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A comparison of communal and separate rearing of families in selective breeding of common carp (*Cyprinus carpio*): Responses to selection

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ABSTRACT

The genetic response in growth traits in a selection program for increased harvest weight in a common carp population in Vietnam is reported. A base population (G_0) was established from six carp stocks using single pair mating. Selection was based on high breeding values for body weight at harvest, with a corresponding control group selected on average breeding values of the population. In the following two selected generations (G_1 and G_2), families were produced using a partial factorial mating design. Each family in G_1 and G_2 was split and reared using communal early rearing (CER) or separate early rearing (SER) methods. Molecular markers were used to maintain pedigree information in CER whereas physical tagging was applied in SER. Both CER and SER were managed under otherwise similar conditions. The data for growth traits were analyzed using a univariate mixed model to estimate breeding values, variance components and response to selection. Response to selection was estimated by two different methods: (i) Comparing the least squares means of the selection and control lines, (ii) Comparing the estimated breeding values of the selection and control lines. In CER, the response to selection for body weight and length varied from 15.0% to 21.4% and 4.0% to 7.2% per generation, respectively, at final measurement. In SER, the responses to selection were lower for both traits, varying from 7.9% to 8.2% and 3.5% to 4.1% per generation for weight and length, respectively. The estimated responses to selection based on least squares means were in good agreement with those calculated from breeding values. Selection under the CER rearing system resulted in greater estimated genetic response relative to SER. The reasons why this may have happened are discussed.

Keywords: Common carp, selective breeding, communal early rearing, separate early rearing, response to selection.

1. Introduction

The efficiency of family-based selection relies on the fact that the environmental deviations of the individuals tend to cancel each other out in the family mean value. This selection method has advantages over other types of selection especially when heritability for a trait of interest is low and when environmental deviations constitute a large part of the phenotypic variance. However, because fish are too small to be individually tagged at (or soon after) spawning they usually remain in their full-sib group until they are large enough to be tagged (5-10 g). This management results in a common (to full-sibs) environmental effect that contributes to the between family variance. From a managerial viewpoint it is desirable to reduce the common environmental component to a minimum by standardization of the environment for all families (Gjedrem, 2005). Thus, individuals from all families should be tagged as early as possible before communal rearing together in the same tank, pond or cage. However, family-based selection based on physical tagging has to accept a minimum period of separate rearing before tagging, which usually introduces a common environmental effect that varies in magnitude according to circumstances.

DNA fingerprinting was proposed as a tool for reconstructing the pedigree of communally reared aquaculture populations (Ferguson and Danzmann, 1998; Hara and Sekino, 2003; Sekino et al., 2003), which would allow high intensity selection programs to take place in production fish farms (Doyle and Herbinger, 1994). According to Rodzen et al. (2004) and Fjalestad et al. (2003), the development of DNA profiling techniques for family identification can reduce the problem of the introduction of environmental effects common to full-sibs and yield a higher selection response since fish are communally reared from a very early stage in the same environmental conditions. However, communal rearing and marker-based parentage assignment often

results in higher variance in family size because of unequal survival and sampling effects.

Mass selection was applied in carp selection programs in the past; however it showed lower selection response after some generations because of uncontrolled family contribution in each generation (Thien, 1993). Recently, more efficient carp selection programs have been established, including control of pedigree information by physically tagging and by genetic tagging methods. The estimation of genetic parameters showed that heritabilities for weight and length ranged from 0.33 to 0.50 in selection lines of European mirror carp (Vandeputte et al., 2004; Kocour et al., 2007; Nielsen et al., 2010) or from 0.14 to 0.30 in Oujiang colour common carp (Wang et al. 2006).

The heritabilities reported for body traits are moderate to high, and the genetic and phenotypic correlations among body traits are very high and positive. Therefore, it is suggested that genetic improvement of common carp for growth-related traits is feasible and that it should be possible to achieve a positive response to selection.

In the present study, we implemented two rearing schemes: i) early communal rearing from very soon after hatching, and ii) separate rearing of families until the fish were large enough to be physically tagged. The main aim of the study was to test the relative efficiency of communal early rearing (CER) and separate early rearing (SER) in the context of a Vietnamese common carp selective breeding program. We used microsatellite markers for parental assignment and pedigree reconstruction to investigate ways of further improving the ongoing breeding program. The genetic parameters, genetic and phenotypic correlations between traits in each rearing method were described by Ninh et al. (2011). In the present paper, we report selection response for growth performance traits in the common carp population under communal early rearing (CER) and separate early rearing (SER) schemes.

2. Materials and methods

2.1. Base populations

The base population (G_0) for the selection program was derived from the best performing animals (based on the estimated breeding values) produced from an incomplete diallel cross involving six carp stocks. A total of 20 crosses (three to nine families per cross) were successfully produced. Separate family rearing was conducted until the fish reached the necessary size for tagging, between 5 and 10 g. Eighty-six families were available for tagging (35 randomly selected fish tagged per family) (Table 1). PIT (Passive Integrated Transponder) tags were used for individual identification. The tagged fish from all families were communally grown out in one pond until harvest. After harvest, brood fish (150 females and 100 males) with high breeding value for harvest body weight were selected from 63 out of the 86 families to form the selection line. The model used to estimate breeding values (EBV) included the fixed effects of crosses and sex, and the random effects of individual fish and full-sib groups.

2.2. Generations 1 and 2 (G_1 and G_2)

2.2.1. Selection population: A partial factorial mating scheme (Berg and Henryon, 1998) was applied to produce the selected families in each generation. Under this mating scheme, one male was mated to two females as follows: Male 1 with females 1 and 2, male 2 with females 2 and 3, and so on to male n with female 1 and n . One hundred and sixteen brood fish selected for the highest breeding values for body weight from the G_0 , comprising 58 females and 58 males, were used to produce the G_1 families. They were produced in two batches, one week apart from each other, and 10 male brooders used in the first batch were re-used in the second one. Within each batch, after the eggs were stripped from a female, they were divided into two approximately equal parts and fertilized by two males to create full-sib and half-sib families. Fertilized eggs

from each full-sib group were incubated separately in upwelling jars. Some families had low hatching rates. A total of 107 selected families were successfully produced in G_1 .

Seventy-seven G_2 families were produced from 73 brooders (40 highest EBV females and 33 highest EBV males), selected from the best 57 families from the communal early rearing group at the final harvest measurement of G_1 (Table 1). The mating scheme and operation were similar to those used in the production of G_1 .

