;  $Q$  is a  $m \times g$  matrix, where  $m$  is the number of individuals in the pedigree and  $g$  is the number of genetic groups, fitted in ASReml using the ‘!G’ qualifier to read the pedigree-derived proportional contribution of each genetic group to the genome of each individual (Gilmour et al. 2014; Wolak and Reid 2017);  $u$  is a vector of random effects with its design

**Table 1** Description of gill raker score categories

Raker score	Description
1	Close to ‘bighead type’; filamentous structure
2	Fused structure; absence of pores
3	Reddish colour stronger; mixed coarse sponge and filamentous structure; primarily filamentous
4	Reddish colour stronger; mixed coarse sponge and filamentous structure; primarily sponge-like
5	Reddish colour appears; coarse sponge-like structure; absence of distinct anterior border
6	Whitish coloured, fine sponge-like fused structure; distinct anterior border; raker area at least double of the gill area

matrix  $Z$ ; and  $e$  is the vector of random residual terms. The model included as fixed effects in  $b$  the overall mean, grow out pond and spawning batch. Furthermore, age at tagging (days), age at assessment (days) and the count of surviving fish per family at tagging were included as covariates in  $b$  after standardisation to have a mean of zero and standard deviation of one (Gilmour et al. 2014).

The random effects in  $u$  were hapa (confounding common nursing environment and full-sibling, specific-combining-ability effects) 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  $G$  is a (co)variance matrix corresponding to  $u$ ,  $R$  is a (co)variance matrix corresponding to  $e$ , and  $0$  is a null matrix. The (co)variance matrix  $G$  was defined as  $G_h \oplus G_a$ , where  $G_h = \sigma_h^2 I$ ,  $G_a = \sigma_a^2 A$ , and  $\oplus$  is the direct sum operation. Furthermore,  $R = \sigma_c^2 I$ ,  $\sigma_h^2$  is the hapa variance,  $\sigma_a^2$  is the additive genetic variance,  $\sigma_c^2$  is the residual variance,  $I$  is an identity matrix and  $A$  is the additive (i.e. numerator) relationship matrix accounting for putative sibship among founders identified in Hamilton et al. (2021) (Fig. 1).

Preliminary analyses of harvest-age weight revealed evidence of heteroscedastic residuals. Accordingly, prior to final analyses, data were square root transformed and transformed data were, again, rescaled to have a mean of zero and phenotypic standard deviation of one within each grow-out pond (Hamilton et al. 2022a; Hamzah et al. 2014).

Variance components, additive genetic correlations and narrow-sense heritabilities for secondary traits were estimated by fitting two separate multivariate models—one including harvest-age weight, gill raker score, relative gut length and pectoral-pelvic fin overlap as response variables; and the other including harvest-age weight, *Lernaea* presence and red spot score as response variables. Harvest-age weight was included in both multivariate models to minimise possible bias resulting from the selection of individuals for study based on estimated total additive genetic values for this trait (Hamilton et al. 2022a; Pollak et al. 1984).

Multivariate models extended the univariate model above with the exception that, for secondary traits, fixed effects in  $b$  included overall mean, grow out pond and post-harvest pond (two levels). In addition, assessor (i.e. the person who undertook the subjective visual assessment) was fitted as a fixed effect for visually-assessed gill raker score and red spot score. (Co) variance matrices  $G_h$ ,  $G_a$  and  $R$  were defined as follows:

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

where the subscripts refer to traits 1 to  $n$  ( $n$  is the number of traits),  $\sigma_h$  denotes the hapa covariance,  $\sigma_a$  denotes the additive genetic covariance and all other terms are as previously described. For each trait, the within genetic group narrow-sense heritability ( $h^2$ ) was estimated as follows:

$$\hat{h}^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_h^2 + \hat{\sigma}_a^2 + \hat{\sigma}_c^2}$$

The significance of  $\hat{\sigma}_h^2$  and  $\hat{\sigma}_a^2$  from zero was tested with a one-tailed likelihood ratio test separately for each trait (Gilmour et al. 2014). The significance of genetic correlations from

zero was tested with a two-tailed likelihood ratio test (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).

Genetic group means were 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) and undertaking a one-tailed likelihood ratio test (Gilmour et al. 2014).

