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Review

Selective breeding of quantitative traits in the common carp (*Cyprinus carpio*): a review

Marc Vandeputte *

INRA, Laboratoire de génétique des poissons (Fish genetics Laboratory), Domaine de Vilvert, 78352 Jouy-en-Josas cedex, France

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Abstract

The common carp is one of the main aquaculture species in the world. Despite this, most of the production is carried out using unselected strains. Selective breeding for fast growth has not proven to be effective in this species, but other traits (disease resistance, shape) could be successfully selected for. Most heritability estimates in the literature are unreliable due to environmental biases, but complementary results from population genetics and comparison of strains seem to indicate that there should be a potential for selective breeding in this species, including selection for growth rate, provided the base populations are variable enough (e.g. synthetic strains). New techniques such as parentage assignment with microsatellites and use of doubled haploid progenies may help describe much more accurately, without environmental bias, the genetic determination of traits of interest in the carp. This could be a new opportunity to design efficient breeding programs in this important species.

Résumé

La sélection des caractères quantitatifs chez la carpe commune (*Cyprinus carpio*). La carpe commune est l'une des principales espèces aquacoles mondiales. Malgré cela, la majorité de la production provient de souches non sélectionnées. La sélection pour la croissance ne s'est pour l'instant pas montrée efficace chez cette espèce, mais d'autres caractères (forme du corps, résistance aux maladies) ont pu être sélectionnés avec succès. La plupart des estimations d'héritabilité de la littérature sont douteuses du fait de biais environnementaux, mais l'ajout des données issues de la génétique des populations et la comparaison de souches montre qu'il doit exister chez cette espèce des potentialités de sélection, y compris pour la croissance, à condition que les populations de base soient suffisamment variables (souches synthétiques en particulier). De nouvelles techniques telles l'assignation de parenté par marqueurs microsatellites et l'utilisation d'haploïdes doublés devraient permettre de décrire beaucoup plus précisément le déterminisme génétique des caractères d'intérêt. Ce pourrait être une occasion pour mettre au point de nouveaux schémas d'amélioration génétique chez cette espèce.

Keywords: Aquaculture; Genetics; Selective breeding; Heritability; *Cyprinus carpio*

1. Introduction

Common carp (*Cyprinus carpio*) are one of the most important cultured fish in the world. More than 2.7 million tonnes of common carp were produced in 2000 (FAO, 2002). Carp are cultivated in a variety of climates, in ponds with various levels of management. As one of the first domesticated fish (Balon, 1995), carp have undergone selective breeding, at least empirically, for centuries. However, the majority of cultivated carp are not produced from selected lines (Hulata, 1995). Several authors have reviewed the work carried out on genetic improvement in this species, including hybridization, crossbreeding, genome manipulations and selective breeding (Wohlfarth, 1986; Hollebecq and Haffray, 1994; Hulata, 1995). They concluded to the possible use of crossbreeding as the main way to improve this species, and to a quite low potential for selective breeding, except for disease resistance. Indeed, the genetic improvement of quantitative traits in carp has to a large extent been achieved through crossbreeding of different lines, which is, however, a onetime event, not offering the possibility for further im-

* Corresponding author.
E-mail address: mvande@jouy.inra.fr (M. Vandeputte).

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provement. By comparison to other aquaculture fish species, very little is known about selective breeding of carp for quantitative traits. Furthermore, there are few documented selective breeding programs in the scientific literature. The aim of this review is to give a deeper insight into selective breeding of economically important quantitative traits (body weight, length, shape and disease resistance), and to evaluate the feasibility of such an approach. The review is composed of three parts. First, existing information about genetic variability and genetic parameters of quantitative traits in common carp is evaluated. Second, the available information on past selective breeding programs is assessed. Finally, possible directions for future selective breeding of carp will be outlined, using recent tools such as isogenic lines or genomic markers.

2. Basic information on genetic variability

Sufficient genetic variability is a prerequisite for selective breeding. Valuable information can be drawn from population genetic studies (although not directly connected with quantitative variation), from investigations on variation of quantitative traits between strains and their crosses, and from within strain heritability estimates.

