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Heritability estimates for growth-related traits using microsatellite parentage assignment in  
juvenile common carp (*Cyprinus carpio* L.)

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## Abstract

Common carp is one of the leading species in world aquaculture, but selective breeding for growth rate has not been actively pursued in this species after unsuccessful selection experiments. We estimated heritability for growth-related traits at 8 weeks of age in Hungarian Synthetic Mirror carp at Vodnany (Czech Republic). Parentage assignment with eight microsatellite markers was used in a full factorial cross of 10 dams x 24 sires. Out of 550 offspring, 95.3 % could be assigned to a single parental pair. Animal model heritability estimates were  $0.34 \pm 0.08$  for weight and length, and  $0.37 \pm 0.08$  for Fulton's condition factor ( $K$ ). Maternal effects and dominance were not significantly different from zero. The genetic correlation between weight and length was 0.98, and negative correlations were found between  $K$  and length (-0.36) and  $K$  and weight (-0.16). It is concluded that selective breeding for increased weight gain can be successful in carp, using indirect selection for length. However, the facts that heritability was estimated at 8 weeks of age and not at harvest weight, as well as a possible amplification of additive variance by competition are limitations to the applicability of the present results.

**Keywords :** common carp, *Cyprinus carpio*, heritability, dominance, maternal effects, growth, genetic correlations, parentage assignment, microsatellites.

## 1. Introduction

Common carp (*Cyprinus carpio* L.) is undoubtedly one of the most cultured fish all over the world, especially in Asia and Central and Eastern Europe. Its annual world-wide production increased from 1 million tonnes in 1991 to 2.7 million tonnes in 2000, which is more than twice the production of all salmonids (FAO 2002). This species is mostly reared in ponds with extensive or intensive management, where at least part of the diet consists of natural food. While procedures to ensure the best conditions for growth are well-known, much remains unknown about the genetic potential of this species.

Although carp was one of the first domesticated fishes (Balon, 1995) and we could assume that it has undergone empirical selective breeding for centuries, quite little is known and documented about this topic in the scientific literature (Vandeputte, 2003). Indeed, the genetic improvement of quantitative traits in carp has been achieved mostly through cross-breeding of strains (Bialowas, 1991; Bakos and Gorda, 1995; Gross and Wohlfarth, 1994; Linhart et al., 2002; Wohlfarth et al., 1987 and Wohlfarth, 1993), while selective breeding showed no effect on genetic improvement of growth (Moav and Wohlfarth, 1976). Hulata (1995) claims that most cultivated carp are not from selected lines.

To assess the utility of selective breeding for growth related traits in common carp, the heritability of those traits has to be known. According to existing data, the heritability is low or intermediate (0.3 or less), but the reliability of most existing heritability estimates in carp is quite low due to confounding with environmental effects or small numbers of breeders used in all experiments (Vandeputte, 2003 for a review).

Selective breeding of carp will have to rely on simple and relatively cheap methods, as many carp-rearing countries cannot afford expensive selective breeding programmes. It has been shown recently on brown trout (*Salmo trutta* L.) that selective breeding by an improved mass selection methodology could yield considerable weight gain (up to 25% per generation,

Vandeputte et al., 2002b). For assessing the possible extension of this method to common carp, a better knowledge of genetic parameters is needed. The recent development of microsatellite markers for common carp (Croijmans et al, 1997) provides the opportunity to identify the familial origin of any individual in a group of common carp, provided that DNA samples of the individual and its parents are available (e.g. Estoup et al., 1998; Fishback et al., 2002). Identification of genealogies may allow the precise estimation of the genetic parameters within strains, using factorial designs which allow the separation of additive, dominance and maternal components of variance (Becker, 1984; Vandeputte et al., 2001) without environmental bias (as all genotypes can be mixed just after fertilization). Although the methods used here to estimate genetic parameters are quite expensive, the information they provide can then be used in simple mass selection programs, which could be applied almost everywhere.

The aim of this study was to estimate the efficiency of microsatellite parentage assignment, the family representation for offspring in a factorial cross, and genetic parameter estimates for growth - related traits in juvenile common carp.