2.2.2. Control population: One hundred fish (60 females and 40 males) in the G_0 and sixty fish (30 females and 30 males) in the G_1 were selected from families with breeding values for body weight close to the overall mean of the population to create a control population. The number of full-sib control families produced was 28 in the G_1 generation and 16 in the G_2 . The plan was to produce 30 control families in each generation. However, some families were lost due to insufficient number of fry (Table 1). Eggs from each female were fertilized by a single male to produce full-sib families and incubated separately in upwelling jars. In all generations, the selection and control lines were contemporaneously maintained and during the course of the experiment the fish of both lines were reared under the same conditions and management practices (Ninh et al., 2011).

2.3. Rearing and data collection

2.3.1. Communal early rearing (CER): About three days after hatching, fry (2,000 individuals per family) from all families were communally reared in a pond at a stocking density of 2,000 individuals per m^2 . The communally reared fingerlings were sampled, weighed and measured at 135 days of age (post hatching) in G_1 and at 88 days in G_2 . The total number of fish sampled and tagged were 1327 in G_1 and 1332 in G_2 . They were correctly assigned to single families using seven microsatellite markers and

represented 113 and 92 families of both the selection and control lines in the G_1 and G_2 generations, respectively. The tagged fish were weighed and measured (standard length) and then restocked in an earthen pond at a stocking density of one individual per m^2 . Further records of weight and standard length were collected at 201 and 396 days old for G_1 and 184 and 317 days old for G_2 (Table 1). Parental assignment and further information about CER fish were reported by Ninh et al. (2011).

2.3.2. Separate early rearing (SER): Individual families of both the selected and control lines were reared separately from larvae to fry. Larvae were first stocked in $1 m^2$ fine net hapas with 0.8 m water depth at a stocking density of about 2,000 individuals per m^2 for each family for 30 days. When the fish had grown to approximately 0.1 g on average, 100 individuals per family were randomly selected and transferred to a $5 m^2$ plastic mesh hapa with 0.8 m water depth. When the fish were about 5-10 g (97-137 days old), 20 randomly chosen individuals per family of G_1 and 35 randomly chosen individuals per family of G_2 were tagged. Selected and control populations of G_2 generation in SER were produced from G_1 CER parent fish (G_1 CER fish reached maturity at one year old but G_1 SER fish did not, so it would not have been possible to produce a contemporaneous G_2 SER generation from G_1 SER parents at this time). The tagged fish of both the selection line and control group were then communally reared in a mono-culture grow-out earthen pond. Wet weight (g) and standard length (cm) of individuals were first collected at the time of tagging (137 and 97 days old in the G_1 and G_2 respectively). The next data collection was carried out when the fish were 204 days old (G_1), and 183 days old (G_2). The third and final data were collected at harvest time, when the fish were 414 and 257 days old for G_1 and G_2 , respectively (Table 1). Further details about management of SER fish are given by Ninh et al. (2011).

2.4. Quantitative genetic analysis

A mixed model to estimate population genetic parameters, as formulated by Ninh et al. (2011), was used to estimate genetic selection responses for body traits (weight and length) in this study. The full model was as follows:

$$y_{ijknpq} = \mu + G_i + L_j + S_k + (G*L)_{ij} + (G*S)_{ik} + (L*S)_{jk} + (G*L*S)_{ijk} + A + I_n + D_p + e_{ijknpq}$$

(Equation 1)

Where y_{ijknpq} is an observation of the individual q ; μ is the overall mean; G_i is the fixed effect of generation ($i = 1, 2, 3$); L_j is the fixed effect of line ($j = 1, 2$ or selection and control); S_k is the fixed effects of sex ($k = 1, 2$ or female and male); A is a linear covariate of age; $G*L$, $G*S$, $L*S$ and $G*L*S$ are the two- and three-way interaction among generation (G), line (L) and sex (S); I_n is the random additive genetic effect of the n^{th} individual; D_p is the random effects of maternal and common environment to full-sibs (and $\frac{1}{4}$ of dominance effect); e_{ijknpq} is the random residual effect associated with individual $ijknpq$.

The pedigree tracing back to the base population was used to avoid possible bias associated with the estimation of selection response. Preliminary analyses were performed in SAS (SAS Institute Inc., 1997). The Proc GLM (General Linear Model) procedure was used to test for significance of the fixed effects and the covariate. The effect of age nested within line and generation was not statistically significant ($P > 0.05$). The F-statistics for the increase in R^2 when changing from linear to polynomial (quadratic or cubic) regressions were also not statistically significant. Two and three factor interactions among the main fixed effects (i.e. $G*L$, $G*S$, $L*S$ and $G*L*S$) were not statistically significant ($P > 0.05$). All factors that failed to show a significant effect

on the traits of interest were removed from the model. A single trait model was used to derive breeding values for body weight (Equation 2).

$$y_{ijknpq} = \mu + G_i + L_j + S_k + A + I_n + D_p + e_{ijknpq} \quad (\text{Equation 2})$$

Where the model abbreviations are as defined above in equation 1.

All computations were carried out separately for each environment (CER and SER) in ASReml (Gilmour et al., 2002).

2.5. Response to selection

The least squares means estimated from the sire and dam mixed model were used to calculate selection response over generations for growth-related traits. The same fixed effects as described above (section 2.4) were used in the model. The random terms fitted in the model were sire within generation and line, and dam within sire, generation and line. The response to selection was calculated as the difference in the least squares means between the selection and control lines. In addition, the selection response was also calculated as the difference in estimated breeding values between the selection and control lines (Equation 1 - see Ninh et al., 2011).

3. Results

3.1. Generation and line differences

Least squares means for weight were all significantly different between selection and control lines in the two generations in CER ($P < 0.05$) (Figures 1 and 2). The difference between selection and control lines was already present at the first time of measurement, and increased with age. In addition, the selection line was 20.6% heavier in G_2 than G_1 at the first time of observation but the differences between the two generations decreased with later ages of measurements. The least squares means of length in the selection line were significantly greater than in the control line. The greatest difference between these two lines was shown at the final harvest data.

In SER, significant differences between the selection and control lines were observed for body weight and length only at final harvest in the G_1 . The mean weight and length at final harvest of the selection population were 8.2% and 3.5%, respectively, greater than the control line ($P < 0.05$). In G_2 , a significant difference ($P < 0.05$) between control and selected lines was also found for only length at the third observation (Figures 3 and 4).

