Genetic parameters for growth and survival in rohu carp (*Labeo rohita*)

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Abstract

Estimates of genetic parameters for growth and survival were obtained from data recorded on 16718 rohu carp (*Labeo rohita*), the offspring of 311 sires and 257 dams from seven year-classes. The fish from the first five year-classes (1993 to 1997) were reared in both mono- and polyculture (together with catla and mrigal) earthen ponds, while the three remaining year-classes (1999 to 2001) were reared in monoculture ponds only. The base population year-classes (1993 and 1994) was crosses between a local farmed stock and five river strains. Body weight was recorded at tagging (6 months of age), on a sample of the fish (16 months of age) and at harvest (20 months of age). Genetic correlation between body weight at harvest in the two production systems was very high, 0.96 ± 0.07, indicating a negligible genotype by production environment interaction for growth in rohu. However, the genetic correlation between survival in these two production systems was of medium magnitude, 0.55 ± 0.24, but with a large standard error. Consequently, in a rohu breeding program, the breeding candidates can be selected for growth based on body weights recorded in monoculture ponds. The estimated heritabilities (and of the effect common to full-sibs, c^2) across the two production systems were

0.22±0.15 (0.66 ± 0.07), 0.38 ± 0.11 (0.28 ± 0.05), 0.34 ± 0.10 (0.23 ± 0.04) and 0.14 ± 0.05 (0.08 ± 0.02) for body weight at tagging, at sampling, at harvest and survival until harvest (on liability scale), respectively. The large c^2 needs to be reduced by rearing each family until tagging size in a more controllable environment, or by pooling a random sample of fry from each family shortly after hatching. The genetic correlation between body weight at sampling and harvest was very high, 0.98 ± 0.01, whereas the genetic correlations of body weight at tagging with body weight at sampling (0.46 ± 0.25) and harvest (0.38 ± 0.27) were of medium magnitude and not significantly different from zero. The low genetic correlations of survival until harvest with body weight at tagging (0.03 ± 0.38), sampling (0.11 ± 0.23) and harvest (0.19 ± 0.22) show that genetic improvement of survival of any significance is only possible through direct selection for survival.

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1. Introduction

World freshwater aquaculture production reached 47.9 million tons in 2016, and 59.7% is destined to carps (FAO, 2018a). India is the third largest aquaculture producer in the world with 4.2 million tons of carps, which is about 73.7% of the total India aquaculture production in 2016 (FAO, 2018a). Catla (*Catla catla*), rohu (*Labeo rohita*) and mrigal (*Cirrhinus mrigala*) are the indigenous major carps species in India, commonly cultured under polyculture system in earthen ponds, often together with grass carp (*Ctenopharyngodon idella*) silver carp (*Hypophthalmichthys molitrix*) and common carp (*Hypophthalmichthys molitrix*). Among the three Indian major carp species, rohu is the most important and preferred by the farmers mainly due to its higher growth rate, market demands and consumer preference (Mahapatra et al., 2006; Nair and Salin, 2007). Since more than a decade ago, with increasing demand for rohu, farmers in India have shifted from three-species to two species polyculture system with rohu and catla (FAO, 2018b).

Since the success of induced spawning technology applied to Indian carps (Choudhuri and Alikunhi, 1957), the number of carp hatcheries in India has increased rapidly (Gupta, S.D. and Rath, S.C. (2006). However, due to the lack of proper management of genetic broodstock resources, carp production in the country experienced a significant deterioration in seed quality and decreased production (Eknath and Doyle, 1990). The urgent need for improved technology and procedures to permanently improve the seed quality was recognized, and in 1993, a project on genetic improvement of rohu carp was initiated at Central Institute of Freshwater Aquaculture (CIFA) in India. The project was executed in collaboration with the Norwegian Institute of Aquaculture Research AS (AKVAFORSK, now a part of the research organization Nofima).

A genetically broad base population is critical for sustainable long-term breeding programs. For the Indian rohu program the base materials were collected from five different

Indian river systems and one domestic farmed stock.

In the first phase of the project the growth and survival of the six stocks of rohu was compared in mono- and polyculture production environment at CIFA (Reddy et al., 2002). This work was followed by a study on the magnitude of heterosis for growth and survival based on two 3x3 diallel crosses of the stocks (Gjerde et al., 2002). The results from these two studies provided fundamental and important insight of the growth and survival performance of rohu strains and their crosses, and contributed substantially to the development of the breeding program.

In this study we present estimates of phenotypic and genetic parameters for growth and survival based on body weight recorded on full- and half-sib families at tagging after a period of separate rearing of the families in earthen nursery ponds, and at sampling and harvest after being reared communally in both a mono- and polyculture system.

2. Material and methods

2.1. The two base population year-classes

Five wild stocks of rohu were sampled as fry or fingerlings from five rivers in India, namely Ganga, Yamuna, Brahmaputra, Sutlej and Gomati and used to establish the two base population year-classes 1993 and 1994 (Table 1). Also included was a farmed (Local) stock available at CIFA that may have been introduced some decades ago from rivers in northern India. The base population year-class 1993 was the offspring from fish sampled from Ganga and Local, while the base population year-class 1994 was offspring from fish sampled from Brahmaputra, Ganga, Gomati, Sutlej, Yamuna and Local. After transfer to CIFA, Bhubaneswar, Orissa the collected fry and fingerlings were quarantined in individual cement cisterns for a period of two weeks. After quarantine the fish from these wild stocks, along with fingerlings from a local farmed stock were individually tagged by fin-clip, M-prociane blue dye, or a combination of these

techniques for identification of origin, and subsequently randomly stocked and communally reared in three earthen ponds for two to three years until they become sexually mature. See Reddy et al. (2002) for more details on the procurement, production and rearing of the two base population year-classes.

