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REVIEW

Quantitative genetic estimates of growth-related traits in the common carp (*Cyprinus carpio* L.): A review

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Abstract The common carp (*Cyrpinus carpio* L.) is the oldest cultured and the most domesticated fish species, as well as one of the most important freshwater fishes in the world. However, scientific studies on evaluating the growth-related quantitative traits in this fish are limited. Heritability, the most important parameter in selective breeding programs, was extensively studied for the growth-related traits. The values varied widely among the experiments and methods used because of the existence of common environmental, dominance and maternal effects. However, correlations in phenotypic and genetic levels first evaluated several years ago were limited. On the other hand, heterosis was widely reported and easily obtained for growth-related traits in the common carp. Meanwhile, genotype environment interaction and prediction of breeding values have been studied recently, and are very important in conducting selective breeding programs. The developmental quantitative genetics of growth-related traits was first analyzed in the common carp for reasonable selection during ontogeny. It is expected that genetic improvement will be achieved by carrying out direct selective breeding in the common carp.

Keywords *Cyprinus carpio* L., growth-related traits, heritability, correlation, heterosis

1 Introduction

The common carp (*Cyrpinus carpio* L.) is the oldest cultured and the most domesticated fish species in the world; it has been cultured for approximately 4000 years (Wohlfarth, 1993; Balon, 1995). Being one of the most important cultured species in the world, its total production reached 3.17 million tons in 2006 (FAO, 2006). Meanwhile, the common carp has developed numerous varieties through a combination of forces from geographic isolation, adaptation, accumulation of mutations, and natural, as well as human selection pressures (Hulata, 1995). The large number of strains or populations of the common carp provides a huge potential to breeders to study the quantitative genetics of growth-related traits for selective breeding and genetic improvement.

Despite its wide distribution and high importance in world aquaculture, very few selective breeding studies of the common carp were documented in the scientific literature, while most of the studies have been conducted empirically (Vandeputte, 2003). Subsequently, genetic analysis of the quantitative traits in the common carp has been poorly carried out, and many estimates of the genetic parameters for growth-related traits in the common carp remain to be studied. This review summarizes studies of the genetic parameters of growth-related traits in the common carp, evaluates the available information on heterosis and breeding potential of the common carp, and discusses the prospects of quantitative traits analysis of this species.

2 Heritability

Heritability is the most important genetic parameter in fish breeding programs and has been the most studied one. It is mathematically defined as the ratio of the heritable genetic variance to the total phenotypic variance. Heritability is classified as either broad sense or narrow sense heritability. Broad sense heritability is the ratio of the total genetic variance to the phenotypic variance, while narrow sense heritability is the ratio of the additive genetic variance to the phenotypic variance. Broad sense heritability contains dominance and epistatic effects that do not respond to selection and is not often used (Gjedrem, 2005). Heritability, particularly narrow sense heritability, has been considered as the primary genetic parameter in

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quantitative genetics. Estimates of heritability for growth-related traits are necessary in fish selection and breeding programs. Reliable estimates of heritability can provide very valuable information for determining reasonable breeding plans and for predicting selection response and breeding values of candidate traits.

A number of heritability estimates of growth-related traits in the common carp have been widely carried out (Table 1). However, as Vandeputte states in his review (2003), heritability estimates vary widely among experiments and methods used; for example, the heritability ranges from 0 to 0.71 for body weight and 0.01 to 0.80 for standard length. It is noteworthy that most estimates show moderate to high heritability, indicating that additive genetic variation exists in the growth-related traits and it is feasible to conduct selective breeding and obtain expected achievement in the common carp.