2.1. Information from population genetics studies

First, population genetics studies show that there are two subspecies of common carp, *C. carpio carpio* from Europe and *C. carpio haematopterus* from Asia (Paaver and Gross, 1990; Balon, 1995; Csizmadia et al., 1995; Kohlmann and Kersten, 1999). The Asian subspecies may be subdivided into strains from Central Asia and East/Southeast Asia (Kohlmann et al., 2002). Within each subspecies, particularly the European one, the genetic distance between populations is low (Cataudella et al., 1987; Kohlmann and Kersten, 1999; Desvignes et al., 2001), and is only revealed when using highly variable markers like microsatellites (Desvignes et al., 2001; Kohlmann et al., 2002; Tanck et al., 2000).

The second major finding of population genetics studies is the lower variability (measured by heterozygosity or mean number of alleles) of domesticated strains of carp when compared with wild strains (Marian, 1987; Kohlmann and Kersten, 1999; Kohlmann et al., 2002). For example, with allozymes, the mean number of alleles per locus ranges from 1.4 to 1.5 in domesticated strains compared to 1.5–1.9 in wild populations (Kohlmann and Kersten, 1999). With microsatellites, a captive stock of Amur carp has 2.7 alleles per locus, compared to 14 in a wild Uzbek population (Kohlmann et al., 2002).

The lower variability of domesticated strains indicates that in many cases, they were propagated with small effective numbers of breeders, resulting in some inbreeding. Although it has to be confirmed with estimates of genetic variation for quantitative traits, this initial inbreeding in the domesticated strains could somehow hamper the possibilities for genetic gain from selective breeding. On the other hand, the structuring of common carp in two subspecies, and the further structuring within these subspecies, is an indication that some strains of common carp have evolved quite independently, and may then show different patterns of genetic variation for quantitative traits, provided there is a genetic basis for the traits of interest. The most interesting source of genetic variability should lie between the two subspecies, which appear to be quite distant, and may then have conserved different alleles influencing the traits of interest. It then seems possible to create synthetic strains with high genetic variability, which may be a good material to start selective breeding programs in this species. However, this is true only if the traits of interest are under additive genetic control, which cannot be inferred from molecular data.

2.2. Information from comparison of strains

Information on the genetic determination of quantitative traits can also be drawn from comparison between strains for these traits. Although differences between strains are not an indication of genetic variability within any particular strain, they show that at the species level, the trait of interest is under genetic control. This increases the probability to find genetic variation within some strains, and may give the opportunity to create additive variation within synthetic strains.

It has to be noted that proper comparison of carp strains (and of pond fish in general) is not an easy job, due to large environmental variation between ponds, which highly interferes with the evaluation of the genetic value of the strains. Methods to correct for environmental variation are, therefore, necessary to obtain accurate estimates of strain breeding values. Two main methods have been described to overcome this problem, communal testing with multiple nursing of progenies (Wohlfarth and Moav, 1972, 1985) and separate (Pokorny et al., 1983; Vandeputte et al., 2002) or communal (Linhart et al., 2002) testing using internal controls identified by their type of scale cover, eventually combined with fin clipping. A combination of multiple nursing and internal control has also been proposed (Gross and Wohlfarth, 1994). However, large differences can still be evaluated with simple replication of ponds as a mean to control environmental variation. Table 1 shows most known cases of differences between strains or their crosses for quantitative traits, in experiments with appropriate environment control methodologies. The types of genetic differences reported represent different components: differences between pure strains include an additive genetic as well as a maternal component; differences between top cross progenies, which are produced by crossing different sire strains on a single dam strain, include an additive and a dominance component; heterosis is only due to dominance and is estimated from diallel crosses.

In most experiments, there was genetic variation between strains of carp. For growth rate, large differences exist between pure strains, the best line in one experiment being often 50–100% larger than the smallest ones. Differences between top cross progenies are in the same range, and

Table 1
Differences between strains and crosses of common carp for weight, survival and flesh yield. Maximum difference in percent of the mean of the worst performing strain, or in percent of the mean of parental strains in case of heterosis. Environment control: C, communal; CMN, communal with multiple nursing; SIC, separate with internal control; CIC, communal with internal control; SR(*n*), separate with *n* replicates by strain. Type of genetic difference: P, between pure lines; TC, between top cross progenies; H, heterosis

