Improvement of Quality in the Common Carp by Crossbreeding

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In order to obtain hybrids that combined the economic advantages of two parent races of the common carp, *Cyprinus carpio*, we produced not only F₁ hybrids of Japanese, Chinese, and various European races, but also progeny of various intercrosses of the F₁ generations, backcrosses, and modified triple or multiple crosses. Definite heterosis was found in seven of twelve F₁ hybrids. Of the F₁ hybrids, the products of a cross between female yamato and male mirror carps (YM) had the highest growth rate. The growth rate and efficiency of feed conversion of the YM exceeded those of both the maternal and the paternal race; the latter (the mirror) had the fastest growth rate and the highest feed-conversion efficiency of any of the parent races used. The YM, due to their high resistance to *Gyrodactylus* or fungus infections, also had a higher survival rate than did either parent race. All YM are scaly, which is a preferred character in Japan. Most progeny from F₁ intercrosses, backcrosses, and triple crosses, however, were economically less desirable than the YM; only the progeny from a multiple cross, (yamato ♀ × scaly German ♂) ♀ × (wild ♀ × mirror ♂) ♂, grew faster and converted feed more efficiently than the YM. The difference between the survival rates of these progeny, the YM F₁ generation, and the yamato carp was negligible. We conclude that the hybrid progeny from the multiple cross are the most economically valuable carp of those studied.

Many races of the common carp, *Cyprinus carpio*, now exist throughout the world. Racial differences in economically desirable characters, such as growth and survival rates, the efficiency with which feed is converted into flesh, catchability by angling, and the ability to escape from a seine, have been studied¹⁻¹²⁾. Crossbreeding is an important method for improving the quality of fish by combining economically desirable characters of parent races and reducing uneconomic characters. Many F₁ hybrids of the carp have been produced especially from European races, and their growth rates, resistance to disease, and catchability by angling have been studied^{4,9,13-17)}. However, the efficiency of the conversion of feed into flesh has scarcely been examined in the cultivated hybrids being compared with the parent races, though the efficiency of feed conversion is a most important issue in carp culture especially in Japan due to intensive artificial feeding.

In an attempt to obtain hybrids with the economic advantages of both parent races, we have produced not only F₁ hybrids, but also many progeny from intercrosses of the F₁ hybrids, back-

crosses, and modified triple or multiple crosses of Japanese, Chinese and European races of the common carp. Here we report the efficiency of feed conversion, the survival rates and the growth rates of these hybrids when they were raised under intensive artificial feeding.

Materials and Methods

The experiments were carried out at the Ueda Branch, Freshwater Fisheries Research Laboratory*³. The following races of carp were used: domesticated Japanese yamato carp originally obtained from a farm in Saku City in 1966 and from one in Suwa City in 1971, Nagano Prefecture; wild carp originally collected from Lake Kasumigaura in 1966 and maintained in captivity since then; domesticated European carps, both scaly and mirror types, transplanted from Germany in 1968; and a Chinese race known as the big-belly carp, transplanted from Taiwan in 1970. The yamato carp from the Saku City farm were used in almost all crosses with this race; those from the Suwa City farm were used only for a cross between female

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wild and male yamato, and for a pure combination of the yamato as a control of its cross. For the F_1 experiment, the adults of the wild and Chinese carps were from the first generation after the capture or transplantation of the race to the laboratory, and those of the other races were of the second generation. For the F_2 , backcross, triple-cross, and multiple-cross experiments, adults of the yamato, scaly German, and mirror carps were of the third generation.

All crosses were carried out by mixing eggs artificially stripped from adult females with spermatozoa from adult males. Three females and four males were used per cross, to reduce the chances of poor viability that might have resulted from the use of only one specimen of each sex, which might have had some unknown undesirable characters. The controls were obtained by fertilizing eggs from a given individual female with spermatozoa from a male of the same race.