2.2. Production of full- and halfsib families

For reproduction, sexually mature male and female breeders were induced by Ovaprim, a synthetic pituitary hormone. Approximately five hours after hormone injection, milt from the males was collected in individual labeled vials, and kept in a refrigerator until used to fertilize the eggs from the artificially stripped females. A nested mating design was used, with males nested with females or vice versa, depending on body size and number of available females at each year-class.

The families in the two base population year-classes were produced using randomly sampled breeders from the six stocks, while the following year-classes were produced using male and female breeders with high breeding value for harvest body weight. To keep the rate of inbreeding at an acceptable level, full- and half-sib mating was avoided. In addition, the number of male and female breeders was restricted to not more than eight animals from each family.

For each year-class (YC) the production of the families took place over a period of 7 to 19 days from mid/late July to late/early August (Table 1).

2.3. Rearing until first feeding

After fertilization, the eggs of each full-sib family were immediately transferred into individual double cloth hapas placed in an earthen pond reservoir, where they hatched after 18 to 20 hours.

Soon after hatching, the inner hapas were removed along with the unfertilized eggs and egg shell. The resulting fullsibs were kept in the hatching hapas (Figure 1A) for about one week, after which a random sample of the fullsibs from each family (about 3000 for the 1993 year-class and 2000 for other year-classes) was transferred to individual 100 m2 nursery ponds. These were established by dividing available 200 m2 earthen ponds with a fine-meshed cloth (Figure 1B). During the about one week hatching period, the outdoor hapas were exposed to excessive heat (36-38 ^{o}C), predation by trash fish which inadvertently entered the hapas from the pond, hapa cutting by crabs and other unmanageable ecological factors. This resulted in low recovery of spawn from a large proportion of the families, and some were completely lost. For the purpose of increase the success rate of family production, after hatching additional random samples of fullsibs from each family were transferred to separate indoor concrete tanks (1200 l) in a wet laboratory (about 2000 individuals for the 1993 year-class and 1000 individuals for the other year-classes, Table 1). These samples were used to restock families that suffered high mortalities in the nursery ponds and thus secured the further rearing of these families in the nursery ponds until tagging size.

The above procedure was used for the first six year-classes, and introduced unwanted environmental effects common to full-sibs (nursery pond or tank effect) and thus biased estimates of genetic parameters. To remedy this situation, a different system was developed for the last two year-classes (2000 and 2001), in which the newly fertilized and swollen eggs were incubated in indoor fiberglass jars (15 l, Figure 1C), after which the spawns migrated with the water flow to a collection hapa placed in front of the incubation jar (Mahapatra and Sahoo, 2003). The new setup resulted in 94.9% (year-class 2000) and 100% (year-class 2001) recovery rate of the number of families produced as compared to an average of 75.8% (varying from 70.1% to 82.0%) for the first six year-classes (Mahapatra and Sahoo, 2003).

146

147 *2.4. Tagging*

148 Rohu is an active swimmer and external tags are not suitable for individual identification
149 (Mahapatra et al., 2001). Thus, the fingerlings were individually tagged with Passive Integrated
150 Transponder (PIT) tags, which was implanted into the abdominal cavity (Mahapatra et al.,
151 2001). A random sample of 50 to 55 fish from each full-sib family were individually tagged.
152 After tagging, the fingerlings were kept overnight in tanks for recovery and monitoring for any
153 mortality.

154

155 *2.5. Production environment*

156 The tagged fish from all families were randomly split and distributed into three 0.1 ha
157 monoculture earthen ponds and two 0.4 ha polyculture earthen ponds at a stocking density of
158 5000 fingerlings per ha. In polyculture, rohu were stocked together with mrigal and catla in the
159 ratio of 1.2:1:1. The stocking density and species ratio used in this study are corresponds to
160 usual practices followed by farmers in India (Chaudhuri et al., 1978). During the grow-out
161 period, supplementary feed consisting of groundnut oil cake and rice bran in a 1:1 ratio (5% of
162 body weight per day during early stages of stocking and 5% at later stages) was used, following
163 the common practice in India. For year-classes 1999, 2000 and 2001, only monoculture was
164 used.

165

166 *2.6. Data structure and recorded traits*

167 A total of eight year-classes were produced, which consisted of records from a total of 16718
168 progenies of 358 full-sib families (Table 1). Year-class 1997 consisted of mainly single pair
169 matings (full-sib families) with very few paternal half-sib families. Over the year-classes, four
170 generations of selection for increased growth rate was performed. In order to establish parent-

offspring genetic ties between the two base populations year-classes 1993 and 1994, some crosses where made between male and female breeders from different year-classes. For instance, year–class 1997 was produced using breeders from year-classes 1994 and 1995. Similarly, year-class 2000 was produced using breeders from year-classes 1996 and 1997. In 1998, severe drought in Orissa prohibited reproduction of nucleus families at CIFA. The following year, a super cyclone hitting the area caused mix-up of full-sib families due to high water levels in the nursery ponds. For that year, only individual (mass) selection for growth was applied.

