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Genetic Aspects of the Transition from Traditional to Modern Fish Farming

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Summary. A theoretical model describing the genetic aspect of the transition from traditional to modern animal husbandry is presented. Traditional races are characterized by high tolerance to harsh environments but a low rate of response to increased management inputs. Modern, artificially-selected breeds are efficient convertors of management inputs to higher production but have a low resistance to harsh environments. Thus, under low-input traditional husbandry, the traditional races are best adapted, while under modern, high-input husbandry, modern breeds are most productive, and in the intermediate zone, hybrids between the two races are capable of closing the 'profit gap' in the shift from traditional to modern husbandry. The domesticated European, and the Chinese Big-belly races of the common carp were tested under many environmental 'treatments' involving variation in density, polyculture, aeration, feeding and fertilization. The Big-belly showed, as expected, high resistance to the poor 'treatments' but low response to environmental improvement. The European breeds performed best in the higher half of the environmental range and their response rates were highest. The F_1 hybrids between the two races excelled in the lower third of the range, exhibiting, there, a high heterosis but only an intermediate rate of response. It was concluded that successful changes from one aquaculture system to another, and particularly the change from traditional to modern husbandry, require a simultaneous search for the most efficient genotype × environment combination and, for each level of modernization of traditional fish farming, the most effective genotype must be identified and utilized. The transition from traditional to modern animal husbandry, including fish farming, is best quantified by the levels of invested inputs, other than labour, that induce higher production of the individual animals. The major management inputs of modern fresh water fish farming are expensive feeding, veterinary care, control of predators, organic and chemical fertilizers that enrich the production of natural fish food, water circulation and aeration. Since all these inputs are rather expensive, the fish have to pay for them by increased production, i.e., faster growth rate. Thus, the *sina qua non* of such a transition is the availability of animal stocks capable of converting increased inputs into economically attractive increased yields. We are all aware of the very great physiological plasticity of farm animals. In the case of the European carp, for example, the same genetic stocks, raised under high stocking density and low feeding level may gain an average weight of 10 to 20 g per fish in a whole year, while under low density and abundant feeding, they may gain over 2 kg in the same period. Such physiological responsiveness may give the wrong impression that all that is needed for the transition to more modern husbandry are improved environmental circumstances. The object of this paper is to point out that the proper choice and changeover of genotypes is equally important for the succesfull implementation of the usually gradual process of fish farming modernization. This demonstration will be based on results of experiments with the European and Chinese races of the common carp, and their F_1 hybrids.

Theory

The transition from traditional to modern livestock farming involves a shift from a husbandry based on seasonally-available natural feedstuffs (e.g., pasture or wastes), with minimum protection from the elements and predators, and no attention to disease or parasite control, to a husbandry based on year-round supplies of high-quality feed, protection from the elements and predatros, increased intervention in natural competition and social structure within the populations, and high levels of sanitation and disease control. In Western Europe and England, this transition began in the late Middle Ages and has continued to the present day. The gradual improvement in environmental inputs was accompanied by conscious selection by animal breeders of genotypes with high responsiveness to these inputs. Simultaneously, the improved environment of modern husbandry caused relaxation of natural selection, and this in turn led to a correlated, undesirable reduction in genetic resistance to harsh environments. Under traditional farming, in contrast, the major selective pressures are those of natural selection for viability in poor and largely uncontrolled environments, while relatively little, if any, conscious selection would have been carried out for increased efficiency of conversion of input to production. As a result of their differing evolution, traditional (henceforth, low-input) and modern