Hatched fry were cultivated in ponds fertilized with soy lees. Two hundred 1- or 2-month-old fry of each cross were cultivated in a separate cemented pond approximately 3.2 m² in area and 0.7 m deep, and containing water constantly maintained at $25 \pm 1^\circ\text{C}$ and flowing at approximately 20 l/min. The number of fry per pond was reduced to 150 after 3 months, 100 after 5 months, and 50 after 7 months. The fish were given pelleted artificial carp feed (Nippai KK) daily, in amounts appropriate to the body weight of the fish; they were fed by hand in the F_1 and F_2 experiments, and by automatic feeder in the backcross, triple-cross, and multiple-cross experiments. More detailed methods are given under the description of each experiment.

Results

F_1 Hybrids

1) Crosses with female mirror, scaly German, and yamato carps

Female mirror, scaly German, and yamato carps were crossed with males of various races on 30 May 1974, in the combinations shown in Table 1. After reaching the age of 1 month, the fry with a mean body weight of 0.35 g in each cross were chosen and were then cultivated for 8 months, from 6 July 1974 to 3 March 1975; thereafter, only the hybrids that showed heterosis and the controls of the parent races were cultivated for 2 more months, to 7 May 1975. Our results for these F_1 hybrids are summarized in Table 1, and the growth curves

Fig. 1. Growth curves of the F_1 hybrids (solid line) showed heterosis, and their parent races (dotted line). M, G, Y, C, and W show mirror, scaly German, yamato, Chinese and wild carp respectively. YM, YG, YC, and YW show F_1 hybrids produced from $Y \times M$, $Y \times G$, $Y \times C$, and $Y \times W$ respectively.

of the hybrids that showed heterosis are given in Fig. 1.

The parent races were ranked for growth on the basis of statistically significant differences on student t-test comparisons of the average body weights of the fish at harvest. The resulting growth-rate hierarchy was as follows: mirror > scaly German $\approx$ yamato > Chinese > wild carp. Thus, the mirror carp had the highest growth rate; the difference between the second- and third-ranking races (scaly German and yamato) was not significant ($p > 0.05$). The same hierarchy was found for the efficiency of feed conversion except that the positions of the scaly German and the yamato carp were reversed; to assess feed-conversion efficiency, we periodically weighed the live fish. The hierarchy for the survival rate among the parent races was as follows: Chinese > yamato > scaly German $\approx$ mirror > wild carp. Many wild carp died as fry, within 3 months of the start of cultivation, becoming malnourished because they did not like the artificial feed. The mirror carp were penultimate in the

Table 1. Cultivation results in the F₁ hybrids produced from crosses with female mirror, scaly German and yamato carps

Crosses	Initial body weight (g)	8-month culture (6 July 1974 to 3 March 1975)					10-month culture (6 July 1974 to 7 May 1975)				
		Average body weight (g)	Survival rate (%)	Growth rate* ¹ (%/day)	Efficiency of feed conversion (%)	Heterosis potency ratio* ²	Average body weight (g)	Survival rate (%)	Growth rate* ¹ (%/day)	Efficiency of feed conversion (%)	Heterosis potency ratio* ²
Mirror ♀											
× Mirror ♂	0.35	302±19* ³	76.7	2.79	89.4		604±61* ³	72.5	2.44	82.1	
× Scaly German ♂	0.35	248±17	89.6	2.71	88.7	0.91					
× Yamato ♂	0.35	248±20	96.0	2.71	86.9	0.91					
× Wild ♂	0.35	168±19	86.0	2.55	77.6	0.97					
Scaly German ♀											
× Scaly German ♂	0.35	245±26	78.7	2.70	84.7		496±95	76.3	2.38	78.4	
× Mirror ♂	0.35	202±17	72.5	2.62	82.5	0.74					
× Yamato ♂	0.35	233±24	86.6	2.68	83.8	0.96					
Yamato ♀											
× Yamato ♂	0.35	242±18	82.6	2.70	86.2		482±45	80.0	2.37	79.8	
× Mirror ♂	0.35	337±29	84.4	2.84	89.6	1.24	856±109	84.4	2.56	85.8	1.58
× Scaly German ♂	0.35	319±24	77.7	2.81	89.3	1.31	738±66	77.7	2.51	84.3	1.51
× Chinese ♂	0.35	269±16	90.6	2.74	86.9	1.25	651±41	90.6	2.47	83.4	1.47
× Wild ♂	0.35	253±35	73.3	2.72	81.9	1.77	590±99	73.3	2.43	78.7	2.09
Wild ♀											
× Wild ♂	0.35	44±8	48.5	2.00	52.0		83±32	42.2	1.79	50.5	
Chinese ♀											
× Chinese ♂	0.35	189±13	90.8	2.60	78.2		406±38	90.8	2.31	74.3	

