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# Wyrównywanie się ciężarów w czasie i zjawisko stabilizacji zmienności w populacji karpiowej selekcjonowanej na szybkość wzrostu

# Equalization of weights with time and the stabilizing effect of variability in a carp population selected for growth

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Abstract — In 1962 the author set up an experiment at the experimental farm Ochaby, Silesia, southern Poland, to investigate the equalization of carp growth and the changes of variability with time under the influence of selection for growth. The existence of compensation growth and of the stabilizing effect of variability in carp populations was demonstrated.

In order to find out how the process of equalization of weigths and the stabilization of variability occurs in a population which is artificially composed of groups differing as to mean weight but at the same time genetically uniform and under the influence of strong selection for the two preceding generations an experiment was set up in 1962 at the experimental farm Ochaby belonging to the Polish Academy of Sciences in the district of Cieczyn, southern Poland. The experiment lasted from 1962 to 1966. The population No 3A1 was taken for the experiment. It was a genetically uniform population because it descended from only one male and one female. This population had undergone strong selection. In the second year of growth the population grew separately in different ponds of the farm hence in different environmental conditions. From three ponds three groups differing in their mean weights were formed and united in one experimental population. The thus formed population was reared afterwards for three years at the same farm always in one pond, that is always in identical environmental conditions. The preceding generations of the experimental population No 3A1 were strongly selected according to the same criteria as the experimental population.

## Methods of the experiment and material of investigated carp

The methods used can be divided into two parts: breeding methods and biometrical methods. The breeding methods consisted in applying in the experiment a population descended from one couple of parents only, i. e. one male and one female, in this way a genetically uniform population being obtained. (In the practice of carp rearing for market purposes this is not done, hence the market populations are not genetically uniform).

In the first year of growth the population grew as a whole in the first transfer pond after which it was stocked in two second transfer ponds. In the second year of life the population stocked in different ponds of the Ochaby farm, the stocking rates for those ponds being different and the carp growing in different and the carp growing in different densities. As a result there were 3 populations from three different ponds with very different mean weights. From these 3 ponds were formed three groups: a) with small mean weight at age $K_2$, called „smalls", b) with average mean weight at age $K_1$, called „averages" and c) with large mean weight at age $K_2$, called „larges". The groups were formed after strict selection, the final selection being less than 1% (Kirpitschnikow 1968). In the third year of life of the population these three groups were united and this group was afterwards considered as the experimental population proper No 3A1. The remaining fishes of the population No 3A1 were sold by the farm. After this the experimental populations No 3A1 was reared and observed at the farm for three years. The whole population was always in the same pond. The find selection was made after the population had attained maturity, i. e. in $K_4$ in Spring. The result of this final selection was the formation of a stock of spawners for farm use. This stock was under observation for one year. The experimental population was a sib-population descending also from the preceding successive sib-populations. These sib-populations were called after Starmach „families".

The group of smalls came from a pond heavily stocked for the production of two-yearlings, and the group of larges came from a pond normally stocked for the production of market size carp in $K_2$. In this pond Pasieczny a heavy infection with dropsy occurred and more than half of the population died out (54%). As a result, the remaining carp grew over the norm and the selection which always favoured the largest, could lead to the formation of a group of very large yearlings which had an average weight 1357 g.

The group of averages was selected earlier than the two remaining groups — at the fry stage. Two hundred of the largest specimens were selected from a population of 31 000 individuals. This group grew separately from the beginning of the second year. The average weight of the selected fry was more than twice as great as the mean weight of the po-

pulation from which they came. The selection of smalls and larges can be regarded in this respect as the second selection. The greatest probability of finding a true jumper (W ł o d e k 1967 b) is during the first selection, i. e. for the averages. This group can therefore be regarded in the experiment as having the best genotypical foundation of swift growth and in fact at the age of $K_5$ they caught up with the average weight of the group of larges.

The criterion of selection was the weight, the health of the fishes also being considered, but the populations selected were very sound with one exception — that from the pond Pasieczny. Exterior features, e. g. scaliness, were purposely not taken into consideration in this population. This, was in order to observe experimentally how the exterior of the fishes forme under severe selection for growth only. A similar criterion was used in the two preceding generations. After selection there were three populations with an uneven number of specimens, the awerage individual weights in these three groups being in the relation 1 : 2 : 3. It is characteristic that this relation did not change after the first wintering. It is also characteristic that the succesive winterings did not spoil the mean relations of the groups attained in the previous autumn. This proves once more that the loss in weight of the carp in winter ponds occurs proportionately (table V and W ł o d e k 1959 b). The application of the same criterion of selection during two consecutive generations led to the formation in the offspring of the $F_3$ population of characteristic scaliness: slightly scaled mirror carp (schwach beschupter Spiegelkarpfen). Ż a r n e c k i (1955/1964) when investigating the growth of the jumpers during their first two years of life made two groups in his experiments: a selected group of jumpers and a selected group of carp detarded in growth. He also (1961) compared a group of non selected averages with selected jumpers. In the present experiment all the compared groups were strictly selected for growth only in one direction. There were no retarded carp. The experimental population No 3A1 came from a long range experiment with inbreeding of carp populations and represented the $F_3$ generation to the initial parents. All tree generations were inbred, all offspring generations were „families", and no inbreeding depression was observed in growth, recundity, exterior, or health. Strong selections were made on large material. The initial spawners for the long range experiment came from different parts of Poland.