The estimation methods of heritability in the common carp include parent-offspring regression (Nenashev, 1966; Zhang et al., 1981), family analysis (Nenashev, 1966;

Table 1 Heritability estimates of growth-related traits at different stages by different designs and methods in the common carp

trait	age/size	design	h^2 (±S.D.)	method	references
weight	27 days	—	0.11	—	Poljarush and ovchenko(1979)*, Kirpichnikov(1999)*
	1 summer	nested (3D, 18S)	0.00±0.07	PO	Nenashev (1966)*
		nested (3D, 18S)	0.34±0.05	S	Nenashev (1966)*
		nested (3D, 18S)	0.44±0.11	D	Nenashev (1966)*
		factorial (3D, 3S)	0.48	S + D	Nagy et al. (1980)*
	2.5 months	—	0.40	PO	Zhang et al. (1981)
	fingerlings	nested(3D, 18S)	0.21	—	Nenashev (1969)*
	30–100 days gain	full-sibs(4D, 4S)	0.29 – 0.30	—	Smisek (1981)*
	110 days	33 androgenetic lines	0.09 (0.03 – 0.17)[a]	AM	Tanck et al. (2001)*
	13 months	5 gynogenetic lines	0.58 (0.23 – 1.00)[a]	AM	Bongers et al. (1997)*
	2 summers	nested (3D, 18S)	0.51±0.08	S	Nenashev (1966)*
		nested (3D, 18S)	0.22±0.07	D	Nenashev (1966)*
	harvest	realized h^2 (up)	< 0	5 gen	Moav and Wohlfarth (1976)*
		realized h^2 (down)	0.3	3 gen	Moav and Wohlfarth (1976)*
	—	realized h^2 (up)	0.20 – 0.29	2 gen	Tran and Nguyen (1993)*
	8 weeks	factorial (10D, 24S)	0.33±0.07	MP	Vandeputte et al. (2004)
	3 growing seasons	factorial (G0–G2; G0: 10D, 24S; G1: 8D, 147S)	0.70±0.08	MPa	Kocour et al. (2007)
	1 summer	factorial(G0–G3; G0: 10D, 24S; G1: 8D, 147S; G2: 8D, 96S)	0.32±0.03	MP	Vandeputte et al. (2008)
	spring		0.29±0.03	MP	Vandeputte et al. (2008)
	2 summers		0.46±0.04	MP	Vandeputte et al. (2008)
	8 months	nested (10S, 30D)	0.25±0.02	S	Wang et al. (2006c)
	20 months	nested (10S, 30D)	0.30±0.03	S	Wang et al. (2006c)
	8 months	diallel	0.10±0.01	MGM	Wang et al. (2006d)
	20 months	diallel	0.15±0.13	MGM	Wang et al. (2006d)
length	1 summer	nested (3D, 18S)	0.04±0.07	PO	Nenashev (1966)*
		nested (3D, 18S)	0.37±0.05	S	Nenashev (1966)*
		nested (3D, 18S)	0.21±0.06	D	Nenashev (1966)*
	2.5 months	—	0.80	PO	Zhang et al. (1981)
	fingerlings	nested (3D, 18S)	0.21	—	Nenashev (1969)*
	110 days	33 androgenetic lines	0.11 (0.04 – 0.21)[a]	AM	Tanck et al. (2001)*
	13 months	5 gynogenetic lines	0.50 (0.14 – 1.00)[a]	AM	Bongers et al. (1997)*
	2 summers	nested (3D, 18S)	0.55±0.08	S	Nenashev (1966)*

(*Continued*)