## Results

The genetic group effect was not found to be significant for any trait (Fig. 2). In contrast, the additive genetic variance within genetic groups was significantly different from zero for all but the health traits of *Lernaea* presence and red spot score (Table 2). The hapa variance was significantly different from zero in the case of harvest-age weight only. However, the hapa variance for harvest-age weight was small in magnitude (0.028 compared with an additive variance of 0.169), indicating that genetic variation in this trait was primarily additive. Estimated narrow sense heritabilities for harvest-age weight and pectoral/pelvic fin overlap were moderate (0.24 and 0.22 respectively) but were low for gill raker score and relative gut length (0.12 and 0.09 respectively).

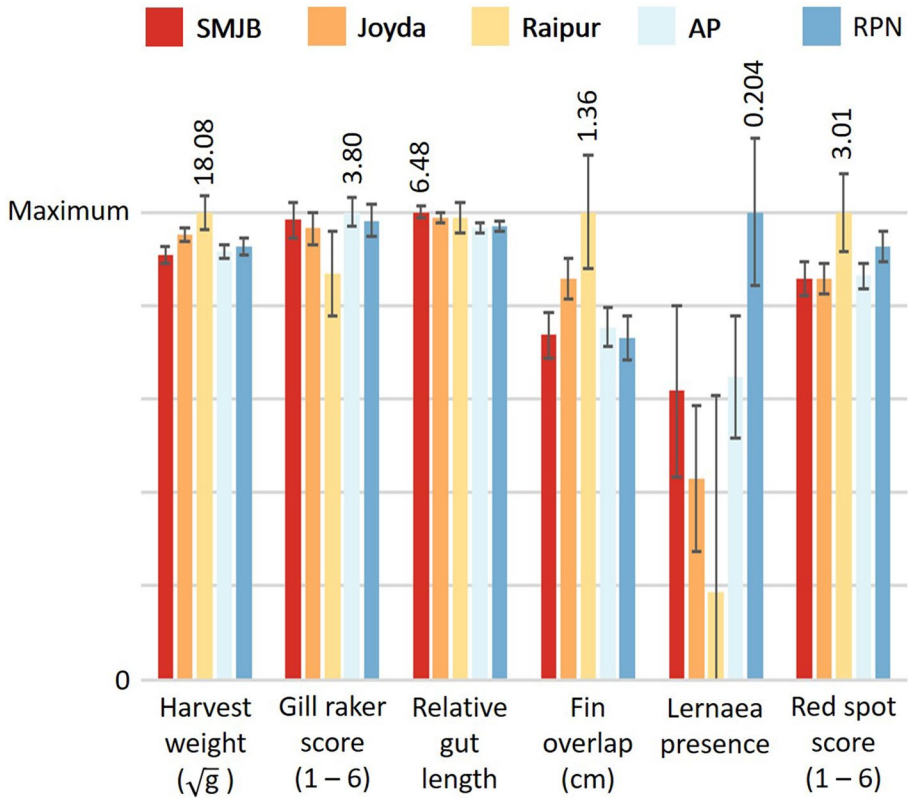
In the case of gill raker score with relative gut length, the genetic correlation was moderately negative ( $-0.62$ ) and significantly different from zero ( $P=0.0414$ ). However, genetic correlations were not significantly different from zero in the case of pectoral/pelvic fin overlap with either gill raker score or relative gut length, and genetic correlations between harvest-age weight and other traits were not significantly different from zero. Genetic correlations with health traits were not estimated, given the small and non-significant additive genetic variances observed in *Lernaea* presence and red spot score (Table 2).

## Discussion

Harvest-age growth was found to exhibit significant additive genetic variation and moderate estimates of heritability within genetic groups, indicating that direct selection for this trait will result in genetic gain across generations. Furthermore, the weak and non-significant additive genetic correlations between this primary trait and studied secondary traits indicated that selection for harvest-age weight is unlikely to result in a correlated response to selection in the secondary traits.

Despite the global significance of silver carp, very few estimates of heritability for, or genetic correlations with, harvest weight are present in the literature (Gheyas et al. 2009; Hamilton et al. 2022b). However, the narrow-sense heritability estimate in the current study ( $\hat{h}^2 = 0.24$ ) was relatively low compared with estimates for harvest weight in silver carp (first estimated by Gheyas et al. (2009) –  $\hat{h}^2 = 0.67$ , 95% confidence interval = 0.42–0.93) and other carp species (summarised in Hamilton et al. 2022b), due in part to the presence of genotype-by-pond (i.e. genotype-by-environment) interaction between the six ponds under study (Hamilton et al. 2022b).