There were differences in size of fish between CER and SER (Figures 5 and 6) although stocking density of those methods were equalized at all cultured stages from nursing to grow-out. The other management techniques were very similar between CER and SER. In addition, progeny in each generation were derived from the same families (same parents). However, the CER fish were three times heavier than the SER in the two selection generations at any of the three measurements. The length of CER fish was almost doubles that of the SER fish in the first two measurements and one half greater at the final measurement.

3.2. Sex differences

In CER, females grew faster than males for all the studied traits (Table 2). Between sex differences were significant for all growth performance traits (weight and length) ($P < 0.05$) except earliest weight and first two length measurements in G_1 . Females at final measurement were 9.1% and 2.1% in G_1 , and 1.2% and 4.0% in G_2 , larger than males for weight and length, respectively.

In SER, growth of females and males showed no significant difference for weight and length at the first and second times of measurement in G_1 and G_2 . However, females were significantly larger than males for all traits at the latest life stage assessed. Females were approximately 13.2% and 3.4% larger than males in weight and length in G_1 . In G_2 , weight and length of females were 13.3% and 5.5% larger than in males (Table 2).

3.3. Responses to selection

3.3.1. Estimated by least squares mean

In CER, selection resulted in significant response for body weight; 15.0% (from G_0 to G_1) and 21.4% (from G_1 to G_2) across measurements. The response to selection for length ranged from 4.0% to 7.2% per generation. When percent genetic gains were expressed as the difference between the lines, there was a decline in response at later measurements in CER but not in SER (Figures 7 and 8).

In SER, the responses to selection were positive but low for all traits, especially for length (2.9% to 3.5%) in G_1 . The G_2 analysis showed greater response to selection for weight at the first and second time of measurements but decreased slightly at the final observation. Overall, responses to selection in all traits were lower at the initial and second measurements than at the final harvest except for weight at the final measurement in G_2 . The response to selection was higher for weight than for length. In

addition, the responses to selection of the selective breeding line were fairly consistent across ages of measurement in both generations.

3.3.2. *Estimated breeding values (EBVs)*

In CER, estimated breeding values (EBVs) were almost zero for the traits studied in the base population G_0 (data not shown). EBVs increased consistently in G_1 and G_2 and were smallest at stocking and highest at the final harvest. Furthermore, the estimated breeding values for the selected population were higher than that for the control population. The genetic gain was calculated as the difference in EBVs between the lines (e.g. 16.7 g in G_1 and 14.7 g in G_2 for weight at the final harvest, corresponding to an average of 15.7 g per generation, Table 3).

In SER, estimated breeding values were smallest at stocking and greatest at the last measurement in both G_1 and G_2 (Table 3). The estimated breeding values (EBV) of growth-related traits were greater in the selection line compared to the control. However, the magnitudes of the difference between two lines for weight were lower in G_1 compared to G_2 . The estimates of selection response obtained by the two different methods were in agreement with each other for both body traits.

4. Discussion

4.1. Performance variation between generations and sex

4.1.1. Variation in performance between generations

There were large differences in size of fish between CER and SER (Figures 5 and 6) although the stocking density for both methods was equalized at all cultured stages from nursing to grow-out. These differences may be due to the habitat and feeding habits of the common carp as a bottom feeder; hapas are not favourable for nursing in the conditions implemented in SER. Separate full-sib family rearing seriously affected the growth rate of the fish.

In CER, generation and environment contributed more to the total variation than the effects of age, line and sex on weight and length (Ninh et al., 2011). The appearance of high variation between generations may be the result of good selection progress that moves forward the mean of the selected population but also included other factors such as variation of age at observation and environmental conditions, for instance weather changes between generations. The strong effect of environment could be explained by differences within and between generations including factors such as rearing conditions, water temperature, feed characteristics and husbandry. The availability of natural feed and bottom sediment in ponds are examples where competition of fish for food and other habitat may have occurred, especially as stocking density was also relatively high in ponds. All of those effects can be partially observed by looking at the different means between lines and generations in Figures 1 and 2. For example in Figure 1, the weight of the control and selection lines in G_2 was similar to the control line and even lower than the selection line in G_1 at tagging. However, both the selection and control lines in G_1 were significantly heavier than that in G_2 at the second and last measurements. Fish age at the time of measurement between ponds and generations was not analyzed as a covariate in the present study however this was demonstrated in tilapia (Ponzoni et al.,

2005; Maluwa et al., 2006), channel catfish (Rezk et al., 2003) and rainbow trout (Fishback et al., 2002).

In SER, Figures 3 and 4 clearly show differences of growth performance between G_1 (control and selection lines) and G_2 (control and selection lines) indicating that environment, grow-out conditions and selection influenced the performance of fish. Growth performance of the fish in each generation was also highly variable due to selection, environment and yearly condition as well as management methods. Change of weather in the spawning season is considered as one of the main effects, which suddenly reduced water temperature and caused longer incubation time for families hatched in one batch which then appeared to affect their growth in later life stages. The yearly conditions including environment and management practices may affect the growth of fish between generations. Growth performance of fish (Figures 3 and 4) showed that size at tagging in G_1 was lower even at higher age compared to in G_2 but fish size in G_1 was larger than in G_2 in the next measurements at the same age. Furthermore, this separate early rearing experiment was designed for comparison with the communal early rearing method.

4.1.2. Sex differences in growth traits

Growth of common carp is affected by sex, that is, females showed bigger size than males, from 1.2% to 9.1% for weight, 2.1% to 4.0% for length at final measurement (Table 2). In other research, common carp could be 7% to 8% heavier at market size (1 kg) in Israel by rearing all-female populations (Cherfas et al., 1996). Kocour et al. (2007) obtained from 4.8% to 6.8% better growth of a three year old all-female population compared to mixed sex, which is consistent with our results.

4.2. Responses to selection

In CER, response to selection for body weight estimated by least squares means from the mixed model ranged from 14.2% to 19.6% at the final harvest in each generation (Figure 7). The rates of response to selection in each generation in our study are similar to SER in findings of 14% in Atlantic salmon (Gjerde, 1986), 13% in rainbow trout (Gjerde, 1986), 10% in coho salmon (Hershberger et al., 1990), 7% to 10% in channel catfish (Rezk et al., 2003) and 10% to 20% in tilapia (Gjedrem and Thodesen, 2005; Ponzoni et al., 2011).