trait	age/size	design	h^2 (±S.D.)	method	references
		nested (3D, 18S)	0.18±0.06	D	Nenashev (1966)*
	8 weeks	factorial (10D, 24S)	0.33±0.08	MP	Vandeputte et al. (2004)
	3 growing seasons	factorial (G0–G2; G0: 10D, 24S; G1: 8D, 147S)	0.69±0.10	MP	Kocour et al. (2007)
	1 summer	factorial (G0–G3; G0: 10D, 24S; G1: 8D, 147S; G2: 8D, 96S)	0.20±0.03	MP	Vandeputte et al. (2008)
	spring		0.22±0.03	MP	Vandeputte et al. (2008)
	2 summers		0.28±0.04	MP	Vandeputte et al. (2008)
	8 months	nested (10S, 30D)	0.35±0.04	S	Wang et al. (2006c)
	20 months	nested (10S, 30D)	0.27±0.03	S	Wang et al. (2006c)
	8 months	diallel	0.01±0.00	MGM	Wang et al. (2006d)
	20 months	diallel	0.71±0.05	MGM	Wang et al. (2006d)
rel. body height	3 growing seasons	factorial (G0–G2; G0: 10D, 24S; G1: 8D, 147S)	0.32±0.06	MP	Kocour et al. (2007)
body height	8 months	nested (10S, 30D)	0.20±0.02	S	Wang et al. (2006c)
	20 months	nested (10S, 30D)	0.18±0.03	S	Wang et al. (2006c)
	8 months	diallel	0.56±0.03	MGM	Wang et al. (2006d)
	20 months	diallel	0.52±0.23	MGM	Wang et al. (2006d)
	2.5 months	—	0.44	PO	Zhang et al. (1981)
rel. body width	3 growing seasons	factorial (G0–G2; G0: 10D, 24S; G1: 8D, 147S)	0.15±0.05	MP	Kocour et al. (2007)
body width	8 months	nested (10S, 30D)	0.22±0.03	S	Wang et al. (2006c)
	20 months	nested (10S, 30D)	0.14±0.03	S	Wang et al. (2006c)
	8 months	diallel	0.33±0.03	MGM	Wang et al. (2006d)
	20 months	diallel	0.13±0.16	MGM	Wang et al. (2006d)
head length	8 months	diallel	0.09±0.10	MGM	Wang et al. (2006d)
rel. head length	3 growing seasons	factorial (G0–G2; G0: 10D, 24S; G1: 8D, 147S)	0.54±0.12	MP	Kocour et al. (2007)
caudal peduncle length	2.5 months	—	0.67	PO	Zhang et al. (1981)
	8 months	diallel	0.32±0.10	MGM	Wang et al. (2006d)
	20 months	diallel	0.71±0.02	MGM	Wang et al. (2006d)
caudal peduncle height	2.5 months	—	0.20	PO	Zhang et al. (1981)
	8 months	diallel	0.28±0.07	MGM	Wang et al. (2006d)
	20 months	diallel	0.38±0.26	MGM	Wang et al. (2006d)
K (Fulton)	8 weeks	factorial (10D, 24S)	0.37±0.07	MP	Vandeputte et al. (2004)
height/length ratio	1 summer	nested (3D, 18S)	0.25±0.09	PO	Nenashev (1966)*
		nested (3D, 18S)	0.42±0.06	S	Nenashev (1966)*
		nested (3D, 18S)	0	D	Nenashev (1966)*
	2 summers	nested (3D, 18S)	0.75±0.09	S	Nenashev (1966)*
		nested (3D, 18S)	0.11±0.05	D	Nenashev (1966)*
	harvest	realized h^2 (up)	0.47±0.06	1 gen	Ankorion et al. (1992)*
		realized h^2 (down)	0.33±0.10	1 gen	Ankorion et al. (1992)*

*: results cited from Vandeputte (2003); S: sire component; D: dam component; AM: animal model; PO: parent-offspring regression; MP: molecular pedigree; MGM: mixed genetic model.

Nagy et al., 1980; Wang et al., 2006c), animal model (Bongers et al., 1997; Tanck et al., 2001), and mixed genetic model (Wang et al., 2006d). The existing environmental effects cause bias in parent-offspring regression. For example, Zhang et al. (1981) first conducted a preliminary estimation of genetic parameters of growth traits of the common carp in China by analyzing the phenotypic variation of three generations of parents, F_1 and F_2. Because the environment has a great effect on different generations, and because genotype and environment interaction gives rise to a bias in estimation, there was an overestimation in the study (0.40 for weight and 0.80 for standard length). The family analysis through nested mating (sires nested within dams, or dams nested within sires) has often been used to estimate heritability; however, it is difficult to reduce the non-additive genetic effects (e.g., dominance, maternal, and common environmental effects). The animal models and mixed genetic models have been developed since the 1970 s and have been frequently used recently in fish breeding programs, because they could efficiently divide the phenotypic variation into additive, dominance, and maternal components. Furthermore, realized heritability evaluation was also occasionally used in the common carp (Ankorion et al., 1992). It is remarkable that molecular pedigree (e.g., microsatellite marker technology) has been recently used to evaluate the genetic parameters (Vandeputte et al., 2004, 2008; Kocour et al., 2007). This method is not influenced by common environmental effects and thus ensures the reliability of the genetic parameters evaluated.