Trait	Age/size	Type of genetic difference	Number of strains or crosses	Maximum difference (%)	Environment control	Reference
Weight	5 weeks	TC	3	9	SIC	Vandeputte et al. (2002)
	1 summer	P	4	65	CMN	Moav et al. (1975)
		P	2	40	CMN	Prinsloo and Schoonbee (1984)
		P	4	49	SIC	Pokorny et al. (1983)
		P	27	99	CMN	Wohlfarth (1993)
		TC	4	93	SIC	Linhart et al. (2002)
		TC	3	20	SIC	Vandeputte et al. (2002)
		H	3	25	CMN	Prinsloo and Schoonbee (1984)
		H	27	34	CMN	Wohlfarth (1993)
		H	8	38	SIC	Bialowas (1991)
	2 summers	P	7	18	SR(1)/C	Bakos and Gorda (1995)
		P	6	44	CMN	Wohlfarth (1993)
		TC	4	88	CIC	Linhart et al. (2002)
		TC	3	7	SIC	Vandeputte et al. (2002)
		H	7	18	SR(1)/C	Bakos and Gorda (1995)
		H	6	21	CMN	Wohlfarth (1993)
	3 summers	P	6	10	SR(3)/C	Bialowas et al. (1997)
		TC	4	56	CIC	Linhart et al. (2002)
		H	6	29	SR(3)/C	Bialowas et al. (1997)
	Harvest	P	3	63	SR(3)	Tran et al. (1987)
Survival	1 summer	TC	4	89	C	Duda et al. (1999)
	2 summers	P	7	78	SR(1)/C	Bakos and Gorda (1995)
		H	7	31	SR(1)/C	Bakos and Gorda (1995)
	3 summers	P	6	214	SR(3)/C	Bialowas et al. (1997)
		H	6	314	SR(3)/C	Bialowas et al. (1997)
KHV[a] resist	Fingerlings	TC	3	375	SR(3)	Shapira et al. (2002)
		P	3	300	SR(3)	Shapira et al. (2002)
Flesh yield	2 summers	P	6	2.1	SR(3)/C	Shapira et al. (2002)
		H	6	2.7	SR(3)/C	Shapira et al. (2002)

[a] Koi Herpes Virus.

heterosis is between 20% and 30% of the parental mean. The differences seem to be larger in younger fish, especially within the same experiment, either for top cross progenies (Linhart et al., 2002), or for heterosis (Wohlfarth, 1993). This would be an indication of the decrease of the dominance component over time, as pointed out by Wohlfarth (1993). Variations between strains and heterosis seem to be also very large for survival, as well as for disease resistance, but much smaller for flesh yield, the phenotypic variation of which is, however, very limited (Cibert et al., 1999).

The large amount of genetic variation observed between strains for the quantitative traits of interest is a good indication of possible additive genetic variance within some strains of this species, and especially within synthetic strains. Although heterosis effects (i.e. non-additive genetic variation) may also play a large role in the determination of performances in this species, as shown by several authors (e.g. Bialowas, 1991; Wohlfarth, 1993), it seems unlikely that they would be the main genetic determinants of performances in common carp, as large differences also exist between pure strains. These differences between pure strains may be biased by maternal effects, but in all pure strain designs reported here, there was an initial phase of separate rearing of progenies. In salmonids, maternal effects quickly decrease during separate rearing of progenies (Chevassus, 1976; McKay et al., 1986), so it seems reasonable to assume that differences between pure strains are mainly due to additive genetic differences.

2.3. Heritability estimates

Many heritability values of quantitative traits have been published in common carp (Table 2). Most of them are larger than 0.2, showing putative additive genetic variation for the quantitative traits of interest. However, they are highly variable among experiments, ranging from 0 to 0.58 for weight, for example. For growth rate, we can see that the heritabilities are very similar for weight and length. Quite unusual results were obtained by Nenashev (1966) with sire heritabilities higher than dam heritabilities in most cases. This is likely to be due to the design used (sires nested within dams with initial separate rearing of progenies), which implies that the sire component contains additive variance, but also dominance and common environment (which is not the case when

Table 2
Heritability (h^2) estimates for some quantitative traits in common carp. Method for h^2 estimation: PO, parent offspring regression; S, sire component; D, dam component; S + D, sire + dam component; AM, additive component from animal model; *X* gen., number of generations for realized h^2