Selection for body weight also resulted in correlated increase in standard length as estimated from the differences in both least squares means and breeding values between the lines in each generation. This is consistent with the theoretical predictions in tilapia by Nguyen et al. (2007). In the present study, the genetic gains calculated by the estimated breeding values were greater than those estimated from phenotypic observation by mixed model. The observed response to selection was 19.6% and 4.8% for weight and length respectively at the final harvest in the G_2 . These results and moderate heritability of traits at different measurements (Ninh et al., 2011) suggest that a rapid rate of genetic improvement is feasible in the selective breeding program for common carp.

Although selection was practiced on CER fish to produce G_2 , a substantial response was also achieved for growth-related traits in SER. The response in each generation of selection, measured as the differences in least squares means and estimated breeding values between the selection and control lines, ranged from 3.3% to 8.2% for growth-related traits at the final harvest in SER.

The results presented here show that the selected lines improved over generations. No genetic gain during five generations of mass selection for growth trait of carp was found by Moav and Wohlfarth (1976). An average improvement of 6% to

7% per generation has been obtained for most species but some other studies indicating average genetic gains of over 10% per generation by applying separate family rearing and selection in coho salmon (Hershberger et al., 1990), Atlantic salmon (Thodesen et al., 1999) and tilapia (Gall and Bakar, 2002; Bolivar and Newkirk, 2002; Ponzoni et al., 2005, 2011). Vandeputte et al. (2008) predicted a positive but low response to mass selection of the best 3%, assuming that the growth trait of carp had heritability of 0.3 and the phenotypic coefficient of variation was 30%. The performance of the selected lines in a selective breeding program improved with advancing generations but a genuine control line did not change much in most studies, for instance, in coho salmon (Hershberger et al., 1990) or rainbow trout (Chevassus et al., 2004).

The genetic gain estimated in our study should be expected to have minimum bias. The models fitted accounted for all possible effects recorded during the course of the selection program. However, there may be numerous other factors which may have had an influence on body traits. Therefore there is still a need to maintain controls. In practice, the actual phenotypic changes corresponding to the expected genetic response to selection can only be estimated accurately when the common environmental (full-sib family) effects are identified (Gall et al., 1993). In our case the common environmental (full-sib family) effects were included as an additional random term in the statistical model when estimating breeding values. However, competition effects that may accompany selection for high growth (Moav and Wohlfarth, 1974) were not accounted for in calculations of genetic gain because these indirect genetic effects are not easily estimated from the current data, unless a strictly designed experiment that requires tremendous facilities (hapas) is assigned for this purpose (Bijma, 2010).

Moav and Wohlfarth (1974) observed increased variance in size between genetically different groups of common carp in communal rearing compared to separate rearing. Vandeputte et al. (2009) observed increased differences in size between

selected and control groups of European sea bass (*Dicentrarchus labrax*) in communal rearing compared to separate rearing. In the former case, the common carp were mixed when large enough to physically mark (by branding), whereas the sea bass were mixed at the egg stage and parentage assigned later using microsatellite markers. In the present study, we compared selected and control groups that were either reared communally from shortly after hatch (CER), or reared separately until large enough to tag and then reared communally until harvest (SER). It is possible that the early period of communal rearing in the CER conditions may have inflated the difference in size between the selection and control groups by harvest time, compared to the SER groups. However, we did not attempt to estimate this separately from the genetic response to selection under the two different conditions. The estimation would have required separate rearing of control and selection fish in several replicate containments.

The selection response achieved is as expected from the moderate to high heritabilities estimated for growth-related traits in CER and SER (Ninh et al., 2011). In the second generation there was greater selection response than in the first generation. The selection responses under CER were almost double those under SER for weight and length (Figures 7 and 8). Whereas response to selection decreased from the first measurement to final harvest in CER it increased with greater age in SER. The G_2 fish in SER were derived from selected parents of the G_1 CER fish as a consequence genetic gain in CER was direct response to the selection, and the estimated gain in SER was correlated response. The selection response may be related to size or stage of development and final harvest size of fish as well as rearing methods. The lower response to selection in SER than in CER could also be partially due to environmental effects on family means or due to genotype by rearing environment interaction that caused lower accuracy in the selection estimates. The advantage of CER over SER is probably greater in common carp than in tilapia because carps seem to adapt less readily

and not as well as tilapia to a hapa environment, where the full-sib groups have to be kept until tagging under SER.

4.3. Conclusions

The present investigation revealed that common carp genetic improvement programs in Vietnam may be successful using either method, communal early rearing (CER) or separate early rearing (SER). However, the responses to selection obtained in this study demonstrate that growth performance of common carp can be improved at a faster rate by CER. For selection using communal rearing of families to provide continuing genetic gain, it is vital that it is used in conjunction with structured mating and marker-based parentage assignment, to provide pedigree information and allow control over effective population size.

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Table 1. Family size, representation and age at measurements in generations 0, 1 and 2 (G_0 , G_1 and G_2 , respectively) of SER and CER.

	Lines	G_0	G_1		G_2	
			CER	SER	CER	SER
Number of families in	Selection	86	93	107	76	77
	Control	-	20	28	16	16
Number of female parents used	Selection	86	58	58	40	40
	Control	-	20	28	16	16
Number of male parents used	Selection	86	58	58	33	33
	Control	-	20	28	15	16
Number of progeny at tagging (assigned) in	Selection	1750	1098	2121	964	2522
	Control	-	186	549	317	488
Number of progeny per full-sib family in	Selection	18-35	1-49	18-20	1-38	30-35
	Control		2-23	18-20	1-43	28-35
Age at first measurement (days)	Selection	382	135	137	88	97
	Control		135	137	88	97
Age at second measurement (days)	Selection	382	201	204	184	183
	Control		201	204	184	183
Age at third measurement (days)	Selection	382	396	414	317	257
	Control		396	414	317	257

Table 2. Least-squares means (\pm S.E.) of traits at different measurements for females and males in G₁ and G₂ obtained from the sire and dam mixed model.