3 Correlation

Correlation, which measures the relative magnitude of covariance between traits, has phenotypic and genetic levels. Genetic correlation, which demonstrates the heritable part in the phenotypic correlation, is also an important parameter in quantitative genetics analysis. The estimates of correlation can indicate changes in the traits that may not be used in selection when selection is practiced on candidate traits. In contrast to extensive evaluation in the heritability, correlation estimate was seldom conducted for the common carp. The first estimate of genetic correlation between weight and length in the common carp was reported in 2004 with a value of 0.98 (Vandeputte, 2004). From then on, the correlations of the growth-related traits in this species have been frequently estimated (Table 2). In general, the correlations between the body weight and length are high: 0.52–0.98 for genetic correlation, and 0.54–0.97 for phenotypic correlation. Moreover, the correlations among weight, height, and width are also relatively high, but widely varied. These results indicate that positive responses in weight can occur if the length, height, and width would be used as indirect breeding indices in practice.

In estimated methods, the recently used molecular markers, microsatellite for example, and pedigree data displayed higher genetic and phenotypic correlation estimates than the conventional methods, such as nested, factorial, and diallel cross design. The results from the low, or absence of environmental effects in the estimated methods were compared to the conventional methods.

4 Heterosis

Heterosis is the phenomenon when the offspring surpasses the average of its parents for one or more traits (Gjedrem, 2005). Heterosis displays different direction from heritability, in particular, the narrow sense heritability. When the narrow sense heritability is low, but the non-additive variation or dominance effect is high, heterosis can be easily achieved by crossbreeding. It is reported that selective breeding was not efficient for genetic improvement of the growth rate in the common carp, but genetic improvement by crossbreeding was easily obtained (Moav and Wohlfarth, 1976; Ankorion et al., 1992; Wohlfarth, 1993; Bakos and Gorda, 1995; Hulata, 1995; Vandeputte, 2003). Meanwhile, significant heterosis in the common carp has also been obtained by crossbreeding in China. For example, the Xingguo red common carp (*C. carpio* var. *singuonensis*) and the Purse red common carp (*C. carpio* var. *wuyuanensis*) have been widely used as parents to make cross combinations, which produced remarkable heterosis in practice (Table 3). In general, crossbreeding is highly successful and heterosis is very easily achieved in the common carp. This result is related with the large number of variants and strains in this species with different gene pools and relatively large genetic distance.

5 Interaction effects

The phenotypic expression of quantitative traits results from both genetic and environmental sources of variation and the interaction between the two (Fishback et al., 2002). It is common for the growth performance to be different among different strains reared in different environments. This mostly results from the genotype×environment (G×E) interaction.

The common carp with numerously different strains containing a variety of differing genetic groups provides an opportunity to study genotype×environment interactions. Although Wohlfarth et al. (1983) delivered the preliminary reports on genotype×environment interaction in the common carp, available literature on genotype×environment interaction in this fish is highly inadequate. In 2007, Wang and Li reported the genotype×environment interaction of growth-related traits in the common carp. They found that body weight