*¹ $G = 100 \frac{\log {}^a Y_T - \log {}^a Y_t}{T - t}$, where Y_T and Y_t are the average body weight recorded at T and t, T being later than t, that of two parent races, *³ Standard error.

*² Computed from the average body weight of the F₁ hybrids against

survival ranking, because at the age of 1 year they were highly susceptible to *Gyrodactylus* infection; fungus infection also lowered their rate of survival. The poor survival of the mirror and wild carp was a repetition of their poor performance when they were grown in running-water ponds with uncontrolled water temperature, as reported earlier¹⁰.

On the other hand, when female yamato carp (Y) were crossed with males of other races, mirror (M), scaly German (G), Chinese (C), and wild (W) carps, the F_1 hybrids (YM, YG, YC, and YW) showed definite heterosis; i.e., most of them had growth rates and efficiencies of feed conversion of that were much higher than those of either parent race. For growth rates, these hybrids ranked the same as their paternal races, i.e., YM, YG, YC, and YW. The YM converted feed most efficiently, and they weighed significantly more ($p < 0.05$) at harvest than their paternal and maternal races. Furthermore, the survival rate of the YM was not only higher than that of the mirror carp, but was also somewhat higher than that of the yamato carp. None of the YM was infected with *Gyrodactylus* or fungus, but some of them died as a result of poor handling when they were weighed monthly. All of them were completely scaly. Most of the F_1 hybrids other than YM, YG, YC, and YW had growth rates and feed-conversion efficiencies intermediate between those of the two parent races. However, the great majority of these hybrids had higher survival rates than those of either parent race, because none of the hybrids were susceptible to *Gyrodactylus* infection, even those from crosses with the female mirror carp.

2) Crosses with female wild carp

Female wild carps were crossed with males of the mirror, scaly German, and yamato carps on 28 May 1977. Fry with a mean body weight of 3.0 g for each cross were chosen when they were about 2 months old and were then cultivated from 22 July 1977 until 19 February 1978. Before the cultivation experiments, each pond was treated with a 1/2,000 formalin solution in order to kill *Gyrodactylus*.

For the parent races, the hierarchies for growth rate and for efficiency of feed conversion were mirror > scaly German $\approx$ yamato > wild carp, the same as that found in the experiments made from 1974 to 1975 and in the preceding section. The survival rates of these parent races varied within a narrow range, from 82.7 to 97.0% (Table 2). *Gyrodactylus* infection was not observed, even in the mirror carp.

The F_1 hybrids from crosses between female wild carp and male scaly German or yamato carp showed heterosis in growth and more efficient feed conversion than did either parent race. The progeny of crosses between female wild and male mirror carps were intermediate in growth rate and efficiency of feed conversion between those of the parent races, although the heterosis potency ratio was 1.67. None of the hybrids from these crosses with female wild carp grew faster than the mirror carp. The survival rates of the hybrids were very similar, ranging from 92.0 to 95.1%.