Rearing method	Time of measurement ^a	Sex	G ₁		G ₂	
			Weight (g)	Length (cm)	Weight (g)	Length (cm)
CER	1	Female	85.01 \pm 1.17 ^a	17.54 \pm 0.07 ^a	102.03 \pm 2.35 ^a	17.85 \pm 0.13 ^a
	1	Male	82.41 \pm 1.27 ^a	17.39 \pm 0.08 ^a	90.86 \pm 2.35 ^b	17.20 \pm 0.14 ^b
	2	Female	277.16 \pm 3.98 ^a	25.64 \pm 0.12 ^a	238.08 \pm 5.33 ^a	24.50 \pm 4.16 ^a
	2	Male	265.96 \pm 4.33 ^b	25.37 \pm 0.13 ^a	208.51 \pm 5.24 ^b	23.59 \pm 0.17 ^b
	3	Female	1028.61 \pm 15.29 ^a	38.91 \pm 0.16 ^a	537.35 \pm 11.91 ^a	30.00 \pm 0.19 ^a
	3	Male	935.33 \pm 16.77 ^b	38.08 \pm 0.19 ^b	528.81 \pm 18.16 ^b	28.79 \pm 0.22 ^b
SER	1	Female	23.26 \pm 0.64 ^a	10.89 \pm 0.09 ^a	35.36 \pm 2.53 ^a	12.34 \pm 0.25 ^a
	1	Male	22.69 \pm 0.68 ^a	10.82 \pm 0.09 ^a	35.20 \pm 2.52 ^a	12.22 \pm 0.25 ^a
	2	Female	83.05 \pm 2.17 ^a	17.44 \pm 0.15 ^a	77.99 \pm 6.45 ^a	16.31 \pm 0.36 ^a
	2	Male	78.74 \pm 2.37 ^a	17.09 \pm 0.16 ^a	73.06 \pm 6.39 ^a	16.11 \pm 0.35 ^a
	3	Female	377.72 \pm 9.83 ^a	28.52 \pm 0.25 ^a	173.04 \pm 11.96 ^a	21.46 \pm 0.41 ^a
	3	Male	328.05 \pm 10.59 ^b	27.54 \pm 0.27 ^b	150.03 \pm 11.43 ^b	20.29 \pm 0.40 ^b

^a Three time of measurements are ages at measurement in Table 1.

Means of traits with different subscript letters are significantly different ($P < 0.05$) for sex at the same time of measurement and same rearing method.

Table 3. Univariate estimated breeding values[‡] (\pm S.E.) of traits at different measurements for lines (control and selection) and generations (G_1 and G_2) relative to G_0 .

Rearing method	Time of measurement ^a	Weight (g)				Length (cm)			
		G_1		G_2		G_1		G_2	
		Control	Selection	Control	Selection	Control	Selection	Control	Selection
CER	1	1.47 \pm 0.67	1.72 \pm 0.52	2.83 \pm 0.67	3.78 \pm 0.42	0.27 \pm 0.05	0.29 \pm 0.03	0.32 \pm 0.04	0.38 \pm 0.02
SER	1	1.54 \pm 0.24	1.65 \pm 0.23	1.62 \pm 0.22	1.70 \pm 0.23	0.11 \pm 0.02	0.115 \pm 0.03	0.14 \pm 0.02	0.145 \pm 0.04
CER	2	14.01 \pm 0.43	16.94 \pm 0.75	10.96 \pm 0.93	15.12 \pm 0.58	0.66 \pm 0.05	0.72 \pm 0.03	0.54 \pm 0.04	0.62 \pm 0.02
SER	2	2.98 \pm 0.67	3.20 \pm 0.80	2.46 \pm 0.44	2.71 \pm 0.58	0.22 \pm 0.02	0.23 \pm 0.03	0.20 \pm 0.02	0.21 \pm 0.04
CER	3	69.30 \pm 2.05	86.00 \pm 2.03	46.78 \pm 1.40	61.53 \pm 1.21	1.95 \pm 0.11	2.07 \pm 0.04	1.64 \pm 0.08	1.72 \pm 0.03
SER	3	9.90 \pm 1.62	10.80 \pm 2.30	7.40 \pm 1.01	8.10 \pm 1.16	0.94 \pm 0.08	0.98 \pm 0.05	0.92 \pm 0.02	0.93 \pm 0.04

^a The three times of measurements are described in detail in Table 1.

[‡] Using animal and dam model (equation 2) as described in section 2.4

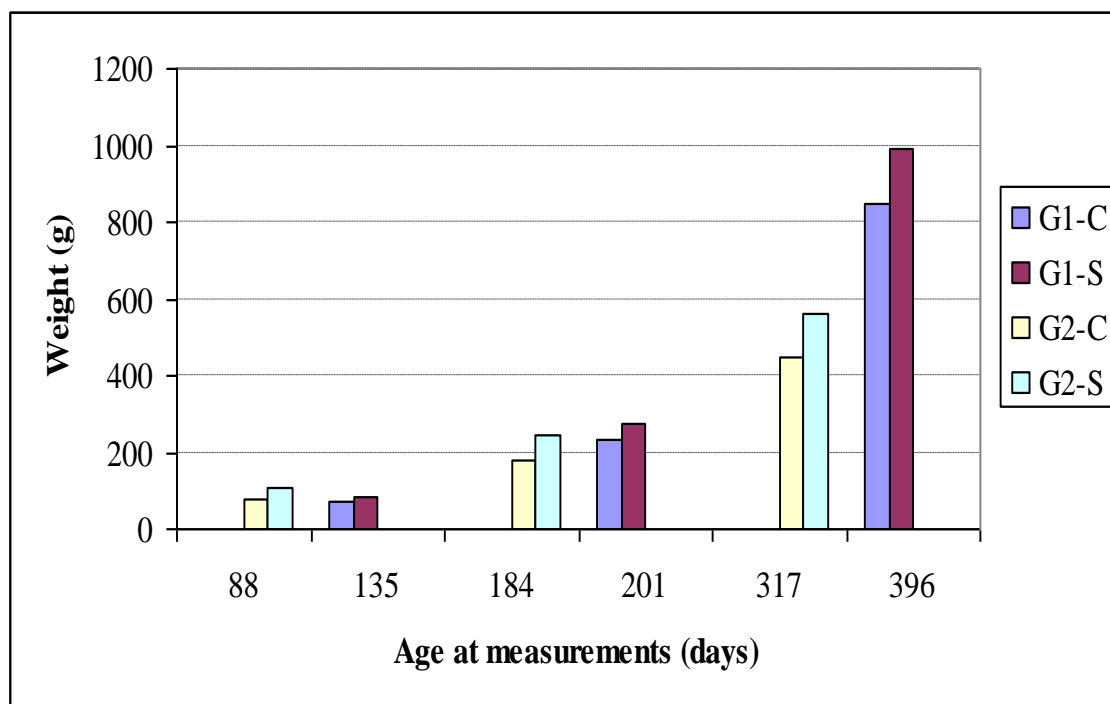


Figure 1. Least squares means of weight at different measurements for each generation (G₁, G₂) and line (C: Control, S: Selection) in CER.