Table 2 Phenotypic and genetic correlations between growth-related traits in the common carp

trait	age/size	design	r (±S.D.)	method	references
weight-length	8 weeks	factorial (10D, 24S)	$r_A = 0.98$	MP	Vandeputte et al. (2004)
	8 months	nested (30D, 10S)	$r_A = 0.80 \pm 0.02$ $r_P = 0.93 \pm 0.07$	S	Wang et al. (2006c)
	20 months	nested (30D, 10S)	$r_A = 0.76 \pm 0.02$ $r_P = 0.93 \pm 0.07$	S	Wang et al. (2006c)
	20 months	diallel	$r_A = 0.52$ $r_P = 0.54$	MGM	Li et al. (2006)
	3 growing seasons	factorial (G0–G2; G0: 10D, 24S; G1: 8D, 147S)	$r_A = 0.97 \pm 0.01$ $r_P = 0.92 \pm 0.02$	MP	Vandeputte et al. (2007)
	1 summer spring 2 summers	factorial (G0–G3; G0: 10D, 24S; G1: 8D, 147S; G2: 8D, 96S)	$r_A = 0.97 \pm 0.01$ $r_P = 0.97 \pm 0.01$	MP	Vandeputte et al. (2008)
weight-height	8 months	nested (30D,10S)	$r_A = 0.62 \pm 0.02$ $r_P = 0.87 \pm 0.07$	S	Wang et al. (2006c)
	20 months	nested (30D,10S)	$r_A = 0.78 \pm 0.02$ $r_P = 0.96 \pm 0.08$	S	Wang et al. (2006c)
	20 months	diallel	$r_A = 0.26$ $r_P = 0.43$	MGM	Li et al. (2006)
weight- rel. body height	3 growing seasons	factorial (G0–G2; G0: 10D, 24S; G1: 8D, 147S)	$r_A = 0.08 \pm 0.11$ $r_P = 0.15 \pm 0.05$	MP	Vandeputte et al. (2007)
weight-width	8 months	nested (30D, 10S)	$r_A = 0.58 \pm 0.02$ $r_P = 0.84 \pm 0.08$	S	Wang et al. (2006c)
	20 months	nested (30D, 10S)	$r_A = 0.74 \pm 0.01$ $r_P = 0.95 \pm 0.12$	S	Wang et al. (2006c)
	20 months	diallel	$r_A = 0.40$ $r_P = 0.74$	MGM	Li et al. (2006)
weight- rel. body width	3 growing seasons	factorial (G0–G2; G0: 10D, 24S; G1: 8D, 147S)	$r_A = 0.34 \pm 0.11$ $r_P = 0.28 \pm 0.05$	MP	Vandeputte et al. (2007)

r_A: genetic correlation; r_P: phenotypic correlation; S: sire component; D: dam component; AM: animal model; PO: parent-offspring regression; MP: molecular pedigree; MGM: mixed genetic model.

Table 3 Some hybrids made by crosses with red common carps in China

hybrid	parental combination
Feng common carp	Xingguo red common carp (♀)×Scatter mirror carp (♂)
He-Yuang common carp	Purse red common carp (♀)×Yuangjiang river carp (♂)
Yue common carp	Purse red common carp (♀)×Xiangjiang river carp (♂)
Tri-hybridization carp	He-Yuang common carp (♀)×Scatter mirror carp (♂)
Lotus common carp	Scatter mirror carp (♀)×Xingguo red common carp (♂)
Allogynogenetic crucian carp	Fangzheng crucian carp (♀)×Xingguo red common carp (♂)
cold resistance strain of Purse red common carp	Helongjiang river carp (♀)×Purse red common carp (♂)

and standard length were weakly controlled by genotype×environment interaction effects; however, body height and width were predominantly caused by genotype×environment interaction. The results not only show that genotype×environment interaction is an important controller of genetic variation in the common carp but also indicate that it is important for aquaculturists to consider the influence of genotype×environment interactions on different traits in genetic improvement programs for the common carp. Furthermore, Wang and Li (2007) first divided the genotype×environment interaction into additive×environment and dominance×environment interactions in quantitative traits of aquatic animals. This is advantageous in that it shows the inheritable magnitude, selection potential, and the magnitude of heterosis of improved traits in different environmental conditions.