## 2. Materials and Methods

### *2.1. Establishment of broodstock and spawning*

The reproduction and culture of common carp was carried out at the Department of Fish Genetics and Breeding, RIFCH, University of South Bohemia at Vodnany in the Czech Republic. A Hungarian Synthetic Mirror strain (HSM) was imported to the Czech Republic during 1975-1985 (Linhart et al., 2002). F<sub>5</sub> individuals from this strain (15 females and 24 males) were chosen for reproduction during 1997. Five-year-old broodstock of HSM taken from breeding ponds in April were stored in two ponds of 0.2 ha separated by sex. Broodfish suitable for stripping were selected in May and kept separately at a hatchery in 4 m<sup>3</sup> tanks with water flow rate of 0.2 l s<sup>-1</sup>, temperature of 18-22 °C and 6-7 mg l<sup>-1</sup> O<sub>2</sub>. Twenty-four HSM sires were injected with a solution of dried carp pituitary at 1 mg kg<sup>-1</sup>, 24 h before stripping at 21 °C. Milt was collected individually from each sire, kept in thin layer in cell culture vessels under aerobic conditions at 0°C for 24 h before fertilisation (Linhart et al., 2003). Twenty-eight dams were randomly divided into 2 groups of 10 and 18 fish and injected twice with dried carp pituitary (0.4 mg kg<sup>-1</sup> and 2.1 mg kg<sup>-1</sup>, 24 h and 12 h before stripping, respectively) at 4 h interval. In each injection group, the dams were checked every 3 hours after the second injection for ovulation, stripped into separate dishes and the best spawns were selected based on visual inspection of egg quality and quantity. Ova were stored in aerobic conditions at 17-19 °C for 2-4 h prior to artificial insemination (Rothbard et al., 1996)

From each of the parents used in the cross, a fin sample was collected and stored in 90% ethanol at room temperature for further genotyping. For each female used, three batches of approximately 0.3 g (around 200 eggs) of unfertilised eggs were weighed to the nearest 0.0001 g. Once weighed, each batch was fixed in 4 % formaldehyde for later counting of eggs number and then calculation of mean egg weight.

## ***2. 2. A factorial design to produce experimental fish***

A full factorial cross (24 sires X 10 dams) was made as follows:

When 3 or 4 good quality spawns were simultaneously available, 50-200 g of eggs per dam (depending on the available amount of eggs for each dam) were pooled into one dish. From each dish, 24 batches of 15g of eggs were taken. Each fifteen-gram batch of eggs was placed into a dish of 50 ml; 500 µl sperm from one sire were added for individual fertilisation. Then the 24 dishes were placed on an orbital agitator with constant 200 rpm rotation speed with deflection 10 mm, and 4 ml of 22°C dechlorinated tap water were added (Linhart et al., 2003). After 1 minute, the twenty-four 15g batches from a given pool of 3-4 dams were grouped in one 360 g batch and egg stickiness was eliminated for 60 minutes in a solution of 33 g l<sup>-1</sup> half fat content milk powder. Each batch was then incubated in one Zuger jar for 4 days at 19-20°C. This operation was repeated three times, producing 3 pools of fertilised eggs in 3 separate jars. Pool 1 represented 3 dams (200 g of eggs from each), pool 2 represented 4 dams (130, 130, 75 and 50 g of eggs), and pool 3 represented 3 dams (130 g of eggs from each).

## ***2.3. Rearing of experimental fish***

At hatching, fry from each jar were kept separately in resorption trays at 19-20°C for 5 days until the beginning of exogenous feeding.

For on-growing to 8 weeks, 3 nursery ponds of 1600 m<sup>2</sup> were used, each being stocked with 16,000 larvae from one of the resorption trays. Pond 42 had the progeny from pool 1, pond 41 from pool 2 and pond 40 from pool 3. Fish grew up to 3 weeks of age on natural food and then were additionally fed on a commercial carp diet KP1, as is typical in the Czech Republic, using standard feeding ratios according to the estimated quantity of zooplankton.

At 8 weeks of age, the ponds were drained, all the fish were counted, and a random sample of 250 fish was taken from each pond, except in pond 40 where only 220 fish were

sampled. These fish were weighed to the nearest 0.01 g, and measured for length (from the tip of the nose to the end of the caudal peduncle) to the nearest mm. Fulton's coefficient of condition ( $K=W/L^3$ ) was calculated for each fish. A fin sample was collected from each fish and stored in 90 % ethanol for further genotyping.