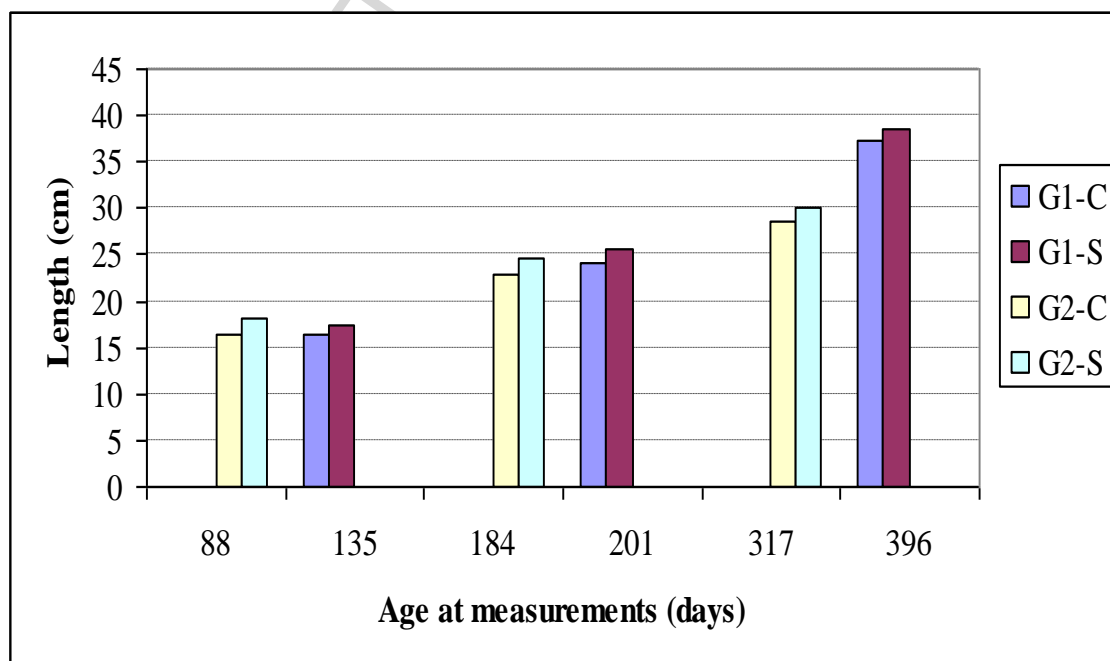


Figure 2. Least squares means of length at different measurements for each generation (G₁, G₂) and line (C: Control, S: Selection) in CER.

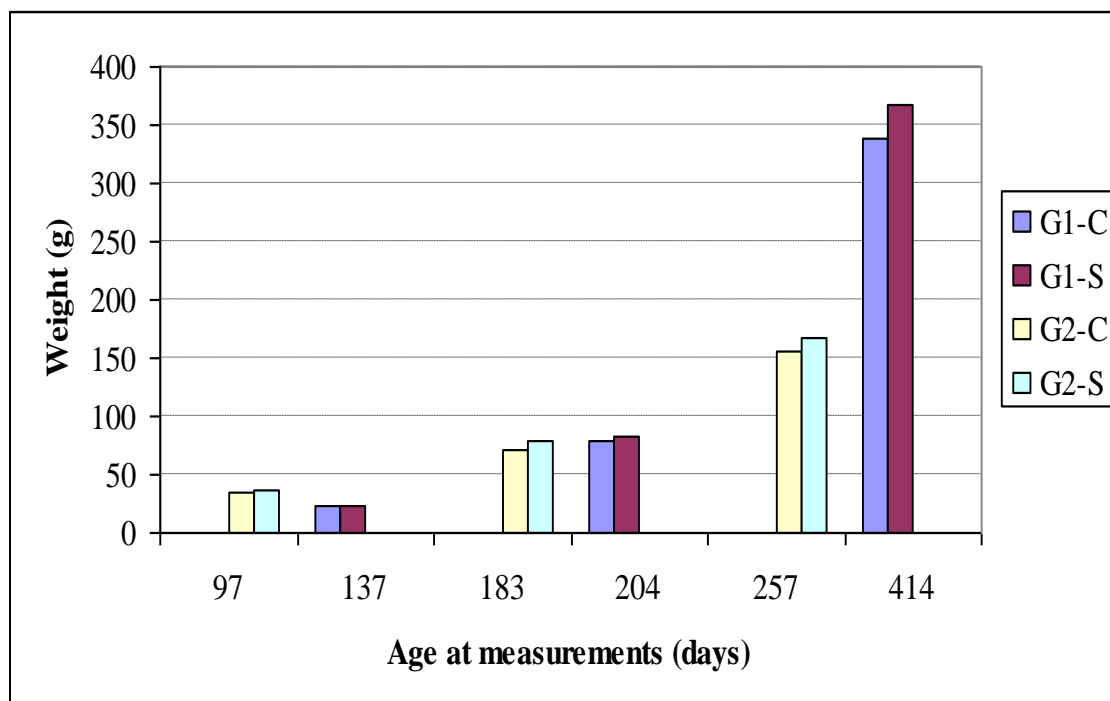


Figure 3. Least squares means of weight at different measurements for each generation (G_1 , G_2) and line (C: Control, S: Selection) in SER.