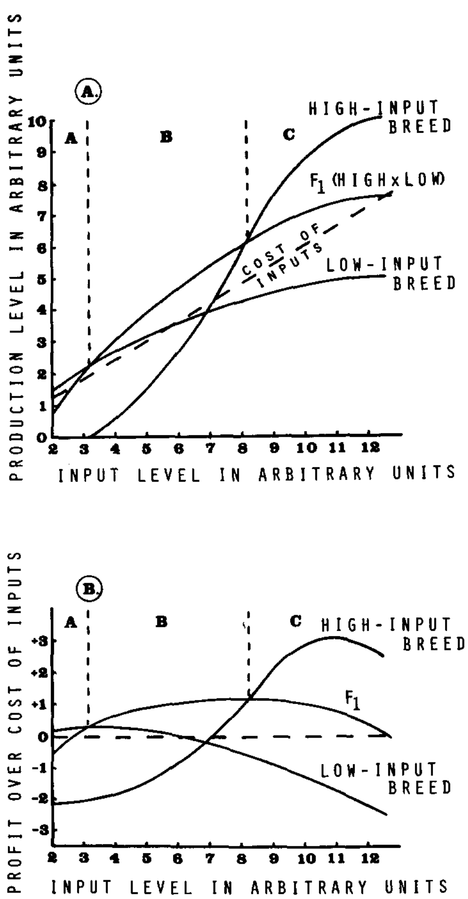

Fig. 1. Theoretical relationships of production and profit with level of management inputs of modern (high-input) and traditional (low-input) breeds and their F_1 hybrid. A. Predicted regressions of production and costs on input level; B. Profit over cost of inputs of the three genotypes

(henceforth, high-input) races respond differently to changes in input levels and this, as we shall see, may have important consequences for the choice of the most productive and profitable genotypes at different regions of the entire spectrum of inputs characterizing a complete transition.

Fig. 1A shows schematically the production (e.g., milk, egg number, growth-rate) of a low-input, high-resistance stock and a high-input, low-resistance stock, and of their F_1 hybrid, at increasing levels of management inputs. At the lowest end of the input range (input levels 2 and 3 in our arbitrary graph), survival is the prime determinant of production; here the low-input breed outproduces the high-input breed. As conditions improve, however, the genetic differences in response eventually reverse the production rankings. At input level 3.3, the F_1 takes the lead. It maintains first place up to level 8.2, when the high-input breed finally has sufficient opportunity to express its superior capacity to convert input into production.

The broken line of Fig. 1A represents assumed cost of the inputs, so that only points above it correspond to positive profits. This is further emphasized in Fig. 1B, which shows profits over inputs for the whole input range, divided into three regions: Region A (input levels 2 to 3.3) where the low-input breed is most profitable but even the highest profit is rather low; Region B (input levels 3.3 to 8.2) where the F_1 is most profitable and larger profits can be made; Region C (input levels above 8.2) where the high-input breed is most profitable and the highest profits are expected. The point of highest profit is reached by the high-input breed at around input level 10. At higher levels, even the high-input breed can not yield at a sufficiently high rate to pay for the marginal costs of the extra inputs. For example, consider the specific input of "area of pond per single fish" (commonly measured inversely as density of stocking). At densities lower than optimal, corresponding to higher input levels, the individual fish would grow at a faster rate, yet yields/hectare and profits would be lower.

Note that in the absence of the F_1 hybrid region B would represent a 'profit gap' that would act as a block to a smooth and gradual transition from traditional to modern husbandry. In principle, the gap can be crossed by a quantum jump in environmental input accompanied by a simultaneous shift from traditional to modern stocks. In practice, this may be difficult to negotiate smoothly. Experience with dairy cattle and poultry in Israel has shown that F_1 crossbreds between local (low-input) and modern, imported breeds perform better than either parent in regions of the environmental spectrum where the traditional breeds can no longer respond adequately to increased environmental input, but the modern breeds can not yet tolerate the residual environmental harshness. The alternative approach, of selecting for increased responsiveness, is essentially an attempt to mimic the progress of European breeders over centuries, and would appear to be time-consuming and wasteful. Farmers can learn new techniques and capital can be applied much more rapidly than most animal stocks can be improved genetically.

Note that the dominance relationships and heterosis exhibited by the F_1 are variables determined by