#### 2.4. Parentage assignment

DNA extraction was performed as follows: a small piece of fin was incubated under continuous agitation at 55°C for 12 hours in 250 µl TNES-Urea extraction buffer (10 mM Tris-HCl pH8, 0.3M NaCl, 10mM EDTA, 1% SDS, 4M Urea) with 10 µl proteinase K. This mixture was then strongly agitated for 5 minutes after addition of 250 µl phenol, then centrifuged for 15 min (10,000 rpm, 15°C). The supernatant (200 µl) was collected and DNA was precipitated with 500 µl ethanol and 20µl 3M sodium acetate. After centrifugation (20 min, 10,000 rpm, 4 °C) ethanol was discarded and the DNA pellet was washed with 750 µl of 70% ethanol, then centrifuged (12 min, 10,000 rpm, 4°C). Ethanol was discarded, the pellet was vacuum-dried, and then re-suspended in 200 µl water at room temperature overnight. DNA concentrations were estimated using a fluorometer at 260 nm OD, and then samples were diluted to a working concentration of 200 ng/µl. Samples were then stored at -20°C.

Due to bad preservation, probably caused by a low quality of one batch of ethanol used for the sample collection, 85 out of 250 samples were not recovered in ponds 41 and 42 (insufficient quality of DNA for microsatellite amplification). Altogether, 550 offspring gave good DNA quality (220 from pond 40, 165 from pond 41, 165 from pond 42). DNA from all parents (24 sires, 10 dams) was also available.

Microsatellite DNA markers described by Crooijmans et al (1997) were used. Seven of them were selected for genotyping (*MFW16*, *MFW26*, *MFW7*, *MFW11*, *MFW18*, *MFW9*, *MFW3*),



1 and were labelled with TAMRA or 6-FAM fluorochromes. PCR conditions were as described  
2 in Crooijmans et al (1997) except for the use of 25 amplification cycles and a final elongation  
3 step of 5 minutes at 72°C. PCR products were electrophoresed through a 7M Urea, 8% 29:1  
4 acrylamide/bisacrylamide gel, and alleles were detected using a fluorescence scanner (FM-  
5 BIO II, Hitachi).

6 All individuals were genotyped for the seven microsatellites. For 48 individuals however, an  
7 eighth microsatellite (*MFW20*) was needed to achieve assignment to a single pair.

8 Parentage assignment was performed by exclusion using a program developed at INRA Fish  
9 Genetics Laboratory with Visual Basic for Microsoft Excel. Due to the structure of data  
10 (dams nested within ponds), some pond\*dam combinations could not occur, and individuals  
11 for which one single “impossible” dam was found were excluded from the analysis. On the  
12 other way, some individuals for which two couples with two different dams were possible  
13 could be assigned to a single couple, excluding the couple with the “impossible” dam.

## 14 ***2.5. Statistical analyses***

15 Due to the nature of the cross, males were expected to be equally represented in the progeny  
16 from all three ponds. The number of observed progeny per male was therefore compared to a  
17 uniform distribution with a chi-square test. In each pond, three to four females were supposed  
18 to be represented. Theoretical proportions of offspring per female were generated using the  
19 weight of eggs from each female in the corresponding pool, as well as the mean weight of  
20 individual eggs from each female, to yield an estimation of the total eggs number from each  
21 female in each pool of eggs. Observed numbers of progeny per female were compared to  
22 these theoretical numbers using a chi-square test.

23 Due to the small value of expected frequencies (lower than 5 in most cases) for each full-sib  
24 family, homogeneity of the number of offspring per full-sib family could not be tested using a

chi-square test. It was tested using Monte Carlo Markov Chain (MCMC) estimates of the likelihood ratio chi-square (SAS® Proc Freq).

For discussing the effects of family sizes, the effective genetic size of the population ( $N_e$ ) was calculated. The basic formula used was :

$$N_e = \frac{4(N-2)}{\left(K_s + \frac{V_s}{K_s}\right) + \left(K_d + \frac{V_d}{K_d}\right) - 2}$$

with  $N$  the offspring sample size,  $K_s$  and  $K_d$  the mean numbers of offspring per sire and per dam, and  $V_s$  and  $V_d$  the variances of  $K_s$  and  $K_d$ . Under the assumption of random family samples within equal family sizes (Poisson distribution) and large offspring sample ( $N > 50$ ),  $N_e$  was calculated with the classical simplified formula:

$$N_e = \frac{4N_s N_d}{N_s + N_d}$$

with  $N_s$  the number of sires, and  $N_d$  the number of dams.