Individual body weights were recorded at tagging (at about 6 months of age), at sampling (14 months of age) and at harvest (20 months of age). Survival rates were calculated based on number of tagged and harvested fish. As the fish were not gutted at harvest, the effect of sex on body weight could not be determined and accounted for in the statistical model.

2.7. Statistical analysis

For body weight recorded at sampling and harvest, heterogeneity of variances across the different levels of the fixed effects (year-classes and ponds) were accounted for by scaling the observed body weight records by the respective standard deviation in the actual level of the fixed effect according to Hill (1984): $y_{ij}^{*} = y_{ij} \frac{\sigma_{y.}}{\sigma_{y_i}}$, where y_{ij} the observed and y_{ij}^{*} is the standardized trait for animal *j* in level i of the actual fixed effect, σ_{y_i} is the observed standard deviation of the trait in level *i* of the fixed effect and $\sigma_{y.}$ is the mean standard deviation of the trait across all levels of the fixed effect. Thus, it is assumed that the magnitude of the heritability for each trait is the same across the different fixed effect subclasses; i.e. that the residual and genetic variances are changing proportionally in these different subclasses.

2.7.1 Estimation of genetic parameters for body weights and survival

For the estimation of genetic parameters for body weight at tagging, at sampling and at harvest, and survival from tagging to until harvest, four different models were fitted in order to investigate the underlying genetic constitution of the traits. The ASReml software (Gilmour et al., 2009) was used for all analyses.

Model 1 was a univariate mixed linear animal model for body weight at tagging to estimate the variance components within and across year-classes. In matrix notation:

$$\mathbf{y}_{bwt} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_c c} + \mathbf{e} \qquad (1)$$

where subscript $\mathbf{y}_{bwt}$ refers to the observed body weight at tagging; $\mathbf{b}$ is the vector of fixed effects; $\mathbf{a}$ is a vector of random additive genetic effects; $\mathbf{c}$ is a vector of random effects common to full-sibs other than additive genetics, which were effects of separate rearing of families until tagging and potential dominance genetic effects (hereafter called effect common to full-sibs, c^2); and $\mathbf{e}$ is a vector of random residuals. The matrices $\mathbf{X}$, $\mathbf{Z_a}$ and $\mathbf{Z_c}$ are the appropriate incidence matrices that assign the individual observations to the right level of the fixed effect, random animal effect and full-sib family effect, respectively. Assumed was that additive genetic effect $\mathbf{a} \sim N(\mathbf{0}, \mathbf{G} \otimes \mathbf{A})$, the effect common to fullsibs $\mathbf{c} \sim N(\mathbf{0}, \mathbf{C} \otimes \mathbf{I})$, and the residual $\mathbf{e} \sim N(\mathbf{0}, \mathbf{R} \otimes \mathbf{I})$; where $\mathbf{G}$, $\mathbf{C}$ and $\mathbf{R}$ are the additive genetic, common full-sib and residual (co)variance matrices among the traits, respectively, $\mathbf{A}$ is the numerator relationship matrix for all animals in all generations including the parents in the base population and $\mathbf{I}$ is an identity matrix of appropriate size.

With Model 2, a trivariate mixed linear animal model was fitted to estimate the genetic

correlation between body weight at harvest in mono- and polyculture systems, including body weight at tagging as the third trait. Expressed in matrix notation:

$$\begin{bmatrix} \mathbf{y}_{\text{bwt}} \\ \mathbf{y}_{\text{bwhM}} \\ \mathbf{y}_{\text{bwhP}} \end{bmatrix} = \mathbf{Xb} + \mathbf{Z}_{\text{a}}\mathbf{a} + \mathbf{Z}_{\text{c}}\mathbf{c} + \mathbf{e} \qquad \textbf{(2)}$$

where $\mathbf{y}_{bwt}$ refers to body weight at tagging, and y_{bwhM} and y_{bwhP} refers to standardized harvest body weights recorded in mono- and polyculture ponds, respectively. In Model 2, the residual correlation between the harvest body weights recorded in mono- and polyculture ponds was set to zero as any given fish was reared in only one of the production system.

Model 3 was bivariate mixed sire-dam threshold model, fitted to estimate the genetic correlation between survival until harvest in mono- and polyculture systems. This model in matrix notation:

$$\begin{bmatrix} \Pr(y_{surv\_m} = 1) \\ \Pr(y_{surv\_p} = 1) \end{bmatrix} = \Phi(\mathbf{Xb} + \mathbf{Z}_{\text{s}}\mathbf{u}_{\text{s}} + \mathbf{Z}_{\text{d}}\mathbf{u}_{\text{d}} + \mathbf{Z}_{\text{c}}\mathbf{c} + \mathbf{e}) \qquad (3)$$

where $\Pr(y_{surv\_m} = 1)$ and $\Pr(y_{surv\_p} = 1)$ are vectors of probabilities of being alive at harvest in mono- and polyculture ponds, respectively; $\mathbf{u}_s$ and $\mathbf{u}_d$ are the vector of ½ the sire and ½ the dam additive genetic values, respectively; $\mathbf{Z}_{\text{s}}$ and $\mathbf{Z}_{\text{d}}$ are the corresponding design matrices.