Trait	Age/size	Design (nb Dams, nb Sires)	h^2 (±S.D.)	Method	Reference
Weight	27 days	?	0.11	?	Poljarush and Ovchenko (1979) in 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)
	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. (2001b)
	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)
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)
	Fingerlings	Nested (3D, 18S)	0.21	?	Nenashev (1969)
	110 days	33 androgenetic lines	0.11 (0.04–0.21)[a]	AM	Tanck et al. (2001b)
	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)
		Nested (3D, 18S)	0.18 ± 0.06	D	Nenashev (1966)
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)
K (Fulton)	110 days	33 androgenetic lines	0.37 (0.20–0.62)[a]	AM	Tanck et al. (2001b)
Dropsy resistance	–	Realized h^2	0.15–0.20	9 gen.	Kirpichnikov (1999)
Cortisol stress response	110 days	33 androgenetic lines	0.60 (0.37–0.90)[a]	AM	Tanck et al. (2001b)
Hypoxia resistance	10 g	Factorial (3D, 3S)	0.51	S + D	Nagy et al. (1980)
Gonad weight	13 months	5 gynogenetic lines	0.75 (0.48–1.00)[a]	AM	Bongers et al. (1997)
Percent deformed larvae	13 months	5 gynogenetic lines	0.31 (0.00–0.69)[a]	AM	Bongers et al. (1997)
Fat content	1 summer	Nested (3D, 18S)	0.22	S + D	Nenashev (1969)

[a] Ninety percent confidence interval.

dams are nested within sires). Thus, the true heritabilities may be considerably lower than those given in this case, especially if common environment exists, which is likely due to the initial rearing of families in unreplicated aquaria: a value as low as 0.05 for c^2 (the share of common environment in phenotypic variance) would imply an upward bias of 0.2 for h^2. The dam heritabilities could be regarded as more reliable in this case, although they may be biased by maternal effects. However, as previously outlined, maternal effects are known to decrease quickly when the progenies are reared separately. Unfortunately, the low number of dams used (three) reduces the reliability of these estimates. The same problem of small number of breeders is seen in the experiments of Nagy et al. (1980), Smisek (1981) and Bongers et al. (1997). In the experiment of Nagy et al., h^2 is also likely biased by maternal effects due to the use of the sire + dam component, and in the experiment of Tanck et al. (2001b), initial rearing of progenies in separate aquaria potentially biases the estimates with common environmental effects. Moreover, rearing in aquaria may have lead to results, which are not applicable in ponds. Parent–offspring regression may be biased upwards by maternal effects and downwards by environment effects. The resulting heritabilities are lower for growth rate (0–0.04) and *H*/*L* ratio (0.25) than sire and dam heritabilities (Nenashev, 1966), indicating either low additive variance or high environmental variance between full-sib families. Altogether, the reliability of most existing heritability estimates in carp is, therefore, quite low. Realized herita-

bilities (which will be detailed in Section 3) may be regarded as more reliable, but may also be biased in some ways by inefficient estimations of the breeding values (e.g. confounding of maternal and/or environmental effects with genetic variation, resulting in low responses), year effects (in the absence of proper controls) or inbreeding. Globally, however, it seems from the existing data taken altogether that the heritability of growth rate, either in weight or in length, should be low to intermediate (0.3 or less) and the one for conformation (*K*, *H*/*L*) should be higher (in the range of 0.3–0.4). For other traits, the number of estimates is much lower, but there seems to be strong genetic variation for cortisol stress response, hypoxia resistance and gonad weight, and lower variation for dropsy resistance, percent of deformed larvae and fat content. Based upon these moderate heritability estimates, together with the relatively long generation intervals of common carp, at least in Europe, several researchers concluded that selective breeding for growth rate in carp was not an interesting way of improvement. Crossbreeding was thought to be more interesting as it uses the amount of dominance variation between carp strains (e.g. Wohlfarth et al., 1987; Bakos and Gorda, 1995). However, as opposed to selective breeding, crossbreeding does not allow further genetic improvement, so the quick results obtained with this method may hamper the possibilities for future progress if crossbreeding is the only method used. A trait like growth rate, if it had a heritability of 0.3 and a phenotypic coefficient of variation of 0.3, could be improved by 20% at each generation by simple mass selection of the best 3%. This seems quite valuable, even with a generation interval of 4–5 years.

Putting together population genetics data, genetic differences between strains and heritability estimates, it can be foreseen that additive genetic variation should exist for many traits in common carp, but not necessarily in all strains, due to a putative loss of variability linked to the use of small numbers of breeders for propagation. Although some strains having enough within-strain additive genetic variance certainly exist, the prior construction of synthetic strains may be a good precautionary action for starting a within-strain selective breeding program. Moreover, although the reliable information seems to be quite scarce, the additive genetic variation is expected to be larger for the shape of the fish than for growth rate. As this last parameter seems more likely to be biased by maternal and/or environmental effects, this difference could be expected.