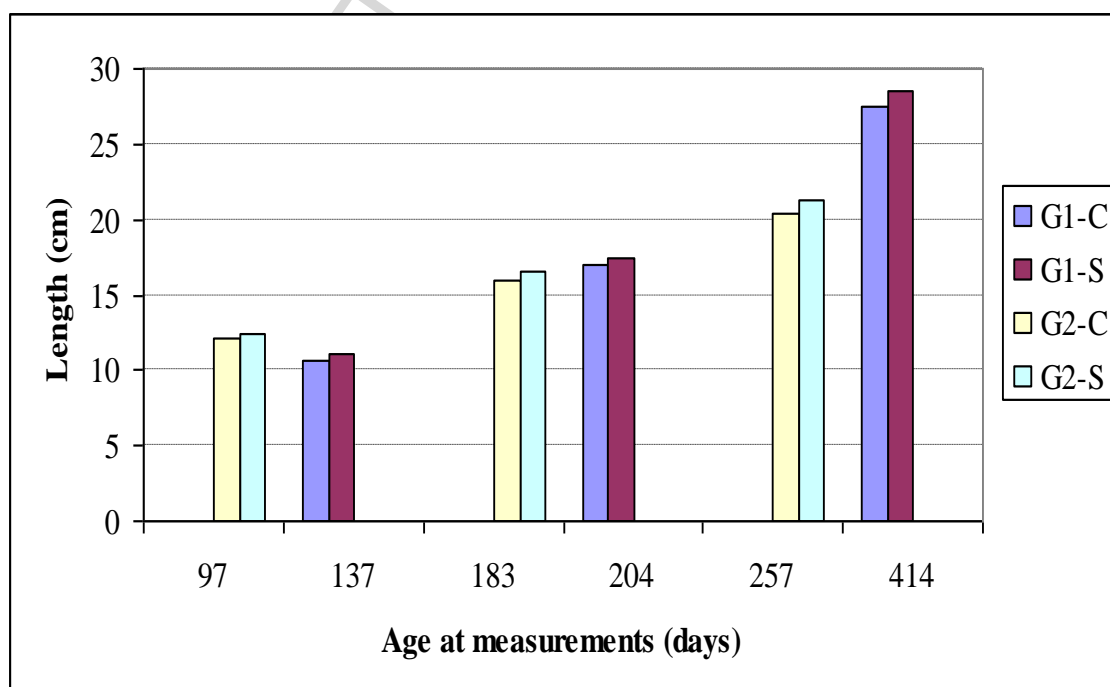


Figure 4. Least squares means of length at different measurements for each generation (G_1 , G_2) and line (C: Control, S: Selection) in SER.

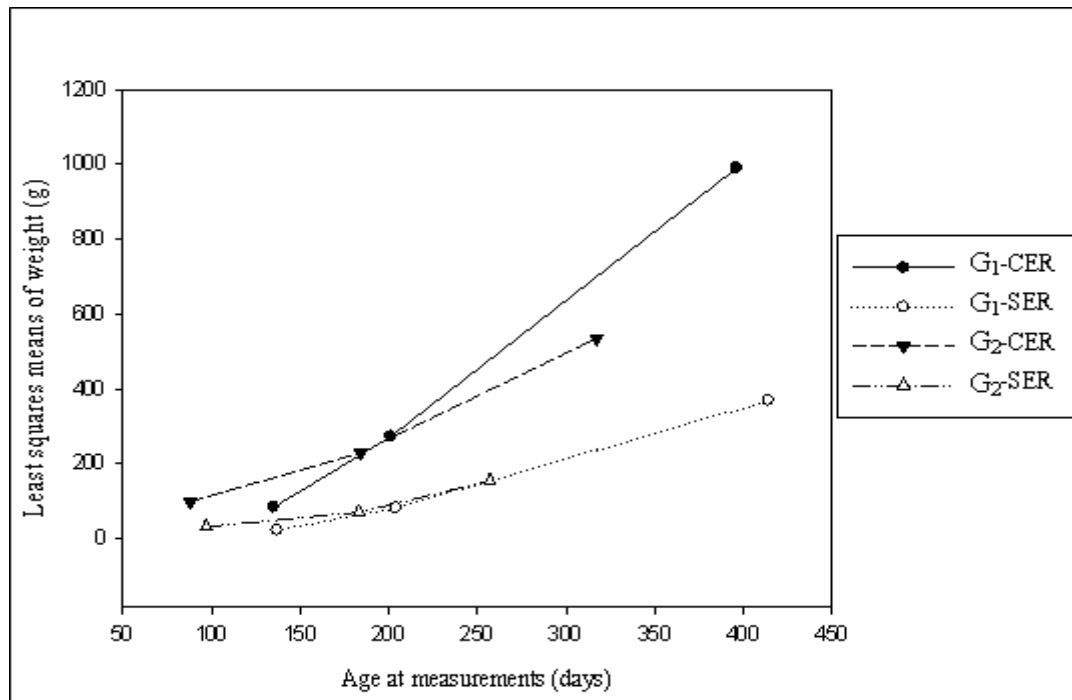


Figure 5. Least squares means of weight at different measurements of selected fish in each generation (G_1 and G_2) and rearing method (CER and SER).

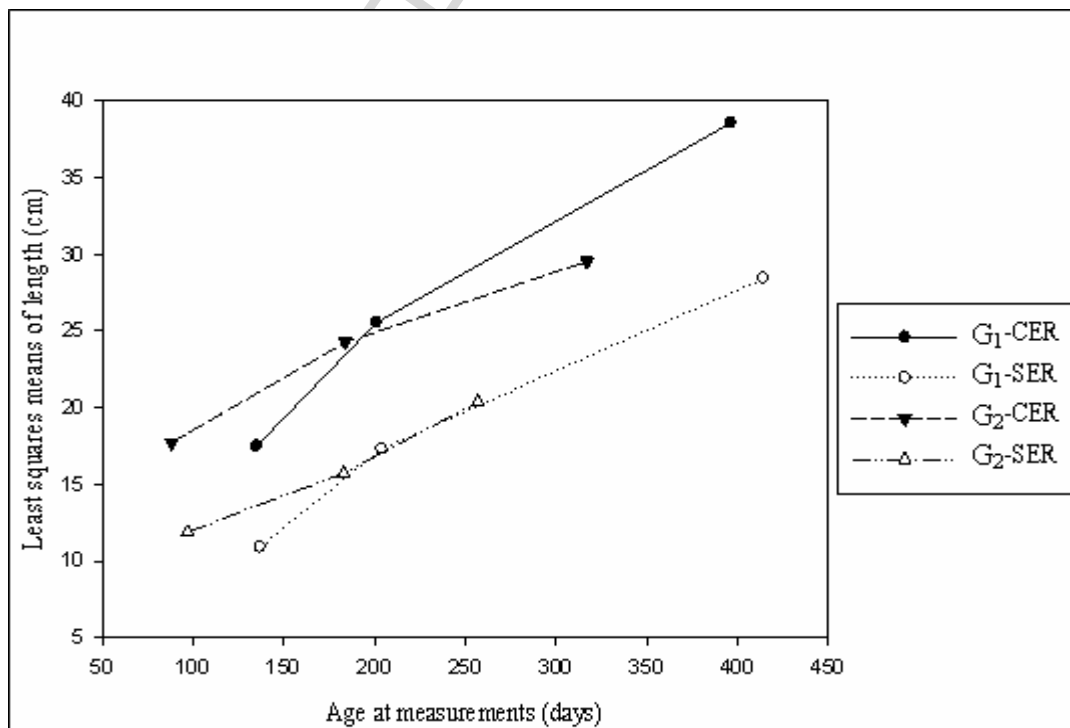


Figure 6. Least squares means of length at different measurements of selected fish in each generation (G_1 and G_2) and rearing method (CER and SER).