On the other hand, epistasis is also an important contributor to phenotypic variation. For example, the additive×additive epistatic effects were significant in traits such as body weight, total length, standard length, head length, snout length, and caudal peduncle length in the common carp; thus epistasis could play an important role in genetic selection and breeding of the common carp (Wang et al., 2006b). It is also noted remarkably that developmental quantitative genetic analysis of growth-related traits in the common carp has been conducted (Wang et al., 2006a), which gave a useful sign for reasonable selection and breeding during the ontogeny.

6 Breeding value prediction

Breeding value (EV) is the ratio of additive effects to phenotype variation in breeding practice. The breeding values or genetic merits of improved strains are sometimes of greater concern to the breeders. However, in breeding practices of the common carp, the breeding values or prediction of genetic merits have not often been conducted, which may be associated with low improvement in selective breeding practices for the common carp. However, the breeding values were found to be very important and useful in the reports of Wang et al. (2006c, 2006d) and Wang and Li (2007). Using the diallel design of three strains in the red common carp, they found that the strain of *C. carpio* var. *color* could increase the body weight and body length in their progeny. Moreover, the strains of *C. carpio* var. *wuyuanensis* could reduce total length, standard length, and caudal peduncle length, but increase body height in their progeny. The *C. carpio* var. *color* was the best strain for genetic improvement through direct selection in different environmental conditions, and the cross-combination of *C. carpio* var. *color* and *C. carpio* var. *singuonensis* was the best for heterosis utilization by hybridization in the three strains of red common carp.

7 Direct selection

It has been widely reported that direct selection always failed in the common carp (see the section of heterosis). However, in China, genetic improvements in growth rate through direct selective breeding in the common carp have been a great success. For instance, for the Xingguo red common carp, a mass selection was initially conducted in 1972 and completed in 1985 after six generations with a 20% increase in weight gain; for the Purse red common carp, a mass selection was conducted during 1969–1979 and the Glass red common carp (*C. carpio* var. *wananensis*) during 1973–1983, and both showed considerable improvements in body weight (Li, 1996; Lou, 1999; Li and Wang, 2001). These red common carps have been cultured in many parts of China and have played a major role in the Chinese carp aquaculture industry. Furthermore, the Jian common carp (*C. carpio* var. *jian*) is a famous case for selective breeding, which combines family selection and gynogenesis after the hybridization between the Yuan wild common carp and the Purse red common carp (Zhang and Sun, 1994). Indeed, genetic improvement through direct selective breeding can give good results for genetically different strains of the common carp.

8 Conclusions and prospect

Fish has become an increasingly important source of protein in many developing countries. Fish and fisheries play important roles in the economies of developing countries, by contributing to animal protein intake, employment generation, household incomes, and foreign exchange earnings (Gupta et al., 2005). The common carp, as one of the most cultured species of fish, has played a very important role in the aquaculture industry. Genetic improvement in important economical traits, such as fast growth, has been a main target in selective breeding and crossbreeding of the common carp. Thus, genetic evaluation of growth-related traits is necessary in breeding programs. Especially, studies on the genotype×environment interaction and breeding values prediction for growth-related traits should be heavily conducted in the selective breeding of the common carp. Developmental quantitative genetic analysis of quantitative traits is a good method to predict reasonable selection stages during ontogeny and has been suggested to be conducted in breeding schedules. In China, the cradle of aquaculture, very few reports on genetic improvement of the common carp have been found in the literature. Thus, aquaculturists should pay more attention to the genetic analysis of quantitative traits and genetic improvement in the common carp.

In addition, the impact of fish diseases is an important issue in developing a sustainable aquaculture industry of economic importance. Aquaculture of common carp is carried out mostly in open environment (earthen ponds), strongly limiting the possibilities for disease control measures (Rakus et al., 2009). Therefore, the disease resistance breeding would increasingly be another objective in common carp breeding schedules.

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