For the progeny of each female, a survival index was calculated using the observed survival in each pond and the observed number of offspring from the given female in this pond :

$$SI_{j(i)} = S_i FP_{j(i)} / IP_{j(i)}$$

Where  $S_{j(i)}$  is the survival index of dam  $j$  in pond  $i$ ,  $S_i$  is the survival in pond  $i$ ,  $FP_{j(i)}$  is the final proportion of offspring from female  $j$  in the sample of offspring from pond  $i$ , and  $IP_{j(i)}$  is the initial proportion of the eggs of female  $j$  in the pool of eggs used for pond  $i$ . This survival index was used in a covariance analysis (SAS Proc Glim, Type III SS) with the following model:

$$Y_{ij} = \mu + P_i + a.c_{j(i)} + e_{ij} \quad (1)$$

where  $Y_{ij}$  is the survival index of dam  $j$  in pond  $i$ ,  $\mu$  is the population mean,  $P_i$  is the fixed effect of pond  $i$ ,  $c_{j(i)}$  is the covariate for dam  $j$  in pond  $i$  (covariates tested were mean individual weight of eggs from the dam, and time of ova storage from stripping to

fertilisation),  $a$  is the regression coefficient of survival on covariate and  $e_{ij}$  is the random residual.

For variance component estimation, the following model was used :

$$Y_{ijkl} = \mu + P_i + s_j + d_{k(i)} + sd_{jk(i)} + e_{ijkl} \quad (2)$$

where  $Y_{ijkl}$  is the performance (weight, length, K) of the individual considered,  $\mu$  is the population mean,  $P_i$  is the fixed effect of pond  $i$ ,  $s_j$  is the random effect of sire  $j$ ,  $d_{k(i)}$  is the random effect of dam  $k$  within pond  $i$ ,  $sd_{jk(i)}$  is the random sire\*dam interaction and  $e_{ijkl}$  is the random residual. This model was adjusted with SAS® Proc Mixed (REML).

This model allowed the estimation of all the variance components:  $\sigma_s^2$  the sire component,  $\sigma_d^2$  the dam component,  $\sigma_{sd}^2$  the sire\*dam interaction component, and  $\sigma_e^2$  the residual component.

Sire heritability was estimated as  $h_s^2 = 4\sigma_s^2 / (\sigma_s^2 + \sigma_d^2 + \sigma_{sd}^2 + \sigma_e^2)$ , dominance ratio as

$d^2 = 4\sigma_{sd}^2 / (\sigma_s^2 + \sigma_d^2 + \sigma_{sd}^2 + \sigma_e^2)$  and global (genetic + environmental) maternal effects ratio as

$m^2 = (\sigma_d^2 - \sigma_s^2) / (\sigma_s^2 + \sigma_d^2 + \sigma_{sd}^2 + \sigma_e^2)$ , and their standard errors approximated as done by Becker (1984) :

$$S.E.(h_s^2) \cong 4 \frac{\sqrt{\text{var}(\sigma_s^2)}}{\sigma_s^2 + \sigma_d^2 + \sigma_{sd}^2 + \sigma_e^2} \quad S.E.(d^2) \cong 4 \frac{\sqrt{\text{var}(\sigma_{sd}^2)}}{\sigma_s^2 + \sigma_d^2 + \sigma_{sd}^2 + \sigma_e^2}$$

$$S.E.(m^2) \cong \frac{\sqrt{\text{var}(\sigma_d^2) + \text{var}(\sigma_s^2)}}{\sigma_s^2 + \sigma_d^2 + \sigma_{sd}^2 + \sigma_e^2}$$

Additionally, single and multiple trait animal models were optimised with VCE4 (Groeneveld, 1998) for estimating heritabilities and global maternal effects (single trait models) as well as genetic correlations between traits (multiple trait model). The general form of these models was as follows :

$$y = Xb + Za + Wm + e \quad (3)$$

where  $y$  is the vector of observed performances,  $b$  is the vector of fixed effects (ponds),  $a$  is the vector of additive genetic values,  $m$  is the vector of maternal effects and  $e$  is the vector of

1 errors.  $X$ ,  $Z$  and  $W$  are known incidence matrices. No standard errors were available for  
2 genetic correlations. Animal models were used as they give better precision for heritability,  
3 and provide direct estimations of genetic correlations. However, the software used does not  
4 allow the estimation of dominance effects, and the sire-dam model with interaction (model 2)  
5 was used therefore.

6

### 3. Results

#### 3.1. Rearing parameters

Egg sizes were quite variable among dams, with a mean egg weight of 1.24 mg, a minimum of 0.97 mg and a maximum of 1.61 mg. On average, the fertilisation rate was 85% in each of the three pools, and the hatching rate was 75%. At 8 weeks post-resorption, the mean length of the juveniles was 54 mm (55, 53, 54 in ponds 40, 41, 42, respectively) and their mean weight was 5.51 g (5.80, 5.18, 5.56 in ponds 40, 41, 42, respectively). The mean coefficient of variation was 11% for length and 29% for weight. Mean survival was 61% (56%, 69%, 59% in ponds 40, 41, 42, respectively).