**Fig. 2** Genetic group means for each trait. Trait means for the genetic group with the greatest value are indicated. Difference between populations were not statistically significant for any trait, according to likelihood ratio tests

The significant additive genetic variation observed for gill raker score and relative gut length and the negative and significant additive genetic correlation between these traits indicate that selection for higher gill raker scores (i.e. for ‘silver-carp-like’ gill rakers with a sponge-like structure) would result in indirect selection for shorter relative gut length (i.e. more ‘bighead-like’ relative gut length) and vice versa. It is unclear if the additive genetic variation observed in these traits resulted from intra-specific variation in ancestral silver carp populations and/or introgression of big head carp genes into the hatchery populations from which WFSCGIP founders were sourced (Hamilton et al. 2021). In any case, genetic change in either of these traits through direct or indirect selection is likely to be constrained by low heritability ( $\hat{h}^2 = 0.12$  for gill raker score and  $\hat{h}^2 = 0.09$  for relative gut length; Table 2) and the seemingly antagonistic additive genetic correlation between them (-0.62; Table 3). In the case of gill raker score, the low heritability estimate observed in our study may, in part, be explained by the subjective nature of assessment, inherent measurement error associated with categorical data and potential for categorical data to violate the assumptions underpinning analyses. Additional training and experience of assessors in gill raker scoring (Taylor et al. 2016), modification of categories (Table 1) and/or adoption of

**Table 2** Estimated genetic parameters (and standard errors) for traits

Trait category	Trait	Hapa variance	Additive variance	Residual variance	Narrow sense heritability
Harvest-age growth	Harvest-age weight	0.028 (0.011) <sup>***</sup>	0.169 (0.04) <sup>***</sup>	0.497 (0.022)	0.24 (0.05)
Feeding and digestive system	Gill raker score	0.000 (0.014) <sup>ns</sup>	0.126 (0.055) <sup>***</sup>	0.885 (0.046)	0.12 (0.05)
	Relative gut length	-0.015 (0.019) <sup>ns</sup>	0.092 (0.040) <sup>**</sup>	0.982 (0.046)	0.09 (0.04)
Morphometric	Pectoral/pelvic fin overlap	-0.038 (0.019) <sup>ns</sup>	0.222 (0.059) <sup>***</sup>	0.822 (0.046)	0.22 (0.06)
Health	<i>Lernaea</i> presence	0.002 (0.003) <sup>ns</sup>	0.000 (0.004) <sup>ns</sup>	0.126 (0.005)	0.00 (0.03)
	Red spot score	0.003 (0.021) <sup>ns</sup>	0.012 (0.032) <sup>ns</sup>	1.008 (0.043)	0.01 (0.03)

<sup>ns</sup> not significantly different from zero; <sup>\*\*</sup>  $P < 0.010$ ; <sup>\*\*\*</sup>  $P < 0.001$ .

alternative approaches to genetic analysis (e.g. the adoption of generalised linear models; Apiolaza 2011; Southey et al. 2003) warrant consideration as a means of improving the accuracy of variance component and heritability estimates for this trait.

The negative direction of the genetic correlation observed between gill raker score and relative gut length was unexpected, particularly given the phenotypic plasticity in gut length observed by Ke et al. (2008)—relative gut length was observed by Ke et al. (2008) to increase when fish were feeding on more phytoplankton. Silver carp—like spongy gill rakers (i.e. fish with high gill raker scores) are putatively specialised to allow the filtration and consumption of diets high in phytoplankton, and longer gut lengths are understood to increase the ability of fish to digest this phytoplankton (Bitterlich and Gnaiger 1984; Ke et al. 2008). However, bighead are also highly capable of filtering phytoplankton from the water column depending on food availability in the environment. Accordingly, drawing a direct relationship between gill raker characteristics (e.g. ‘sponginess’ as an indicator of pore size) and the composition/size of filtered plankton is overly simplistic (Battonyai et al. 2015; Cohen and Hernandez 2018; Kolar et al. 2005; Lu et al. 2020), and there is evidently a need to better understand (i) the role of phenotypic plasticity (and ontology) in feeding apparatus and internal gut morphology (Ke et al. 2008; Walleiser et al. 2014); (ii) the implications of altering feeding and digestive system traits in the context of carp polyculture systems—changes in gill raker morphology and/or relative gut length have the potential to affect the ability of silver carp to fill its accepted niche in polyculture systems and, by extension, pond food webs and the productivity of polyculture systems more generally (Cohen and Hernandez 2018; Drenner et al. 1984; Wahab et al. 2011); and (iii) the genetic mechanisms (i.e. linkage disequilibrium and/or pleiotropy) underpinning the additive genetic correlation observed in the current study. However, in the absence of a detailed understanding of these factors, ongoing monitoring of feeding and digestive system traits in silver carp breeding programs may be justified, particularly in the case of gill raker score which can be simply and rapidly assessed on living fish.