F_2 Hybrids

F_2 hybrids were produced by intercrossing the F_1

Table 2. Cultivation results in the F_1 hybrids produced from crosses with female wild carp

Crosses	Initial body weight (g)	7-month culture (22 July 1977 to 19 February 1978)				
		Average body weight (g)	Survival rate (%)	Growth rate* ¹ (%/day)	Efficiency of feed conversion (%)	Heterosis potency ratio* ²
Wild ♀						
× Wild ♂	3.0	89 ± 5* ³	90.2	1.62	53.6	
× Mirror ♂	3.0	470 ± 12	95.1	2.42	87.6	1.43
× Scaly German ♂	3.0	430 ± 10	92.0	2.37	86.3	1.72
× Yamato ♂	3.0	413 ± 13	93.0	2.35	84.6	1.67
Mirror ♀						
× Mirror ♂	3.0	570 ± 10	97.0	2.51	93.3	
Scaly German ♂						
× Scaly German ♂	3.0	410 ± 7	82.7	2.35	84.8	
Yamato ♀						
× Yamato ♂	3.0	405 ± 10	97.0	2.34	84.5	

*¹ $G = 100 \frac{\log * Y_T - \log * Y_t}{T - t}$, where Y_T and Y_t are the body weight recorded at T and t, T being later than t, *² Computed from the average body weight of the F_1 hybrids against that of two parent races, *³ Standard error.

Table 3. Cultivation results in the F_2 hybrids compared with those in the F_1 hybrids and the parental races. YM and YG show F_1 hybrids produced from yamato ♀ × mirror ♂ and yamato ♀ × scaly German ♂ respectively.

Crosses	Initial body weight (g)	7-month culture (19 August 1975 to 19 March 1976)				
		Average body weight (g)	Survival rate (%)	Growth rate* ¹ (%/day)	Efficiency of feed conversion (%)	Heterosis potency ratio* ²
Mirror	2.5	581 ± 16* ³	93.5	2.52	80.7	
Scaly German	2.5	524 ± 17	97.3	2.47	79.8	
Yamato	2.5	300 ± 14	100	2.21	71.2	
YM	2.5	597 ± 27	100	2.53	80.8	1.36
YG	2.5	600 ± 19	99.0	2.53	82.7	1.46
YM ♀ × YM ♂ (F_2)	2.5	607 ± 21	91.0	2.54	80.8	1.02
YG ♀ × YG ♂ (F_2)	2.5	474 ± 21	98.0	2.43	78.9	0.79

*¹ $G = 100 \frac{\log^e Y_T - \log^e Y_t}{T - t}$, where Y_T and Y_t are the body weight recorded at T and t , T being later than t , *² Computed from the average body weight of the F_1 and F_2 hybrids against that of two parent races, *³ Standard error.

YM or YG hybrids, which had showed remarkable heterosis in the 1974/75 experiment. In addition, F_1 YM and YG hybrids, and controls, were produced again from carp bred in 1974, for comparison with the F_2 . Each pond was treated in advance with a 1/2,000 formalin solution. One-month-old fry with a mean body weight of 2.5 g in each cross were selected for cultivation for 7 months thereafter, from 19 August 1975 to 19 March 1976.

Of the parent races, the mirror carp had the fastest growth rate, the scaly German carp intermediate, and the yamato carp lowest (Table 3); the racial differences in average body weights at harvest were significant.

Both of the newly produced F_1 YM and YG hybrids showed heterosis, as in the 1974/75 experiment; that is, the growth rates and efficiencies of feed conversion exceeded those of either parent race.

Table 4. Ratio of the scaly and mirror-type carps in the F_2 hybrids produced from the F_1 yamato-mirror hybrid (YM), scored on four-month-old fry

Item	Scaly	Mirror	Total
Observed	930	313	1243
Expected	932.2	310.8	1243
Ratio	3	1	
$\chi^2_{(1)} = 0.021, p = 0.90-0.80$			

The F_2 progeny of the YM hybrids grew faster and converted feed somewhat more efficiently than did the F_1 , although the mean body weights of harvested F_2 and F_1 specimens were not significantly different. Among the products of the YG cross,

the growth rate and the feed-conversion efficiency were lower for the F_2 than for the F_1 generation. The differences between the survival rates of the two crosses were negligible. In the F_2 progeny from YM crosses, the scaly and the mirror-type carps segregated in a ratio 3:1 (Table 4). The mirror type has no scales on a band running along the length of the fish on the central part of each side.