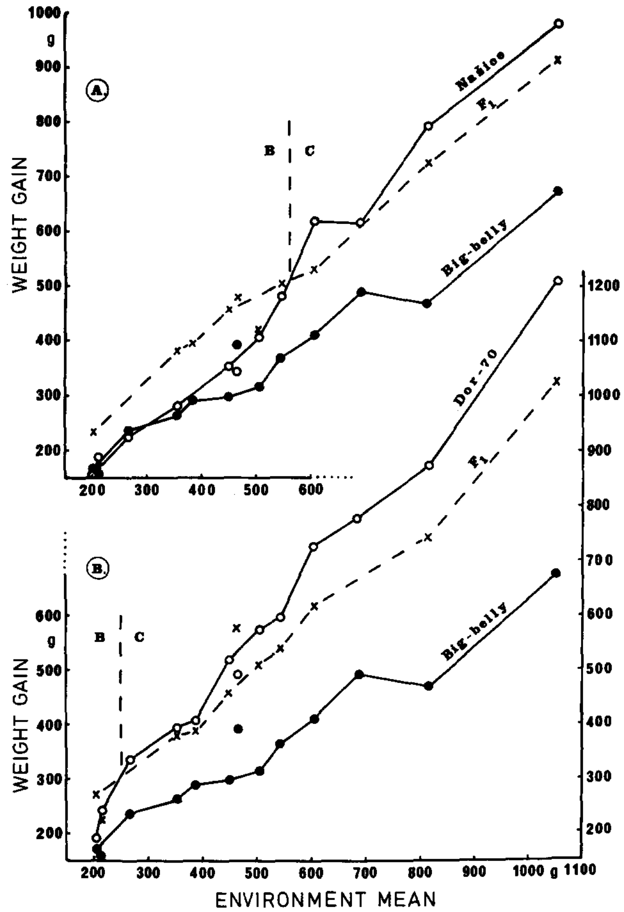

Fig.2. The regressions of weight gain on the quality of the environment as measured by the mean weight gains of all genotypes tested under a given environment. (For further details see text and Table 1.) A. Big-belly (Chinese, traditional breed), Našice (European, modern inbred) and their F_1 hybrid; B. Big-belly, Dor-70 (European, modern breed) and their F_1 hybrid

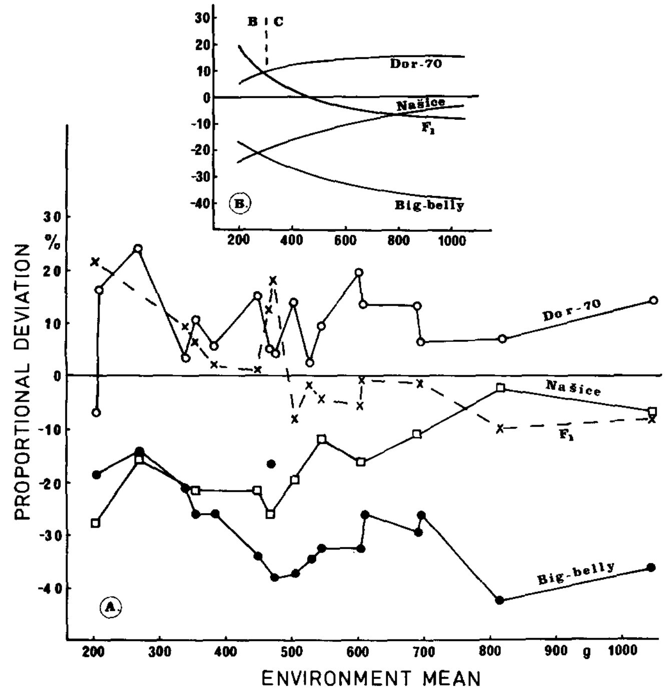

Fig.3. The regressions of proportional (x) deviations of weight gains from environmental means on the environmental means. (F_1 is mean of Našice × Big-belly and Dor-70 × Big-belly.) A. Observed results (taken from Table 1); B. Expected regressions of the observed results

the input level (Bucio-Alanis et al., 1969; Knight 1973): that is, only in region B does the F_1 exceed its two parents; in other regions, it is more or less intermediate. The heterosis exhibited in region B need not be explained in terms of over-dominance or products of individual loci. Rather, it is a necessary result, given certain reasonable assumptions as to the functional relationships between productivity and its components - response to input and viability (Moav 1966).

Experimental Results

Big-belly is the common name of the major race of the common carp (*Cyprinus carpio* L.) of China. It has been grown and bred in Chinese fish farms for over 2000 years. During this period, it has, as a rule, been exposed to very harsh environments, and has not apparently been subjected to artificial selection for growth-rate (Drews 1961; Bardach et al., 1972; Wohlfarth et al., 1975). It is therefore a typical traditional breed.

The evolutionary history of the domesticated European race of the common carp took a different path. It had been kept under relatively high input levels (low stocking densities, regular feeding with grains, and predator and disease control). Also, it underwent continuous, strong selection for rapid growth-rate at the hands of the breeders (Mann 1961). It is thus a typical modern breed.