Pectoral/pelvic fin overlap is a morphometric characteristic used to distinguish between bighead, silver carp and their hybrids (Kolar et al. 2005; Rajts 2004). This trait is quantitative, easy to assess, and non-lethal and exhibited both significant additive genetic variation and a moderate estimate for heritability in our study. However, genetic correlations between pectoral-pelvic fin overlap and other traits were weak and not significantly different from zero (Table 3)—indicating that assessment of this trait in silver carp breeding populations would be of limited or no utility, particularly given that pectoral-pelvic fin overlap itself has no obvious intrinsic fitness or economic value.

The lack of significant additive genetic variation in disease traits suggested that additive genetic variation in *Lernaea* spp. resistance is not under strong genetic control in silver carp. However, it is possible that this result is an artefact of the study environment, specific fish population and/or method of assessment and analysis (i.e. as a presence-absence trait)

**Table 3** Additive genetic correlations (and standard errors) between traits

	Harvest-age weight	Gill raker score	Relative gut length
Gill raker score	0.12 (0.24) <sup>ns</sup>		
Relative gut length	0.24 (0.22) <sup>ns</sup>	−0.62 (0.28)*	
Pectoral/pelvic fin overlap	0.07 (0.18) <sup>ns</sup>	−0.18 (0.25) <sup>ns</sup>	0.06 (0.24) <sup>ns</sup>

<sup>ns</sup> not significantly different from zero; \*  $P < 0.05$

adopted in our study. If resistance to *Lernaea* spp. in silver carp is to be monitored in silver carp genetic improvement programs, alternative approaches to assessment are required and/or appropriate direct challenge tests developed—noting that the costs associated with the development and implementation of the second of these options would be substantial. Such approaches have successfully been developed and implemented for ectoparasites in multiple finfish genetic improvement programs (Gharbi et al. 2015; Houston 2017; Taylor et al. 2016), in numerous cases revealing significant additive genetic variation in susceptibility to ectoparasites, and—as might be expected, given the multitude of traits, species, challenge systems, and environments encompassed by such studies—highly variable estimates of genetic correlations with harvest weight (e.g. Bassini et al. 2019; Gjerde et al. 2011; Lhorente et al. 2012; Papapetrou et al. 2021; Yáñez et al. 2014).

## Conclusion

Selection for harvest-age weight is unlikely to result in a correlated response to selection in the studied secondary traits. However, ongoing monitoring of gill raker score may be justified in silver carp genetic improvement programs—given it can be simply and rapidly assessed on living fish, it will allow more precise estimation of genetic parameters (e.g. the additive genetic correlation between harvest-age weight and gill raker score), and the potential for genetic change in this trait across generations caused by factors other than indirect selection (e.g. genetic drift). The methods used to assess health traits in this study were not effective and alternative approaches to assessment, and/or appropriate direct challenge tests developed, if resistance to *Lernaea* spp. in silver carp is to be monitored or selected for.

## Supplementary information

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**Author contribution** According to CRediT (Contributor Roles Taxonomy), author contributions were as follows:

Matthew G Hamilton: conceptualisation, data curation, formal analysis, methodology, project administration, project administration, supervision, writing—original draft. Mohammed Yeasin: conceptualisation, investigation, methodology, project administration, supervision, writing—review and editing. Vishnumurthy Mohan Chadag: conceptualisation, methodology, writing—review and editing. Jérôme Delamare-Deboutteville: conceptualisation, methodology, writing—review and editing. Partho Pratim Debnath: conceptualisation, methodology, investigation, writing—review and editing. John AH Benzie: conceptualisation, funding acquisition, supervision, writing—review and editing.

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## Declarations

**Competing interests** The authors declare no competing interests.

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