Finally Model 4 was a multivariate mixed sire and dam model for estimation of (co)variance components for survival until harvest and body weight at tagging, at sampling, and at harvest. Model 4 in matrix notation:

$$\begin{bmatrix} \mathbf{y}_{\text{surv}} \\ \mathbf{y}_{\text{bwt}} \\ \mathbf{y}_{\text{bws}} \\ \mathbf{y}_{\text{bwh}} \end{bmatrix} = \mathbf{Xb} + \mathbf{Z}_{\text{s}}\mathbf{u}_{\text{s}} + \mathbf{Z}_{\text{d}}\mathbf{u}_{\text{d}} + \mathbf{Z}_{\text{c}}\mathbf{c} + \mathbf{e} \qquad \textbf{(4)}$$

where y_{surv} refers to survival records (1 = alive at harvest; 0 = dead during the period from tagging to harvest), y_{bws} and y_{bwh} refer to standardized body weights recorded at sampling and

242 harvest, respectively. The survival trait was in threshold scale, as defined for Model 3.

243

244 The fixed effect fitted in Model 1 was the overall mean for the analysis within year-class, and
245 the year-class effect for the analysis across year-classes. For Model 2, year-class was fitted as
246 a fixed effect for body weight at tagging, and the combined year-class by production system by
247 replicated ponds within production system for body weight at harvest in two above mentioned
248 production systems. The survival model (Model 3) included the same fixed effect as the one
249 fitted for body weight at harvest in Model 2. Lastly, the fixed effects fitted in Model 4 were the
250 same as included in Model 2 and Model 3. In all models a fixed effect of age, with from three
251 to five different levels depending on the year-class that represents the date on which the families
252 were produced, was also included but was found to be not significant (P>0.05) and therefore
253 excluded from the final models.

254

255 Heritability for each body weight trait was calculated as $h^2 = \frac{\sigma_a^2}{\sigma_p^2}$, and the relative importance
256 of $c^2 = \frac{\sigma_c^2}{\sigma_p^2}$, where σ_a^2 denotes additive genetic variance, and σ_c^2 as variance of c^2. The
257 phenotypic variance was calculated as, $\sigma_p^2 = \sigma_a^2 + \sigma_c^2 + \sigma_e^2$, where σ_e^2 denotes the error
258 variance.

259

260 Heritability for survival was calculated as $h^2 = \frac{4\sigma_{sd}^2}{2\sigma_{sd}^2 + \sigma_c^2 + \sigma_e^2}$, where σ_e^2 equals to 1.0 and
261 $\sigma_{sd}^2 = \sigma_s^2 = \sigma_d^2 = 1/4\sigma_a^2$, which was obtained through the model function *and(dam,1)* in the
262 ASReml software (Gilmour et al., 2009).

263

264 A log likelihood ratio test (see Chapter 13 in Lynch and Walsh, 1997) was used to test if the

estimated genetic correlation between survival in the two production systems was significantly different from zero. However, as such a test is not defined for a threshold model, the tested correlation was obtained from a linear model similar to Model 3. The likelihood ratio was defined as $LR = -2Log[(L_F)/(L_E)] = -2[LogL_F - LogL_E]$, where $LogL_F$ is the log likelihood value when the genetic correlation was fixed to zero and $LogL_E$ is the log likelihood value for the estimated genetic correlation. The genetic correlation is considered significantly different from zero, if LR was significantly different from zero using a chi-square statistic (χ^2_r) with r = 1 degree of freedom.

The magnitude of the estimated genetic correlation between harvest body weight, or between survival until harvest, in mono- and poly-culture reflect the degree of re-ranking of families in the two production systems. The magnitude of this correlation was used as an estimate of the magnitude of the genotype by environment interaction (GxE) for growth and survival in the two production systems.

3. Results

3.1. Descriptive statistics for body weights and survival

Mean body weight of rohu recorded at tagging, at sampling and at harvest, varied considerable between the year-classes, production systems (mono- and polyculture) and replicated ponds within production systems (Table 2). For the first five year-classes (1993 to 1997) with fish reared in both production system, body weight at sampling and harvest were on average 14% and 21% larger in monoculture than in polyculture ponds, respectively. The coefficient of variation (CV) of body weight was particularly high at tagging, on average 63%, but much lower at sampling and harvest, on average 36% and 31%, respectively. CVs of body weight were generally higher in polyculture, 40% at sampling and 32% at harvest, compared to

290 monoculture ponds with CV of 27% for both.

291

292 The average survival rate across all the tested year-classes was low (65%), and with large
293 variation between replicated mono- and polyculture ponds in most year-classes (Table 2). Large
294 variation for survival was also seen between year-classes, for example survival rate of 91% in
295 1994 compared to 41% in 1999. For year-classes 1993 to 1997 in which the fish were reared in
296 both production systems, survival was on average marginally higher in the monoculture (71%),
297 than in the polyculture ponds (67%).

298

299 *3.2. Genetic parameters for body weight at tagging*

300 Based on results from Model 1, the within year-class heritability estimates for body weigh at
301 tagging varied considerably among the year-classes, ranging fromzero to 0.64 (Table 3). The c^2
302 was relatively high and also highly variable (range 0.22 to 0.96). Across all year-classes, the
303 heritability estimate was zero and $c^2$was very high, 0.78 ± 0.03 (Table 3).