3. Selective breeding experiments

Several selective breeding programs have been reported in common carp. Selection for disease resistance or cold resistance yielded positive responses, whereas the success of selection for growth rate is more controversial.

It has to be noted that only few breeding programs have been published in the scientific literature with enough details to evaluate their results on an objective basis. Moreover, some of them consist of crosses between lines in order to combine some of their advantages, but do not necessarily imply selection of families and/or individuals on the basis of their performance for the trait(s) required. In this paper, this selection of line crosses will not be considered, although it can yield very interesting results.

Many programs conducted in the USSR, reported crossings of initially more or less distant broodstocks in order to increase genetic diversity, and then mass selection for growth rate, exterior traits and viability, or for adaptation to special environmental conditions (cold or hot temperature) (Kirpichnikov, 1987). Unfortunately, no figures are given for evaluating the gain produced in most of these programs. For two of them, however, we have more details.

The first one led to the selection of a fast growing, cold tolerant carp, the Ropsha carp (Kirpichnikov et al., 1974; Babouchkine, 1987). It was obtained by crossing the cold tolerant Amur wild carp with the fast growing Galician carp. Various intercrosses, backcrosses and progeny testings were used to obtain a cold resistant carp, homozygous for scale cover genes (genotype SSnn), which was then mass selected for growth rate for five generations. The results show a large improvement of cold tolerance (from 30–40% to 77.4% winter survival). No data were given for the efficiency of the selection for growth rate.

The second detailed Russian breeding program is the selection of a dropsy-resistant strain, the Krasnodar carp (Kirpichnikov et al., 1993). Fish were mass selected as survivors when they were reared with infected conspecifics. The selection pressure was 30–35% per generation for nine generations, and the estimation of realized heritability was 0.15–0.20 (Kirpichnikov, 1999). The fish were also mass selected for growth rate, with an average intensity of 0.5–1.4% per generation. Selection for growth rate is reported to be successful, but no figures are given (Kirpichnikov et al., 1993).

Another mass selection experiment for dropsy resistance was reported by Schäperclaus (1962). The selection intensity was not given, but the selected line (average of 65 ponds) suffered only 11.5% mortality while in non-selected fish (average of 76 ponds) the mortality was 57%. In Vietnam, mass selection for growth rate (Tran and Nguyen, 1993) produced an increase in body weight over two generations, with a realized heritability of 0.20–0.29 in one line. In this experiment, however, it seems that only one line out of the three selected ones responded to selection (data not given for the other two lines).

These experiments show that disease resistance may be selected for, but that selection on growth rate, although often claimed to be successful, is not supported by strong scientific evidence.

More details are available on selection for growth related traits in two Israeli experiments: the first one was individual divergent selection for growth rate on five generations (Moav and Wohlfarth, 1976). The up-selected line showed a small response in the first generation, then its performance de-

creased under that of the control line until generation 5. Down selection was more efficient, yielding a realized heritability of 0.3 in the first three generations. In generations 4 and 5, the performance of the down selected line stabilized. The main explanation given by the authors was that the strain used would be at a selection plateau, this hypothesis being supported by two major facts: first, in several previous one-generation selection experiments (Moav and Wohlfarth, 1966), the results were comparable, with an inability to increase growth rate by selection, but quite a good efficiency of downward selection. Second, progeny tests showed high genetic variance of weight gain (Moav and Wohlfarth, 1966). Additionally, strong genotype by environment interactions (especially between years and ponds) may also have explained the lack of response, and it is well known that this type of interactions exists in carp (Moav et al., 1975; Wohlfarth et al., 1983; Gross and Wohlfarth, 1994). However, as mass spawnings were used in this experiment to produce each generation, it also seems possible that (1) not all breeders introduced participated in the reproduction, resulting in increased inbreeding; (2) differences in fertilization time and hatching time may have occurred between females; (3) subsequently, the best performing individuals may have been offspring of the earliest spawners, and may not necessarily have been the individuals with the best breeding values for growth. Indeed, it has been shown that maternal effects (represented by the time of spawning) have a dramatic influence on the early life of common carp (Wohlfarth and Moav, 1970). All this may have led to selection of genetically average fish, and may also have induced a high inbreeding rate.