The female was from local stock, whose ascendency was not known, and the male was imported by Prof. S t a r m a c h from the north of Poland from the Mazury lake district, from the pond farm at Montowo. Its ascendency was also unknown, being only supposed that it came from stocks selected in this region before the second world war. A short history of the breeding and selection of those populations that precede the experimental population is given in Table I.

Table I. A short history of the material of carp used for the experiment in growth at the experimental farm Ochaby (according to Włodek 1959 and other unpublished data)

| Generation of breeders | Age of breeders at breeding | Name of farm | Date of last selection | Date of spawning | Name of spawning pond | No of breeders ♂ | No of breeders ♀ | Average weight of the population (index) ♂ | Average weight of the population (index) ♀ | Individual average weight of breeders (index) ♂ | Individual average weight of breeders (index) ♀ | Offspring generation: Generation | Offspring generation: No of population |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $P_0$ | ? | Ochaby | not known | 29.V.1954 | Podbór | 416 | 4155 | 100 | 100 | ? | ? | $F_1$ | 3 |
| | | | | | Mazury local | | | | | | | | |
| $F_1$ | $K_4$ | " | 25.X.1957 | 24.V.1958 | Lebioda | 306 | 342 | 100 | 100 | 145 | 105 | $F_2$ | 3A |
| $F_2$ | $K_4$ | " | 8.V.1962 | 14.VI1962 | Lebioda | 1359 | 1356 | 100 | 100 | 118 | 125 | $F_3$ | 3A1 |
| $F_3$ | $K_4$ | " | 27.IV1966 | farm spawns | | | | | | | | $F_4$ | |

Selections of the experimental population:

Selection 1. — the catching of the whole population 3A1 from the wintering pond for fry — Karaś Górny — and the selection of a group of fishes which in the next year would be called the „averages". The 200 largest individuals were selected from 31 000.

Selection 2 — the fishing of the pond Lasek; the population stocked in this pond was destined for the production of twoyearlings. Here 86 largest individuals were selected out of 9866; also fished was the pond Pasieczny, whose population was stocked for producting market size fishes in $K_2$. Here selected were 42 largest individuals out of 5947 remaining in this pond after the attack of dropsy. The carp found in this pond had cicatrized wounds but were on the whole sound.

Selection 3 — after the wintering of $K_4$'s the whole experimental population was caught and from the 247 individuals a stock of the best 78 spawners was selected on the basis of their individual achievement during their life. This stock was investigated during a further year.

The severity of selections was under 1% (Kirpitschnikow 1968) in the first three cases, but the severity of the selection of spawners was not so strong, since the spawners were from populations already strictly selected.

As can be seen from Tables II and III, even groups were not formed, this fact stressing the importance of selection in the experiment: only the largest in $K_1$ and $K_2$ were taken into the experimental population. Such a population also had the greatest probability of rapid growth, because the probability of choosing the true jumpers was great, especially in the group of „averages". The aim of the selection was to provide for the experiment carp from the initial population that would grow as rapidly as possible.

The experimental population was individually marked in Spring 1964, that is after selections. During the first two years of common growth of the groups, the losses in the marks were not great but during the third year, i.e.after the maturation of spawners, the losses were great (Table III).

The biometrical methods consisted in that every fish in the experimental population proper was weighed twice a year. The weighing took

Table II. The growth experiment with population No 3A1 at the experimental farm Ochaby in the years 1962-1966. Experimental population No 3A1 before selection.