304

305 *3.3. Genetic parameters for harvest body weight and survival in mono- and polyculture*
306 *ponds*

307 Genetic parameter estimates for harvest body weight (Model 2) and survival (Model 3) are
308 presented in Table 4. For harvest body weight, the heritability was low but statistically
309 significantly different from zero, and of same magnitude in the two production systems
310 (0.10). The heritability for survival was higher in polyculture (0.21 ± 0.07) than in
311 monoculture (0.10 ± 0.05), but not statistically significantly different. The results from
312 Model 2 showed that estimated heritability for body weight at tagging was low and not
313 significantly different from zero (0.06 ± 0.04) and with a large c^2 (0.70 ± 0.05).

314

315 Genetic correlation between harvest body weight in the two production systems was very
316 high (0.96 ± 0.07), and of medium magnitude for survival, (0.55 ± 0.24; P=0.06).
317
318 *3.4. Genetic parameters for the three different body weight traits and survival across mono-*
319 *and polyculture ponds*
320
321 Due to genetic correlations of very high and medium magnitude between mono- and
322 polyculture ponds for harvest body weight and survival, respectively, (Table 4), combined
323 parameter estimates across the two production systems could be obtained from the
324 multivariate Model 4 analysis (Table 5). For body weight at tagging, the heritability was of
325 medium magnitude but with a large standard error (0.22 ± 0.15), while the c^2 was high (0.66
326 ± 0.07). The heritability for body weight at sampling and harvest were of medium
327 magnitude (0.38 ± 0.11 and 0.34 ± 0.10, respectively). The $c^2$for these two traits were also
328 of medium magnitude, but slightly lower than their respective heritabilities (0.28 ± 0.05
329 and 0.23 ± 0.04). These two estimates were substantially lower compared to the estimate
330 for body weight at tagging. For survival until harvest, the heritability was 0.14 ± 0.05 and
331 the c^2 0.08 ± 0.02.
332
333 The genetic and residual correlations among the traits from Model 4 are presented in Table
334 6. The genetic correlations between survival until harvest and body weigh at tagging was
335 close to zero (0.03 ± 0.38), whereas, the genetic correlation of survival with body weight
336 at sampling and harvest were both positive (0.11 ± 0.23 and 0.19 ± 0.22, respectively), but
337 not significantly different from zero (P>0.05). The genetic correlations of body weight at
338 tagging with body weight at sampling and harvest were high (0.46 ± 0.25 and 0.38 ± 0.27,
339 respectively), but not significantly different from zero as well (P>0.05). On the other hand,
340 the genetic correlation between body weight at sampling and harvest was close to unity

341 (0.98 ± 0.01). The residual correlations among the traits were of the same magnitude as the
342 genetic correlations (Table 6).
343
344 **4. Discussion**
345
346 *4.1. Descriptive statistics for body weights and survival*
347 The fish material used within year-class was the same in all mono- and polyculture ponds.
348 Hence the large variation in mean harvest weight and survival between year-classes,
349 between the two production systems within year-class and between replicated ponds within
350 production system and year-class, suggests that environmental effects varied substantially
351 between the two production systems and between replicated ponds within year-class. This
352 is likely due to variation in parameters such as water temperature, soil quality, feeding
353 procedures, or fish density; variables that are more challenging to control in in a pond
354 culture as compared to a more intensive cage or tank culture system. Nevertheless, efforts
355 should be made to obtain better production results in the low performing production units
356 through improvements in the management practices.
357
358 The higher CV for body weight at tagging (64) compared to weights recorded at sampling
359 (37) and harvest (30), indicate stronger competition for e.g. food among the fingerlings at
360 early age. Similar results are reported in grass carp (*Ctenopharyngodon idella*, Fu et al.,
361 2016), common carp (*Cyprinus carpio*, Wang et al., 2006; Nielsen et al., 2010), and
362 rainbow trout (*Oncorhynchus mykiss*, Su et al., 1996). However, in a study by Ninh et al.
363 (2011) on common carp, the CV of body weight was similar at about 3, 6 and 10 months
364 of age. According to Hecht and Pienaar (1993), cannibalism often occurs during the early
365 rearing stages in most fish species. In rohu, this may be due to insufficient supply of natural

366 produced nutrients in the nursery ponds. The higher CVs for body weight at sampling and
367 harvest in polyculture as compared to in monoculture ponds, combined with the lower
368 survival in polyculture, indicate higher competition among the animals in the polyculture
369 system.
370
371 *4.2. Heritabilities*
372 For body weight at tagging (6 month of age), the estimated heritability across generations
373 from Model 1 (0.00) and Model 2 (0.10) were low, consistent with results reported for body
374 weight recorded at an early age in common carp (zero by Vandeputte, 2003; 0.12 by Nielsen
375 et al., 2010). On the other hand, the estimated heritability for this trait from Model 4 was
376 of medium magnitude, and similar to reported estimates for body weight in common carp
377 at two months of age (0.33 by Vandeputte et al., 2004) and four months of age (0.39 and
378 0.49 by Ninh et al., 2011). In silver carp, a higher estimate (0.67) at six months of age was
379 reported by Gheyas et al., (2009). The highly variable heritability estimates obtained for
380 body weight at tagging across year-classes from Models 1 and 4 suggest that the extremely
381 low estimate from Model 1 likely is significantly biased downward by confounding
382 between additive genetic effects and effects common to full-sibs. Such confounding is, at
383 least partly, accounted for in the multivariate Model 4.
384
385 For body weight recorded at sampling and harvest, the heritabilities were of medium
386 magnitude and within the range of reported heritabilities for body weight at harvest in
387 aquaculture species (Atlantic salmon by Gjerde et al., 1994; silver barb by Hussain et al.,
388 2002; coho salmon by Neira et al., 2004; Nile tilapia by Ponzoni et al., 2005). Studies in
389 common carp reported higher heritabilities for this trait (0.70 by Kocour et al., 2007; 0.50
390 by Nielsen et al., 2010). Despite the relatively high c^2 in the present study, the magnitude