Backcross, Triple Cross, and Multiple Cross

For this group of experiments, we used adult F_1 hybrids from crosses between female yamato and male mirror (YM), female yamato and male scaly German (YG), female wild and male mirror (WM), and female yamato and male Chinese carps (YC). These F_1 specimens had been bred in 1974 and showed heterosis, as already mentioned. Hybrid progeny were produced from two backcrosses (Y ♀ × YM ♂ and Y ♀ × YG ♂), three modified triple crosses (YM ♀ × YG ♂, YG ♀ × YM ♂, and YC ♀ × YM ♂), and a multiple cross (YG ♀ × WM ♂) on 15 July 1978. For comparison with these hybrid progeny, F_1 YM and YG hybrids, and the Y controls, were again produced from specimens bred in 1974. One-month-old fry with a mean body weight of 1.1 g in each combination were selected for cultivation for 6 months.

Both F_1 YM and YG hybrids had remarkably higher growth rates and greater efficiency of feed conversion than did the Y (Table 5). This result was the same as for the F_1 obtained in 1974 and 1975. The growth rates of all the progeny from backcrosses and triple crosses were almost the same as or lower than those of the F_1 hybrids, whereas

Table 5. Cultivation results in the hybrids produced from backcrosses, modified triple crosses and multiple cross, compared with those in the F₁ hybrids and the yamato carp. YM, YG, YC and WM show F₁ hybrids from yamato ♀ × mirror ♂, yamato ♀ × scaly German ♂, yamato ♀ × Chinese ♂, and wild ♀ × mirror ♂ respectively.

Crosses	Initial body weight (g)	6-month culture (1 August 1978 to 31 January 1979)			
		Average body weight (g)	Survival rate (%)	Growth rate* ¹ (%/day)	Efficiency of feed conversion (%)
Yamato	1.1	140 ± 6* ²	100	2.69	74.1
YM	1.1	448 ± 9	100	3.33	103.0
YG	1.1	412 ± 7	100	3.29	99.2
Y ♀ × YM ♂	1.1	432 ± 9	97.2	3.31	99.8
Y ♀ × YG ♂	1.1	392 ± 8	98.3	3.26	99.0
YM ♀ × YG ♂	1.1	415 ± 10	98.9	3.29	100.2
YG ♀ × YM ♂	1.1	392 ± 8	98.8	3.26	99.2
YC ♀ × YM ♂	1.1	200 ± 9	100	2.89	81.3
YG ♀ × WM ♂	1.1	472 ± 17	96.1	3.36	104.6

*¹ $G = 100 \frac{\log^e Y_T - \log^e Y_t}{T - t}$, where Y_T and Y_t are the body weight recorded at T and t , T being later than t , *² Standard error.

Fig. 2. Growth curves of the multiple-cross hybrids (solid line). Compared with that of the yamato-mirror F₁ hybrids (solid line) or the control of the yamato carp (dotted line). YG-WM; multiple-cross hybrids produced from (yamato ♀ × scaly German ♂) ♀ × (wild ♀ × mirror ♂) ♂, YM; F₁ hybrids produced from yamato ♀ × mirror ♂, Y; yamato.

the progeny from the multiple cross had a higher growth rate and a greater efficiency of feed conversion than did any of the other hybrid progeny

(Fig. 2). The differences between the average body weights of harvested multiple-cross progeny and those of the YM and Y were significant.

All the survival rates in these experiments were very similar, ranging from 96.1 to 100%. There were no *Gyrodactylus* or fungus infections in this group, although none of the ponds was treated with formalin. The progeny from all the crosses were scaly, even when the parents were F₁ hybrids produced from crosses with the mirror carp.

Discussion

The ranking of the parent races in growth rate and efficiency of feed conversion was mirror > scaly German ≈ yamato > wild carp in the F₁ experiments, with specimens bred in 1974/75 and those bred in 1977/78. This rank is the same as that reported by SUZUKI *et al.*¹⁰⁾ for carps cultivated in outdoor ponds with standing or running water at uncontrolled temperatures. Moreover, a higher growth rate and greater efficiency of feed conversion was found in the mirror carp than in the yamato carp when they were reared in plastic tanks maintained at 25 or 30°C¹⁰⁾. These results suggest that the racial differences in growth rate and feed-conversion efficiency are greatly affected by genetic factors. The Chinese carp ranked between the yamato and wild carps. Slower growth of the Chinese than of the mirror carp was also reported by MOAV *et al.*⁸⁾, although those authors did not examine the efficiency of feed conversion. The Chinese carp may not have been domesti-

cated as long as the yamato and European carps.