#### 3.2. Parentage assignment

550 individuals were available for parentage assignment, of which 518 could be assigned directly to a single parental pair (Table 1). Two individuals, however, were considered as not assigned as the dam identified should have had no offspring in their pond of origin. Similarly, 24 individuals were assigned to two parental pairs, and 8 of those were considered assigned to one pair as one of the two dams identified was not supposed to have any offspring in the given pond. Altogether, 95.3 % of the offspring could be assigned to a single parental pair, 3.1 % to more than one pair and 1.6 % could not be assigned. For variance component estimation, the two offspring of dam 4 were removed from the analysis as they notably perturbed the estimation of maternal effects, so only 522 individuals were used.

#### 3.3. Differential family representations

The representation of the offspring in the different families is given in Table 2. The observed numbers of offspring per sire were different from the expected numbers ( $\chi^2=45.9$ , 23 d.f.,  $P<0.01$ ). However, two males (7 and 23) had an important contribution to the chi-square, and there was no more representation distortion when they were removed from the analysis ( $\chi^2=29.2$ , 21 d.f.,  $P>0.1$ ). Representation of dams was tested within ponds. Within pond 40

(dams 1, 2, 3) there was a large distortion of dam representation ( $\chi^2=24.3$ , 2 *d.f.*,  $P<0.001$ ).

The same was seen for dams 4 to 7 in pond 41 ( $\chi^2=127$ , 3 *d.f.*,  $P<0.001$ ). In this case, it has to be noted that dam 7 gave no offspring in the sample, and dam 4 gave only 2 offspring.

Removing these two dams, the contributions from the two remaining ones were in the expected proportions ( $\chi^2=2.3$ , 1 *d.f.*,  $P>0.3$ ). In pond 42, the observed frequencies per dam also differed from their expectations, but to a lesser extent ( $\chi^2=8.7$ , 2 *d.f.*,  $P<0.05$ ). The MCMC estimate of the likelihood ratio chi-square for homogeneity was not significant ( $P>0.1$ ), showing an independent effect of sire and dam on the full-sib family survival. Covariance analysis on dam offspring survival showed no effect of the covariates on the survival index ( $P>0.5$  for egg weight,  $P>0.8$  for ova storage time).

### **3.4. Genetic parameters**

The fixed effect of pond was not significant in model 2 ( $P>0.36$  for weight,  $P>0.50$  for length and  $P>0.43$  for  $K$ ).

Genetic parameters for weight, length and Fulton's coefficient ( $K$ ) are shown in Table 3.

Heritability estimates were significantly different from zero for all three traits studied, and all fall in the 0.3-0.4 range. Estimates derived from animal model were more precise (standard error divided by two) than those derived from sire-dam model with interaction. Maternal effects for all three traits did not significantly differ from zero. Dominance ratio estimations were positive (although not significantly different from zero) for weight and length and null for Fulton's coefficient. Multi-trait animal model heritabilities, genetic and phenotypic correlations are shown in Table 4. Heritability estimates were slightly lower than with single trait animal model for weight and length, and similar for  $K$ . The genetic correlation between length and weight was very high (0.976), and negative genetic correlations could be observed between  $K$  and length (-0.364) or weight (-0.159). Phenotypic correlations were quite comparable to genetic correlations, although showing a lower absolute value.

## **4. Discussion**

### ***4.1. Rearing parameters***

The quality of rearing was very satisfactory, with a good homogeneity between ponds for survival and growth rates. Hatching rates were as high as normal standards, despite the manipulations of the eggs (pooling, individual fertilisations). This shows that this type of factorial cross is practically applicable in a hatchery with good technical competence.

### ***4.2. Parentage assignment***

The efficiency of parentage assignment (>95 % for a 10 X 24 factorial cross) was very high, with eight markers used. In other species, eight microsatellites have the theoretical capability of assigning 95% or more of the offspring to the right parents in a 140 X 140 factorial cross in turbot, and in a 34 X 34 factorial in rainbow trout (Estoup et al., 1998). The microsatellites in this theoretical study had a mean number of 14.1 alleles in turbot, and 8.4 and in rainbow trout. In our case, the mean number of alleles in the population is 7.75 for the eight microsatellites, so the expected performances are supposed to be a little below those in rainbow trout. Practically in rainbow trout, 14 multiplexed microsatellites allowed 91-95% assignment of the progeny to one parental pair in a 48 X 2 factorial cross (Fishback et al., 2002), or 10 microsatellites allowed 90% assignation in two 2 X 46 factorial crosses (Chevassus et al., 2002). In this case, our results are quite comparable, but with more families (240 compared to 96 or 92) and fewer markers used. Microsatellite parentage assignment in carp can then be rated as very satisfactory.