The second Israeli experiment was done on divergent selection for shape (height/length ratio) in one generation. This one showed a high-realized heritability for this trait (0.47 upwards, 0.33 downwards (Ankorion et al., 1992)), but no clear correlation with growth rate, thus hampering the possibility of using *H*/*L* ratio to indirectly select for growth rate as it was expected.

These results show that at least some traits (disease resistance, shape) may be selected for in the common carp, thus showing that additive genetic variation does exist in this species. The case of growth rate is more controversial, as the only really documented experiment was unsuccessful, and the other ones claim to be successful, but without appropriate scientific evidence. Heritability estimates for growth rate would lead to optimism, even though at present all of them are likely to be biased upwards. More research is therefore needed, and new techniques such as genotyping or doubled haploids may help to get a more precise description of the genetic control of productive traits in carp, and its interaction with the environment. They may also give the opportunity to increase the efficiency of selection methods by including family information in the evaluation of breeders.

4. Prospects for new developments

Many of the difficulties reported here in setting up well controlled experiments for the estimation of genetic parameters and for selective breeding in the carp arise from the inability to tag fish at hatching, and the subsequent need to rear families separated until tagging in many different ponds, thus increasing environmental variance and confounding it with genetic effects. The number of families required to obtain precise estimates of genetic parameters is high (Vandeputte et al., 2001; Dupont-Nivet et al., 2002), and incompatible with the number of ponds usually available in experimental stations. A posteriori reassignment of mixed progenies to their parents with genetic markers would be an effective way to solve this problem. The control of crossing and larval rearing methodologies also has to be improved to ensure the maximal participation of parental broodstock in the reproduction, as well as the best possible equilibrium in family sizes.

4.1. Markers for parentage assignment

A first approach to the use of markers for identifying progenies to their parents was done in the early 1980s (Moav et al., 1976; Brody et al., 1976, 1980, 1981; Smisek, 1980). However, the low variability of the allozymes used allowed to use limited crossing designs only (max. 3 sires × 3 dams), moreover, with parents selected for their allozyme genotype. Recently, microsatellite markers have been developed in common carp (Croijmans et al., 1997; Aliah et al., 1999; David et al., 2001; Tanck et al., 2001a). More than 89 markers are available (Table 3), with a mean number of alleles between 4 and 7, and high heterozygosities (60–80%) in outbred populations. It should be noted that the number of

Table 3
Microsatellite markers available in common carp, with main characteristics in the population tested. N/A: not available

Number of markers	Mean number of alleles (min-max)	Population(s) tested	Mean heterozygosity (%)	References
32	4.7 (2–7)	Three outbred fish	60.4	Croijmans et al. (1997)
		Three inbred fish	51.1	
		Two clones	0.0	
3	6.7 (5–9)	10 koi fish	40.7	Aliah et al. (1999)
		24 wild fish	77.8	
47	4.0 (1–8)	Nine fish	N/A	David et al. (2001)
7	4.7 (1–7)	Seven fish	N/A	Tanck et al. (2001a)

alleles is largely underestimated in the publications originally describing the markers, due to the very small size of the fish samples. When using larger samples from various carp strains, the number of alleles could be much larger. For example, a mean number of 14 alleles at four loci was found in an Uzbek population (Kohlmann et al., 2002), compared with 5.75 in the test population in the original paper (Croijmans et al., 1997). Across 10 populations, loci MFW28 and MFW7 have 20 and 41 alleles in Kohlmann et al. (2002), compared to seven and six, respectively, in the original paper (Croijmans et al., 1997).