The yamato carp from both Saku City and Suwa City ranked between the mirror and Chinese carps in growth rate and efficiency of feed conversion, and did not differ significantly from the scaly German carp in growth rate. Thus, the carp from the two localities may have identical genetic factors responsible for growth.

As we have already reported elsewhere, the mirror carp has many economic advantages over the Japanese carp, such as faster growth rate, more efficient feed conversion, and greater catchability by angling¹⁰⁻¹²). The mirror carp, however, is highly susceptible to *Gyrodactylus* and fungus infections when it is cultivated in ponds untreated with formalin, or in standing-water, running-water, or fertilized ponds¹⁰). In addition, scaleless carp such as the mirror are not generally well accepted in Japan.

Of the F_1 hybrids, the yamato-mirror (YM) hybrids had the highest growth rate and feed-conversion efficiency exceeding not only those of the maternal race, the yamato, but also those of the paternal race, the mirror carp and, because they did not get *Gyrodactylus* or fungus infections, a better survival rate than that of either parent race. Such heterosis in YM was also observed in experiments both in 1974 to 1975 and in 1975 to 1976. These results may have been greatly affected by factors responsible for superior growth of the paternal mirror and strong resistance to diseases of the maternal yamato. In addition, all YM are completely scaly. Since the other F_1 hybrids produced by crosses with the mirror carp also were not infected with *Gyrodactylus*, it seems that susceptibility to this disease is controlled by recessive genetic factors. When HINES *et al.*¹⁷) crossed an inbred strain that is susceptible to epidermal epithelioma with a second inbred strain that is susceptible to a swim-bladder inflammation, the offspring, as well as the offspring of either of these strains crossed with one of various other strains, did not show a single instance of either disease. These authors believed that susceptibility to these two diseases is controlled by recessive genetic factors, which is our supposition in the present case.

The yamato carp has been more widely cultivated by intensive feeding with pelleted artificial feed than has any other race of carp, and it yields the highest annual harvest of any cultivated freshwater fish in Japan. The YM surpassed the yamato's average efficiency of feed conversion by

6.0 and 9.6% in the two experiments, 1974/75 and 1975/76. Furthermore, the average efficiency of feed conversion of the YM exceeded that of the yamato carp by 28.9% when automatic feeding was used, in the 1978/79 experiment. In most fish farms in Japan, the yamato carp needs two or more years to reach marketable size, approximately 800g average body weight. The YM, however could reach marketable size within only one year, thus saving at least 6% on artificial feeds.

On the other hand, most of the progeny from intercrosses of F_1 hybrids, backcrosses, and triple crosses were less good economically than the YM, that is, either the growth rate or the efficiency of feed conversion was much lower than that of the YM. Only the F_2 hybrids from the YM somewhat surpassed the F_1 in growth rate, but this difference was not statistically significant. Be that as it may, even if the growth rate of the YM F_2 generation is really higher than that of the F_1 , the economic value of the F_2 may be lower, because one-third of the F_2 were of the mirror type, that is, were scaleless on the central part of the sides, as was also found by earlier workers^{2,18}). On the other hand, since the progeny from the multiple cross, YG ♀ × WM ♂, grew faster and converted feed more efficiently than did the YM F_1 generation, had a negligible difference in survival rate from those of the F_1 generation of YM or yamato carp, and were all scaly, we judge that of the carps we have studied, the progeny from this multiple cross YG ♀ × WM ♂ are the most economically valuable for carp culture.

Since bodily proportions suitable for cooking habits and catchability by angling are also economically important characters in carp, these qualities of various hybrids will be discussed elsewhere.

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