Our data on the responsiveness of European, Big-belly carp and their F_1 hybrids to increasing levels

Table 1. Weight gains of two European carp breeds (Našice and Dor), the Chinese Big-belly (BB) carp and European × Chinese crossbreds under varying environmental 'treatments'

Year	Major features of treatment							Mean corrected weight gains, in g, of tested groups					
	No.	Pond area (m²)	Ponds no.	No. groups tested	Stocking density carp/ha	Poly-culture[a]	Feeding[b]	BB	BB×Nas	BB×Dor	Nas	Dor	Mean[c]
1971	1	400	4	12	10700		grain	264	378	383	279	394	357
	2	400	4	12	6500		grain	297	454	457	352	517	450
	3	400	4	12	6500		grain	367	505	535	479	593	545
	4	400	4	12	3200		grain	468	725	740	795	874	815
	5	20000	1	13	2500		grain	283	395	386	-	403	382
1972	1	400	8	14	12300	8000	pellets	232	-	-	228	334	270
	2	400	8	14	4100	2600	pellets	486	-	-	615	779	690
										BB×White[d]			
1973	1	400	4	15	8800	10000	pellets	269	-	371	-	351	340
	2[e]	400	4	15	8800	10000	pellets	338	-	553	-	489	470
	3	400	4	15	8800	2000	pellets	403	-	518	-	540	528
	4[e]	400	4	15	8800	2000	pellets	452	-	608	-	693	610
	5	15000	1	15	3500	4000	pellets	512	-	686	-	737	695
1974	1	400	4	10	11400	8250	grain	152	170	222	183	242	208
	2	1000	2	10	12000		pellets	169	230	271	149	193	207
	3	400	2	10	3050	3050	cow manure	389	477	574	345	490	467
	4	400	4	10	11400	8250	pellets	316	418	506	406	575	504
	5	400	4	10	3300	3050	grain	409	528	617	507	724	608
	6	400	4	10	3300	3050	pellets	675	918	1025	977	1208	1058
r[f]								0.974	0.992	0.995	0.995	0.993	
b[f]								0.577	0.792	0.881	1.00	1.145	
a[f]								63.5	72.3	65.0	-72.1	-24.1	

a Number of fish other than common carp, per hectare.
b The pellets were made of crushed grain and fish meal.
c Mean over all the tested groups, including those not mentioned in the present paper.
d In 1973 the only inter-race hybrid tested was Big-belly cross to a local (European) group called White, hence it was substituted for the BB × Dor hybrid.
e Treatments 2 and 4 of 1973 were aerated.
f r, b and a designate, respectively, the coefficients of correlation and regression and the x-axis intercept of the regression of weight gains of individual groups on the ponds means (treatment means) of all the tested groups. (Treatments 1 and 3 of 1974 were excluded from the computation).

of environmental inputs originated from extensive large-scale experiments carried out at Dor, from 1971-1974. In the course of the experiment, the mean weight gain (corrected for differences in initial weights; Wohlfarth and Moav, 1972: Moav and Wohlfarth, 1973) were obtained for about a dozen European inbreds and crossbreds, a single group of Big-belly carp, and several F_1 hybrids between the European and Chinese races. The range of initial weights was 15-40 g, and the test lasted for about 120 days. All these stocks were subjected to various environmental "treatments" covering a wide range of environmental inputs. To represent the European race we have chosen only two breeds - Našice produced by selective breeding in the Yugoslavian fish farm of that name, and Dor-70, developed by a selection programme at Dor. Table 1 summarizes the results obtained with these two European breeds, their respective hybrids with the Big-belly, and Big-belly itself. The mean weight gains of all the groups of carp tested within each treatment (right-hand column of Table 1) is taken as a measure of the quality of the environmental input. Fig. 2A and 2B show, respectively, the regressions of mean weight gains on pond means for Big-belly, Našice and their F_1 hybrid, and for Big-belly, Dor-70 and their F_1 hybrid. It is clear that the two European breeds have steeper slopes (higher regression coefficients) than the Big-belly carp, and the slopes of the F_1 hybrids are intermediate to those of their parents.