These highly variable markers generally make it possible to assign any offspring to its parents even in large crosses, provided DNA samples of the parents are available (Herbinger et al., 1995; Estoup et al., 1998). For example, eight selected microsatellites have the theoretical capability of assigning 95% or more of the offspring to the right parents in a 140 × 140 factorial cross in turbot, and in a 34 × 34 factorial cross in rainbow trout (Estoup et al., 1998). The microsatellites mentioned here had a mean number of alleles and a mean heterozygosity of 14.1 and 0.84 in turbot, and 8.4 and 0.80 in rainbow trout, respectively. The performance for common carp microsatellites would then be expected to be close to that of rainbow trout microsatellites. Practically, 14 multiplexed microsatellites allowed the assignation of 91–95% of the progeny to one parental pair in a 48 × 2 factorial cross in rainbow trout (Fishback et al., 2002). In common carp, recent results showed that more than 90% of the offspring of a 24 × 10 factorial cross were assigned to a single parental pair with seven microsatellites (Mauger, personal communication). This 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). It is likely that this type of study would give a better understanding of the genetic determination of quantitative traits in the carp, as well as give opportunities to study genotype by environment interactions at the family level. A better knowledge of genetic parameters and of the genetic structure (differential family survivals influencing the effective number of breeders) can certainly yield very interesting results for practical breeding programs (how to cross the fish, how many breeders to use, at which age to select, which criteria to use) without any need to use markers at each generation, and then without additional costs for the routine breeding programs.

Apart from allowing a better estimation of genetic parameters, identification of individuals through genotyping may also allow the use of familial, combined or BLUP selection free of environmental bias through avoiding any initial separate rearing phase. The cost of such an approach might, however, be dissuasive, as several thousands of individuals would have to be genotyped at each generation, with a cost around 15–30 € per individual. More simply, markers can also improve breeding programs through a better control of inbreeding, avoiding mating of relatives, without the need to genotype the whole population, like in "walk-back" selection (Doyle and Herbinger, 1995). With this type of procedures, the number of individuals to be genotyped is more in the range of a few hundreds per generation, which is less unthinkable in practice. The use of markers may also allow the identification and use of quantitative trait loci (QTLs) for selective breeding, however, this requires a high density genetic map which does not exist yet in common carp (Tanck, 2000), but seems to be in progress in China (Hulata, personal communication). But again, the cost of this approach would be very high (several hundreds of individuals to genotype for tens of markers in the initial phase, then all candidates to genotype for a few markers at each generation) and it may, therefore, be impractical in most carp breeding countries.

4.2. Use of doubled haploid (DH) progenies

Another new tool for genetic studies in the common carp is the use of doubled haploid (DH) androgenetic or gynogenetic progenies. Although gynogenesis has been developed in the 1970s in common carp (Cherfas, 1975), only recently have DH progenies been used as tools for estimation of genetic parameters. Since the genetic variation between DH families is much higher than the variation between full- and half-sib families, heritability estimates are improved when $h^2 \leq 0.35$ when using DH progenies (Bijma et al., 1997; Bongers et al., 1998). This method has already been used to estimate the heritability of cortisol stress response, morphometric and reproductive traits in the common carp (Bongers et al., 1997; Tanck et al., 2001b, see Table 2) with quite a good precision. Unfortunately in these experiments, the genetic groups were reared in single aquaria, without replication, and the heritability estimates may, therefore, suffer from environmental bias. Moreover, the fish were not in a common (pond) production system and also experienced restricted feeding, which may have made the estimated growth related parameters different from what they would be in real life. However, the use of these DH in communal ponds, together with genotyping, may allow a substantial improvement in the precision of the parameters estimated. Another benefit of this type of progenies is the ability to produce accurate values for individual genotypes, as many measurements can be done on replicated fish representing only one genotype. Due to the large additive variance between families (twice the additive genetic variance in the base population), DH progenies are also a way to produce extreme genotypes, which may be very useful to quickly select efficient genotypes, for example for disease resistance (Quillet, 1994). The major drawbacks of DH progenies are the practical difficulties to implement androgenesis in practice, and the low viability of the progenies due to inbreeding. This may hamper the proposed use of DH progenies in ponds.

5. Conclusion

Although selective breeding especially for growth rate in the common carp had moderate success in the past, new methodologies such as microsatellites for parentage assignment and use of DH progenies may now give the opportunity to go much deeper in the description of the within strain genetic variation of quantitative traits in this species. A better knowledge of the genetic basis of production traits may help to understand the contradictory results about selective breeding that have been observed in the past, as everything indicates that there should be genetic variation for growth rate in the common carp, but selection for growth rate has never been proven to be efficient. This initial phase would be quite costly (especially with the use of marker technology) and financial support will be necessary, but it seems quite likely that the knowledge generated may result in simple recommendations that may improve practical breeding programs in which the recurrent use of markers would not necessarily be needed. It is too early to say if this would lead to effective further genetic improvement, but it is worth trying to improve this species, which is one of the most important ones at the world level.

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