391 of the estimated heritabilities for body weight at harvest in rohu clearly demonstrate that
392 growth rate in rohu can be increased through selection.
393
394 The estimates of heritabilities for survival until harvest were within the range as reported
395 in published literatures for Nile tilapia (0.03 to 0.14 by Charo-Karisa et al., 2006; 0.20 and
396 0.27 by Luan et al., 2008; 0.12 by Rezk et al., 2009), common carp (0.2 by Nielsen et al.,
397 2010), and other aquaculture species summarized by Gjedrem (2005, pp. 66-70).
398
399 The heritability estimates for in particular harvest body weight may be biased downwards
400 as it was not possible to account the recorded body weights for a possible sex effect. As we
401 have not found any published paper on the magnitude of the sex effect on growth in rohu
402 carp the magnitude of this possible bias is not possible to quantify. This may also have
403 caused an unknown downward biased of the effect common to fullsibs for body weight (see
404 4.3), as well as an unknown bias on the estimated genetic and residual correlations (see
405 4.4).
406
407 *4.3. Effect common to fullsibs*
408 The very high magnitude of the c^2 for body weight at tagging (ranged from 0.66 to 0.78
409 obtained from different models across all the year-classes) falls far outside the range earlier
410 reported for common carp (0.24 by Nielsen et al., 2010 and 0.30 by Ninh et al., 2011). This
411 strongly indicates that standardizing the rearing environment in the small nursery ponds
412 during the separate rearing period used in the present study is far more difficult than in
413 small tanks as used in the two referred to studies.
414
415 As expected, the c^2 was substantially lower at sampling (after the fish were reared

communally in 6 and 14 months after tagging, respectively), and similar to those observed in Atlantic salmon (Gunnes and Gjedrem, 1978), chinook salmon (Winkelmen and Peterson, 1994) and Nile tilapia (Nguyen et al., 2010). However, this effect was still of substantial magnitude at harvest, likely causing a reduction in the heritability and selection accuracy, and ultimately reduced response to selection for increased growth. For survival until harvest, the estimated c^2 was relatively low, but slightly higher than those reported for aquaculture species (e.g. 0 to 0.04 by Charo-Karisa et al., 2006; 0.015 by Rezk et al., 2009).

In the present study, substantial efforts were made to standardize environmental effects across the nursery ponds (i.e. preparation of the ponds prior to stocking, stocking density, feeding regime, etc.), but the results demonstrate that significant environmental differences remained. In hindsight, we believe that the restocking of some of the nursery ponds with fish from the wet-lab may have contributed to the large c^2 . Furthermore, fingerlings from some of the year-classes (1994, 1995, 1997, 2001) were tagged at a higher body weight than necessary, which prolonged the nursery period of separate rearing.

For rectifying the issue for nursery, a trial with rearing of rohu in ten outdoor circular fiberglass tanks (water volume of 1 m^3) from first feeding until tagging size was conducted. A sample of fry from year-classes 2001 and 2002 were reared in these tanks with water supply from a nearby earthen pond enriched with zooplankton. For the purpose of improving the rearing condition, a layer of soil with thickness of 5 cm was put on the bottom of five of the tanks. In both, with and without soil, plastic tank environments, the fingerlings stop growing when they reached the size of 2.5 to 3 g and the cause of this stunted growth was unidentified (Anonymous, 2003), but likely due to insufficient amount of food. Thus, new trials on nursing the fry in similar type of fiberglass tanks need to be

441 conducted, for example, with supplemented feeding with live food like rotifers and artemia.
442 However, if acceptable growth rate until tagging size cannot be obtained in tanks,
443 alternative strategies to the nursery ponds need to be considered.
444
445 As stated above, the high magnitude of the c^2 for harvest body size reduce the expected
446 genetic gain for growth. If the c^2 effect cannot not be substantially reduced by improved
447 standardization measures, an alternative is to pool a given number of spawn or fry from all
448 the families, at an early age (for example, shortly after hatching) and trace them to their
449 parents through the use parental assignment by genetic markers. This method has been
450 successfully demonstrated in common carp (Ninh et al., 2011) and grass carp (Fu et al.,
451 2016), for which the pooling took place three days after hatching and at fertilization (mass
452 spawning), respectively. In both these studies, the c^2 estimated for harvest body growth was
453 close to zero.
454
455 *4.4. Correlations*
456 The genetic correlations of body weight at tagging with body weight at sampling and
457 harvest were of medium magnitude (0.38 to 0.49), while it was very high between body
458 weight at sampling and harvest (0.98). These results show that selection for increasing
459 harvest body weight will result in correlated genetic response of early growth; and
460 moreover that although selection for increased growth rate ideally should take place close
461 to desirable market size of fish, it is not that critical as to when this recording is done.
462
463 Most of the estimates reported in literature showed the same magnitude of genetic
464 correlation between body weights recorded at different ages as in our study (for example,
465 0.80 to 0.98 for common carp by Ninh et al., 2011; 0.87 for grass carp by Fu et al., 2016;