### ***4.3. Differential survivals***

The “survivals” studied here are a combination of fertilisation rate, hatching rate and post-hatching survival, due to the mixing of families just after fertilisation. The pattern of differential survivals observed here is consistent with that seen in salmonid studies, with a small effect of sire and a large effect of dam. As in Herbinger et al. (1995), the effect of sires

on survival is only due to a very limited number of sires, and the effect of dams is very large. A large dam effect was also seen in Fishback et al. (2002) on rainbow trout, with 12 dams out of 48 (25%) giving no progeny. In our case, one dam (10%) gave no progeny, and one dam (10%) gave less than 1% of the offspring. There was a large effect of both sire and dam on differential survival in seabass (Garcia de Leon et al., 1998) and in Atlantic halibut (Jackson et al., 2003). Indeed, a dam effect on survival is usual in fish, and often is related to egg size (Bagenal, 1969; Beacham and Murray, 1985; Rana, 1985; Marteinsdottir and Able, 1992; Wallace and Aasjord, 1984). We see here that egg size had no effect on early survival, in accordance with recent results in salmonids (Jonsson and Svavarsson, 2000; Vandeputte et al., 2002a), and with the finding of Lahnsteiner et al. (2001) that egg size is not a good predictor of egg quality in carp. No effect of time of egg storage time from stripping to fertilisation was seen, in accordance with the results of Rothbard et al. (1996).

The relatively good equilibrium of family sizes implicates a significant but moderate reduction of the effective genetic size ( $N_e$ ) of the offspring sample. With the simple assumption that all 10 dams and all 24 sires participated equally in the production of juveniles, the expected  $N_e$  was 28.2, while the real  $N_e$ , taking into account the true variance in family size, was 22.3, a reduction of 21%. If we considered the expected variance in family size due to the initial known differences in egg numbers used from each dam, the theoretical  $N_e$  would have been 26.8, the reduction in  $N_e$  then being 17%. Then, we can conclude that using the type of controlled factorial mating described here, hatchery managers can rely on effective numbers of breeders 20 percent smaller than the ones they can calculate *a priori*.

This reduction is much smaller than what can occur in uncontrolled breeding schemes, especially natural or semi-natural reproduction, where  $N_e$  can be as low as 25 % of the number of breeders used (e.g. red sea bream, Perez-Enriquez et al., 1999).



#### 1    **4.4. Genetic parameters**

2    The heritability estimates obtained for growth rate were rather high (0.34-0.39). Nenashev  
3    (1966) and Nagy et al. (1980) found similar results ( $h^2=0.34-0.44$  and 0.48, respectively),  
4    however with experimental designs very likely to produce upward biased estimates. Other  
5    authors (Nenashev, 1969; Smisek, 1981; Tanck et al., 2001) found lower estimates, in the  
6    range 0-0.30. However, our estimate is the first one to be derived from more than 30 breeders  
7    without any evident source of bias, due to the factorial nature of the cross, and therefore this  
8    high value may be considered with confidence. With such values, one can expect significant  
9    selection gains (in the range of 20-25 % per generation following selection of the 2 % of  
10    heaviest fish). This is in contrast with the observations by Moav and Wohlfarth (1976), who  
11    saw no genetic gain during 5 generations of mass selection for growth rate in carp. However,  
12    it is quite likely that this last experiment was perturbed by the genetic composition of this  
13    particular population, and possibly also by high inbreeding, due to breeding beings done as  
14    mass spawnings, allowing a large under-representation of the breeders used. Still, the  
15    possibility that our HSM population may not respond to selection as well as theory predicts  
16    cannot be ruled out, especially if we consider that all families being reared communally in our  
17    experiment, some amplification of differences between families may occur due to  
18    competition. This amplification has been demonstrated for carp strains by Moav and  
19    Wohlfarth (1974) who showed that the variance between strains means was almost four times  
20    higher when carp strains were reared communally instead of separately. Nevertheless, as the  
21    normal management of strains is to be reared separately, the normal management of families  
22    in an outbred population is to be reared communally, so, hopefully, realized heritability  
23    should not be four times less than our estimated heritability. However, a definitive answer to  
24    this question will only be possible through the achievement of an experimental selective  
25    breeding programme on the HSM strain.