A different graphical presentation of the results of Table 1 is given in Fig. 3. Here the results were transformed to proportional deviations from pond means. That is, the treatment omit mean was subtracted from each observation and the difference was divided again by the treatment omit mean. Although the Dor-70 × Big-belly F_1 had a consistent advantage over the Našice ×

Table 2. A comparison of observed with predicted (expected) mean corrected weight gains in ponds where liquid cow manure substituted grain feeding (predicted values derived from the regression lines of Fig.2)

Genetic group	Mean corrected weight gains in g		
	Observed	Expected	% deviation
European			
Našice	345	365	- 5.5 %
Dor-70	490	530	- 7.5 %
Chinese			
Big-belly	389	300	+29.7 %
Hybrids			
Našice×BB	477	460	+ 3.7 %
Dor×BB	574	460	+24.8 %

Big-belly F_1, the differences between them were usually small. For this reason, and to reduce the 'error' variance, the two were combined. In 1973, neither of these two hybrids was tested. In order not to lose the results of this year, the two missing hybrids were replaced in Fig.3 by a third inter-race hybrid, White × Big-belly (White is a locally developed European carp, marked by the three recessive body coloration genes, Gold, Blue and Grey (Wohlfarth and Moav 1970)).

Fig.3 emphasizes the specific genetic responsiveness to environmental variation, independent of scale effects (Moav et al. 1975). Fig.3 helps us, among other things, to demonstrate the wide difference between the two European groups, Dor-70 and Našice. The poor performance of the latter is attributable, primarily, to inbreeding depression. The proportional difference between the two increases as the environment becomes less favourable, suggesting that Našice is more sensitive to environmental deterioration. This would accord with our interpretation of Našice as an inbred. The difference between these two groups is also manifested by the different input-points at which the F_1 hybrids begin to exceed their European parents. This point is around 550 g for Našice, but only 250 g with Dor-70 (Fig.2).

Ever under the poorest environments of this series of experiments, a region where Big-belly had the highest growth-rate was not reached. However, we do have one set of results which seems to illustrate quite well the specific capabilities of the Big-belly. In 1974 two experimental ponds received a daily ration of liquid cow manure in place of all additional feeding (treatment 3). Although the average growth rate was quite high (467 g), there were considerable differences from the other 'treatments' in the response of the genetic stocks. Table 2 compares the expected production of the various genetic groups, as estimated from the regression lines of Fig.2, and their actual production. Under this treatment all the European strains produced less than expected, while the inter-race F_1 hybrids produced more than expected and the Big-belly much more than expected. These results fit our evolutionary model very neatly. The Big-belly evolved in the fish ponds of China where it was fed almost exclusively with animal wastes, while the domesticated European carp was fed regularly with grains. It also shows the complexities encountered in experiments of the present type when inputs of a different nature are mixed together.

Discussion and Conclusions

Present-day fish husbandry is under considerable pressure to change. Pressures act in two directions: on traditional fish farms to increase yields by improved husbandry techniques; and simultaneously, because of the great rise in cost of high-quality feed, modern fish husbandry is under pressure to 'shift down' and substitute cheaper but lower-quality waste products for high-quality feed, while maintaining high-yield levels. Our results show that, in both cases, proper choice of genotypes is crucial to the success of shifts in environmental inputs. Any attempts to gradually increase management inputs in the vast area where the Big-belly is cultivated by traditional methods would be severely handicapped, unless accompanied by substitution with a more responsive stock. Similarly, attempts to utilize wastes in place of high-quality feed require stocks able to thrive on such wastes. In both instances, we have found that hybrid derivatives between the Chinese Big-belly and the domesticated European carp are able to play an important role.

In a broader context, our results illustrate and emphasize that, once a wide range of environments is taken into consideration, powerful genotype × environment interactions are to be expected. This holds true particularly for finfish aquaculture, where yields per unit of water-surface area range from a few hundred kg/ha in omit ponds without feeding or manuring to omit 2000 tons/ha when fish are raised in cages in omit flowing water and fed with proteinrich feed (Bardach et al., 1972). Here, the conventional assertion that "environmental improvement is the major and primary requirement for increasing production and profitability, and genetics can provide only the final 'fine-tuning' of the system" is clearly unjustified. Furthermore, the viewpoint that genetics and husbandry are two independent approaches to increased production is wrong. The two are strongly interrelated aspects of a single system and the strong genotype × environment interactions make them inseparable. In summary, the present results clearly demonstrate that, because of the very wide range of management practices in aquaculture, a simultaneous search for the most successful genotype × environment combinations becomes obligatory, and for each level of modernization of traditional farming (or traditionalization of modern farming), the most effective specific genotype must be identified and utilized.

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