466 0.61 to 0.85 for sea bass by Saillant et al., 2006). An exception is in the common carp study
467 by Nielsen et al. (2010), reporting relatively low genetic correlations (-0.54 to 0.47) for
468 body weights recorded across different seasons, except for a correlation close to unity
469 (0.98) between body weight at first autumn and second spring. The authors concluded that
470 the low genetic correlations could be due to different water temperature during summer and
471 winter.
472
473 The very high genetic correlation between harvest body weight in mono- and polyculture
474 ponds (0.96 ± 0.07) clearly demonstrates that the families rank very similar for growth in
475 the two production systems, and that genotype by production system interaction for growth
476 in rohu is negligible. Consequently, in a selective breeding program for rohu with the
477 objective to serve both production systems, the breeding candidates can be selected for
478 growth based growth performance recorded in monoculture ponds, which requires less
479 pond testing area than in polyculture ponds. This finding is supported by earlier reports
480 from this project, which showed a high estimated correlation (0.89) between the additive
481 genetic performance of pure stocks and stock crosses of rohu for harvest body weight in
482 mono- and polyculture ponds (Gjerde et al., 2002), and a negligible rohu stock by mono-
483 vs. polyculture ponds interaction (< 1% of the total variation) for harvest body weight
484 (Reddy et al., 2002). However, for survival until harvest the magnitude of the genetic
485 correlation (0.55) indicated a substantial genotype by production system interaction. To our
486 knowledge, these are the first estimates of the magnitude of genotype by mono- vs.
487 polyculture interaction for a trait in aquaculture species.
488
489 The genetic correlations of survival until harvest with the three body weight traits were all
490 low, which suggest that selection for growth rate only will produce a marginal favorable

491 correlated response in survival. Consequently, for genetic improvement of survival in rohu,
492 the trait must be directly selected for.
493
494 **5. Conclusion**
495 This study demonstrates significant genetic variation for growth in rohu, and a negligible
496 genotype by production system interaction for the trait. Consequently, selection for growth
497 rate based on growth data recorded in either system will produce genetic gain for growth
498 also in the other system. As testing in polyculture is more demanding both with respect to
499 management and required pond area, testing the fish in monoculture is recommended. For
500 improved selection accuracy and selection response for growth, high c^2 effect for harvest
501 body weight as documented in this study must be reduced by improved measures to
502 standardize the rearing environment during the period of separate rearing of the families,
503 or alternatively by pooling a random sample of the fry from each family shortly after
504 hatching and subsequently recover pedigree by parental assignment by use of genetic
505 markers.
506
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629 Table 1. Number of sires and dams used to produce the eight different year-classes, and the
630 number of fish stocked and harvested. Year-class 1998 families could not be produced because
631 of drought.
632

Generation	Population	Year-class	Production date	No. of sires	No. of dams	Progeny	
						Tagged	Harvested
0	1	1993	13.07 - 21.07	**57**[1]	20	3021	1547
0	2	1994	11.07 - 06.08	37	**57**	2896	2625
1	1	1995	28.07 – 04.08	**42**	26	1802	1394
1	2	1996	18.07 – 01.08	37	**55**	2594	1425
2	1	1997	13.07 – 30.07	31	**40**	2021	1407
3	1	1999	12.07 – 30.07	- [2]		918	373
3	2	2000	13.07 – 01.08	**54**	30	1538	575
4	1	2001	17.07 – 04.08	**53**	29	1928	1352
Total				311	257	16718	10698

633 [1] Bolded figures represent the number of full-sib families produced in each year-class; total number of full-sib
634 families produced over eight year-classes was 358.
635 [2] Due to super cyclone in 1999, with high water levels in the nursery ponds, neighboring full-sib families were
636 mixed.

Table 2. Descriptive statistics for body weight (g) at tagging (6 months of age), sampling (14 months of age), harvest (20 months of age) and survival from tagging until harvest for each year-class in replicated mono- (M) and polyculture (P) ponds at CIFA.