One limitation of our present work is the fact that genetic parameters are estimated only at 8 weeks of age, and their validity for growth to harvest is questionable. Although we do not know formal estimations of genetic correlations between early growth and harvest size in carp, we can remark that the ranking of 3 strains is the same at 5 weeks and 2 summers in Vandeputte et al. 2002c, although the differences are not significant. The rankings also do not change between juvenile and adult crossbreds in the 1982, 83 and 84 experiments reported in Wohlfarth 1993, and a positive correlation between the growth of strains at 1 summer and 3 summers can be seen in Linhart et al 2002. Altogether, these results tend to show that a genetic correlation exists between early and late growth in common carp, and so our results should also at least partially apply for later growth.

Regarding the shape of the fish (Fulton's  $K$ ), the heritability was high (0.37-0.41), in accordance with the results of Ankorion et al. (1992) who found a realized heritability of 0.47 upwards and 0.33 downwards for another measure of shape (Height/Length ratio). This confirms that shape may be easily selected for in common carp.

In our study, maternal effects were zero or close to zero. This result was quite unexpected, as it had been shown in the past that maternal effects were very strong on the early growth rate of carp (Hulata et al., 1976). In this last study, maternal effects were generated by maternal age (correlated to egg size) and differences in hatching time, and both showed marked effects on the growth performance of the fry. Here, as all families within the same pond were fertilized at the same time, only egg size was expected to have an effect, but none was seen, although some females have very different egg sizes (from 0.97 to 1.60 mg). However, the total number of degrees of freedom to estimate the maternal component of variance was low (5), due to the nesting of dams within ponds and to the (near) absence of offspring for two dams. Therefore, this result indicating no maternal effects should be taken cautiously, and needs confirmation. This information is very important because if maternal effects are known

1 to disappear quickly in salmonids when families are reared separately (Chevassus, 1976;  
2 McKay et al., 1986), this does not hold true when families are mixed from the egg stage  
3 (Chevassus et al., 2002), and this can interfere with the identification of the best individuals in  
4 mass selection procedures.

5 This study is the first one to propose an estimation of within-strain dominance variation in  
6 carp, and the values obtained are low (0.12 or less) and not significantly different from zero.

7 This is a little surprising, as exploitation of heterosis is widely used for crossbreeding of carps  
8 (see Hulata, 1995 for a review), and heterosis requires the existence of dominance variation.

9 However, the precision of the estimation is quite low, due to the disequilibrium in family  
10 sizes and the small size of full-sib families, which generates a lot of missing values (see Table  
11 2). The lack of within strain dominance variation may be a characteristic of the HSM stock,  
12 but would need confirmation, although it is much less important for practical within strain  
13 selective breeding than the level of maternal effects.

14 Our study also gives the first estimates of genetic correlations between growth-related traits in  
15 the common carp. The genetic correlation between length and weight is very close to unity  
16 (0.976) and the heritabilities of length and weight are similar, so selection on length (which is  
17 much easier to apply in the field) should give approximately the same results on weight as  
18 direct selection on weight. Interestingly, there is a negative correlation between length and  $K$   
19 (-0.36), so selection on length should produce heavier, but leaner fish, which might be an  
20 advantage for increasing fillet yield, although there is only a trend towards better fillet yields  
21 in leaner fish (Cibert et al., 1999, Vandeputte, unpublished data). Negative genetic  
22 correlations between length and  $K$  also exist in rainbow trout (Fishback et al., 2002), although  
23 to a lesser extent. More surprisingly, weight also has a negative, although smaller, correlation  
24 with  $K$  (-0.16), which is not seen in rainbow trout. In carp, it was traditionally speculated that  
25 a high height/length ( $H/L$ ) ratio (implying a high  $K$ ) would be positively correlated with

weight gain, and the traditional method for selecting broodstock in Europe was to keep the largest individuals with the highest  $H/L$  ratio (Hofmann, 1975 in Ankorion et al. 1992). Ankorion et al. (1992) found a negative association between weight and  $H/L$  ratio, but concluded it was probably not significant due to the small magnitude of the correlated responses. Our results are in the same direction as their finding, and then it seems quite probable that high-backed fish, which in many countries are preferred by the consumers, have a lower growth potential and should not be selected. It is valid especially if the objective is to market carp fillets, for which the high backed shape (triangular) has even a negative impact on consumer acceptance, at least in the Czech Republic.