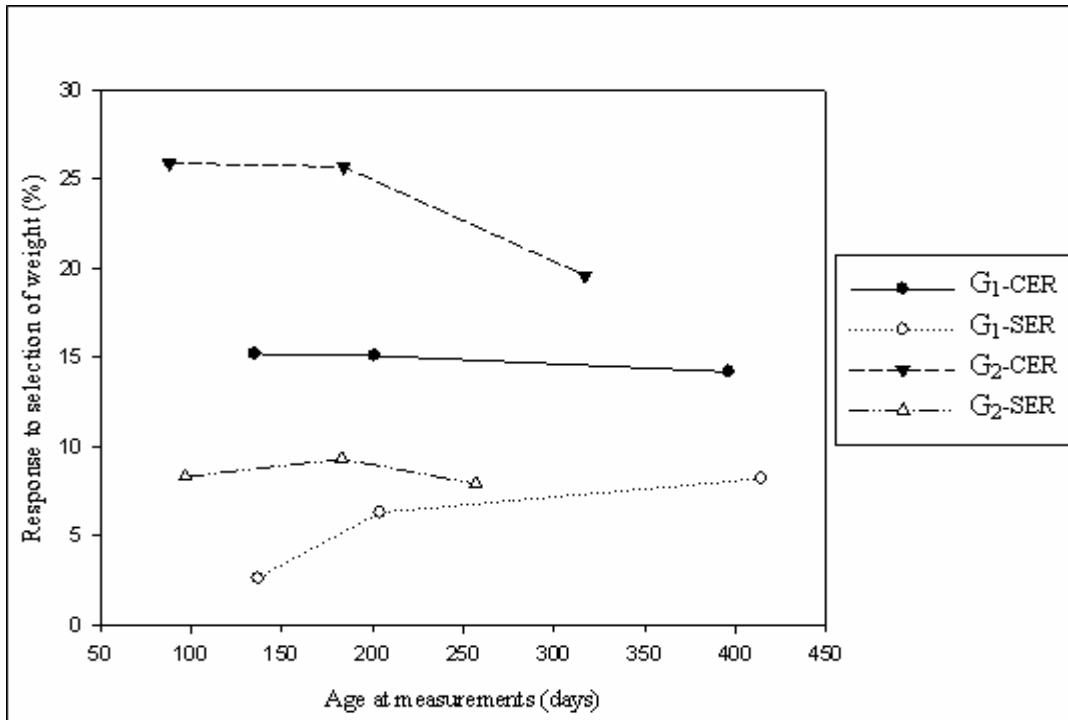


Figure 7. Response to selection of weight at different measurements in each generation (G₁ and G₂) and rearing methods (CER and SER).

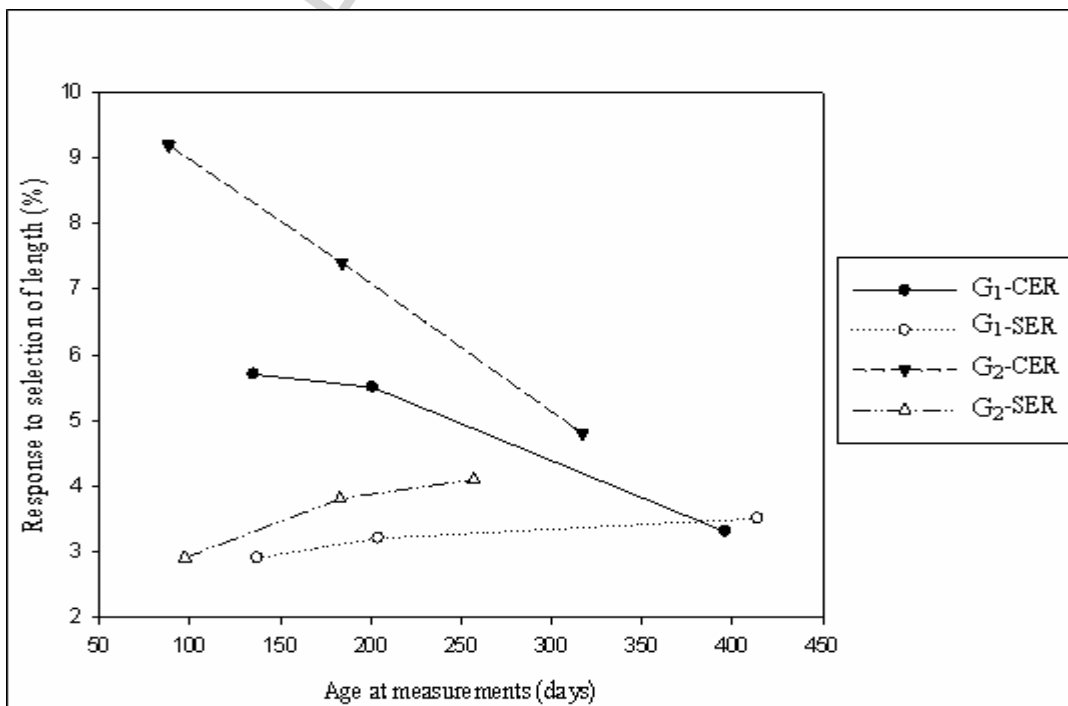


Figure 8. Response to selection of length at different measurements in each generation (G₁ and G₂) and rearing method (CER and SER).

Highlights

We reared common carp families in communal early rearing (CER) or separate early rearing (SER) conditions.

Responses to selection for growth performance were moderate to high in CER and SER.

Growth performance of common carp can be improved at a faster rate by CER.

ACCEPTED MANUSCRIPT