Year-class	Pond	Tagging			Sampling			Harvest			Survival (%)
		N	Mean	CV (%)	N	Mean	CV (%)	N	Mean	CV (%)	
1993	M-1	513	17.7	50.0	332	192	28.9	395	397	26.2	77.0
	M-2	513	11.4	41.4	160	300	19.4	180	529	19.9	35.1
	M-3	513	11.2	40.5	107	529	19.9	109	902	15.8	21.2
	P-1	741	11.5	45.0	221	103	61.3	556	213	38.3	75.0
	P-2	741	11.8	45.6	139	151	43.4	307	351	24.0	41.4
1994	M-1	513	31.7	52.6	390	304	22.2	482	401	27.3	94.0
	M-2	509	32.6	52.5	355	181	28.1	482	322	23.7	94.7
	M-3	513	32.6	56.6	437	207	27.0	484	311	27.8	94.3
	P-1	684	30.1	45.3	133	267	34.5	572	360	36.9	83.6
	P-2	677	31.1	49.8	295	167	41.5	605	213	44.9	89.4
1995	M-1	306	25.1	65.4	206	178	35.3	245	302	31.9	80.1
	M-2	308	24.7	64.6	192	167	32.9	263	290	28.0	85.4
	M-3	308	24.9	65.6	228	180	26.5	290	336	25.5	94.2
	P-1	440	24.2	69.0	109	147	40.2	270	236	41.1	61.4
	P-2	440	24.2	63.5	130	244	29.7	326	396	26.2	74.1
1996	M-1	434	18.3	63.0	167	270	28.7	262	384	26.9	60.4
	M-2	434	18.3	63.4	143	368	20.1	194	512	20.1	44.7
	M-3	433	18.4	61.7	108	245	29.8	299	349	25.2	69.1
	P-1	646	19.1	61.4	179	350	43.6	373	469	42.1	57.7
	P-2	647	19.0	59.3	188	396	24.1	297	512	22.4	45.9
1997	M-1	361	24.6	81.4	170	211	51.1	287	442	43.3	79.5
	M-2	364	24.8	85.3	-	-	-	193	868	29.5	53.0
	M-3	363	25.3	84.1	-	-	-	277	568	30.5	76.3
	P-1	464	25.9	83.7	-	-	-	306	664	19.9	65.9
	P-2	469	24.9	80.6	-	-	-	344	394	28.1	73.3
1999[2]	M1	460	18.2	47.7	-	-	-	189	705	19.2	41.1
	M2	458	17.9	49.5	-	-	-	184	742	24.5	40.2
2000	M-1	510	16.6	65.6	188	185	43.9	203	313	41.8	39.8
	M-2	514	16.6	68.1	-	-	-	159	235	58.9	30.9
	M-3	514	16.7	70.6	-	-	-	213	298	24.4	41.4
2001	M-1	639	27.5	86.3	189	166	71.7	378	339	58.3	59.2
	M-2	645	27.5	88.6	331	190	59.8	463	388	54.4	71.8
	M-3	644	27.9	86.2	315	230	37.0	511	401	30.1	79.3

Table 3. Estimates of heritabilities (h^2) and effect common to full-sibs (c^2) with its standard error (s.e.) for body weight at tagging for each of the seven year-classes and across all of them, obtained from Model 1.

Year-class	h^2 ± s.e.	c^2 ± s.e.
1993	0.64 ± 0.37	0.22 ± 0.16
1994	0.07 ± 0.82	0.69 ± 0.41
1995	0.16 ± 0.44	0.57 ± 0.22
1996	0.31 ± ne	0.69 ± ne
1997	0.00 ± 0.00	0.88 ± 0.02
2000	0.26 ± 0.09	0.74 ± 0.09
2001	0.04 ± ne	0.96 ± ne
All	0.00 ± 0.04	0.78 ± 0.03

ne = not estimable

Table 4. Estimates of heritability (h^2) and of the effect common to full-sibs (c^2) with its standard error (s.e.) for body weight at harvest (Model 2) and survival until harvest (Model 3) within production system, and of the genetic (r_g) and effect common to full-sibs (r_c) correlations between the same trait in mono- and polyculture systems.

Trait	Parameter	Monoculture	Polyculture
Body weight at harvest	h^2	0.10 ± 0.03	0.10 ± 0.04
	c^2	0.26 ± 0.04	0.31 ± 0.05
	r_g	0.96 ± 0.07	
	r_c	0.73 ± 0.06	
Survival until harvest	h^2	0.10 ± 0.05	0.21 ± 0.07
	c^2	0.12 ± 0.03	0.06 ± 0.03
	r_g	0.55 ± 0.24	
	r_c	0.82 ± 0.20	

Table 5. Estimates of heritability (h^2) and of the effect common to full-sibs (c^2) with its standard error (s.e.) for survival until harvest and for body weight (Bw) at tagging, sampling and harvest, across mono- and polyculture ponds (Model 4).

Trait	h^2 ± se	c^2 ± se
Survival until harvest	0.14 ± 0.05	0.08 ± 0.02
Bw at tagging	0.22 ± 0.15	0.66 ± 0.07
Bw at sampling	0.38 ± 0.11	0.28 ± 0.05
Bw at harvest	0.34 ± 0.10	0.23 ± 0.04

8

Table 6. Estimates of genetic (above diagonal) with its standard error (± s.e.) and residual (below diagonal) correlations between survival from tagging until harvest, body weight (Bw) at tagging, at sampling and harvest, across mono- and polyculture ponds (Model 4).

Trait	Survival	Bw at tagging	Bw at sampling	Bw at harvest
Survival	-	0.03 ± 0.38	0.11 ± 0.23	0.19 ± 0.22
Bw at tagging	0.08	-	0.46 ± 0.25	0.38 ± 0.27
Bw at sampling	0.04	0.59	-	0.98 ± 0.01
Bw at harvest	0.04	0.52	0.88	-

(A)

(B)

(C)

Figure 1. Hatching hapas (A), nursery ponds (B) and an indoor fiberglass jar and collection hapa (C).