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## Tables

**Table 1:** Overall success of parentage assignment for 550 offspring of 10 dams and 24 sires of common carp using 7 or 8 microsatellite markers.

	Number	Proportion
Assigned to a single parental pair	516	93.8 %
Assigned to one parental pair after inferences based on experimental design	8	1.5 %
<b>Total assigned to one single parental pair</b>	<b>524</b>	<b>95.3 %</b>
Assigned to 2 parental pairs	16	2.9 %
Assigned to 3 parental pairs	1	0.2 %
<b>Total assigned to more than one parental pair</b>	<b>17</b>	<b>3.1 %</b>
Not assigned	7	1.2 %
Assigned to an impossible pair after inferences based on experimental design	2	0.4 %
<b>Total not assigned</b>	<b>9</b>	<b>1.6 %</b>
<b>Total number of offspring</b>	<b>550</b>	<b>100 %</b>



Table 2: Number of offspring identified for each of the families generated in the full factorial cross

		Dam										Observed total per sire	Expected total per sire
		1	2	3	4	5	6	7	8	9	10		
Sire	1	3	2	1	-	3	2	-	1	3	3	18	21.8
	2	2	1	-	-	4	-	-	3	3	2	15	21.8
	3	2	3	4	1	6	2	-	5	3	2	28	21.8
	4	6	4	4	-	3	4	-	5	-	3	29	21.8
	5	6	-	2	-	-	2	-	5	2	2	19	21.8
	6	2	2	4	-	6	1	-	1	-	2	18	21.8
	7	8	4	5	-	4	5	-	2	5	3	36	21.8
	8	5	3	2	-	4	6	-	2	5	3	30	21.8
	9	5	1	2	-	2	6	-	3	3	-	22	21.8
	10	3	1	3	-	4	1	-	3	2	2	19	21.8
	11	-	3	6	-	2	3	-	1	-	4	19	21.8
	12	6	3	-	-	-	2	-	1	4	4	20	21.8
	13	6	2	4	-	5	3	-	1	1	2	24	21.8
	14	4	1	5	-	8	4	-	-	2	3	27	21.8
	15	2	2	5	-	7	-	-	1	3	2	22	21.8
	16	4	1	1	-	5	1	-	-	3	2	17	21.8
	17	3	4	2	-	4	6	-	1	1	2	23	21.8
	18	2	2	4	-	4	3	-	2	2	-	19	21.8
	19	2	1	3	-	5	2	-	2	1	-	16	21.8
	20	3	-	3	1	7	2	-	2	4	-	22	21.8
	21	7	1	3	-	9	2	-	6	3	2	33	21.8
	22	4	4	7	-	4	1	-	2	4	2	28	21.8
	23	1	-	-	-	1	1	-	2	4	-	9	21.8
	24	2	2	-	-	-	1	-	2	3	1	11	21.8
Observed total per dam		88	47	70	2	97	60	0	53	61	46	524	
Expected total per dam		59	74	72	51	59	28	21	50	47	63		

Table 3: Genetic parameter (heritability, maternal effects, dominance) estimates for weight, length and condition factor ( $K$ ) at 8 weeks post-resorption in common carp, using sire-dam model with interaction (Model 2) or single-trait animal model (Model 3). NE: not estimated

<b>Trait</b>	<b>Model</b>	<b><math>h^2 \pm \text{S.E.}</math></b>	<b><math>m^2 \pm \text{S.E.}</math></b>	<b><math>d^2 \pm \text{S.E.}</math></b>
Weight	sire-dam	$0.38 \pm 0.149$	$0.03 \pm 0.061$	$0.084 \pm 0.154$
	animal	$0.34 \pm 0.078$	0	NE
Length	sire-dam	$0.39 \pm 0.176$	$0.05 \pm 0.059$	$0.12 \pm 0.156$
	animal	$0.34 \pm 0.076$	0	NE
$K$ (Fulton)	sire-dam	$0.41 \pm 0.172$	$0.03 \pm 0.067$	0
	animal	$0.37 \pm 0.082$	0	NE

1 Table 4: Multi-trait animal model heritabilities (diagonal), genetic correlations (bold) and  
 2 phenotypic correlations (italics) for growth-related traits in 8 week-old common carp.

3

	Length	Weight	<i>K</i> (Fulton)
Length	0.318	<b>0.976</b>	<b>-0.364</b>
Weight	<i>0.965</i>	0.318	<b>-0.159</b>
<i>K</i> (Fulton)	<i>-0.228</i>	<i>-0.027</i>	0.364

4