| Name of pond | Date | Farm data | | | | Data from biometrical measurements | | | | Remarks |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Age | Number of indiv. | kg | average individ. weight in g | Number of indiv. | kg | average individ. weight in g | v % | |
| Year 1962 | | | | | | | | | | |
| Spawning pond Lebioda | 14.VI.1962 | $K_4$ | ♂ 1359 x ♀ 1356 | | | | | | | popul. 3A |
| I transfer pond Lebioda | 19.VI.1962 | $K_0$ | 100000 | let through from the spawning pond | | | | | | |
| Stockings of the II transfer ponds: | | | | | | | | | | |
| the pond Społeczny | 14.VII.1962 | $K_V$ | 32000 | | | | | | | |
| the pond Leśny | 16.VII.1962 | $K_V$ | 48000 | | | | | | | |
| Fishing of the II transfer ponds | | | | | | | | | | |
| the pond Społeczny | 18.X.1962 | $K_1$ | 12950 | 279.0 | 21.5 | 30 | 0.46 | 15.4 | 29.3 | |
| the pond Leśny | 18.X.1962 | $K_1$ | 24100 | 440.0 | 18.3 | 30 | 0.50 | 16.6 | 38.4 | |
| wintering in the pond Karaś górny | 18.X.1962 | $K_1$ | 37050 | 719.0 | 19.4 | 60 | 0.96 | 16.0 | 34.5 | |
| Year 1963 | | | | | | | | | | |
| Fishing of the pond Karaś górny | 23.IV.1963 | $K_1$ | 31000 | | | 60 | 0.88 | 14.7 | 44.7 | Selection |
| Stocking of ponds: | | | | | | | | | | |
| the pond Lasek | 23.IV.1963 | $K_1$ | 15000 | 255.0 | 17.0 | | | | | |
| the pond Wencel (selected fishes) | 23.IV.1963 | $K_1$ | 200 | 8.7 | 43.7 | | | | | Selects |
| the pond Pasieczny | 23.IV.1963 | $K_1$ | 13000 | 225.0 | 17.0 | | | | | |
| Fishing of the ponds: | | | | | | | | | | |
| the pond Lasek (two-yearlings) | 31.X.1963 | $K_2$ | 9866 | 2252.0 | 228.3 | 29 | 6.0 | 208.1 | 27.1 | Selection |
| the pond Wencel (selects) | 19.X.1963 | $K_2$ | 181 | 177.0 | 977.9 | 28 | 27.9 | 996.1 | 14.9 | selects |
| the pond Pasieczny (market size) | 11.X.1963 | $K_2$ | 5947 | 4947.0 | 831.8 | 29 | 28.6 | 986.5 | 18.0 | Selection |
| The effects of selection: | | | | | | | | | | |
| the group of smalls from the pond Lasek | | $K_2$ | 86 | 40.0 | 463.1 | | | | | Selects |
| the group of averages from the pond Wencel | | $K_2$ | 181 | 177.0 | 977.9 | | | | | " |
| the group of larges from the pond Pasieczny | | $K_2$ | 42 | 57.0 | 1357.1 | | | | | " |
| to the wintering pond Bagna VI the experimental population No 3A1 | | $K_2$ | 309 | 274.0 | 886.7 | | | | | Selects |

Table III. The growth experiment with population No. 3A1 at the experimental farm Ochaby in the years 1962-1966. Experimental population No. 3A1 after selection

| Year | Groups in the experimental population and names of ponds | Date | Age | Number of individuals | kg | Average individual weight in g | v % | Remarks |
|---|---|---|---|---|---|---|---|---|
| 1964 | Fishing of the wintering pond Bagna VI and stocking of pond Wencel | 18.IV.1964 | $K_2$ | 306 | 249.4 | 815.1 | 35.0 | Marking |
| | in this population the group of smalls | | $K_2$ | 84 | 36.2 | 431.2 | 19.4 | from |
| | " " " " " " averages | | $K_2$ | 182 | 163.2 | 896.5 | 13.9 | No 3-1 |
| | " " " " " " larges | | $K_2$ | 40 | 50.0 | 1250.5 | 7.6 | to No |
| | | | | | | | | 3-306 |
| | Fishing of the pond Wencel | 3.XI.1964 | $K_3$ | 274 | 731.0 | 2667.9 | 12.5 | |
| | in this population the group of smalls | | $K_3$ | 76 | 184.9 | 2432.6 | 10.0 | |
| | " " " " " " averages | | $K_3$ | 164 | 439.5 | 2680.1 | 10.3 | |
| | " " " " " " larges | | $K_3$ | 34 | 106.6 | 3134.8 | 7.3 | |
| | to the wintering pond Bagna VIII | 3.XI.1964 | $K_3$ | 274 | 731.0 | 2667.9 | 12.5 | |
| 1965 | Fishing of the wintering pond Bagna VIII | 6.V. 1965 | $K_3$ | 279 | 682.8 | 2447.5 | 13.1 | |
| | Stocking of the pond Karaś górny | 6.V. 1965 | $K_3$ | 266 | 652.7 | 2453.8 | 13.0 | |
| | in this population the group of smalls | | $K_3$ | 74 | 162.3 | 2193.0 | 8.1 | |
| | " " " " " " averages | | $K_3$ | 157 | 389.1 | 2478.0 | 10.5 | |
| | " " " " " " larges | | $K_3$ | 35 | 101.4 | 2896.7 | 8.3 | |
| | Fishing of the pond Karaś górny | 15.X. 1965 | $K_4$ | 248 | 959.5 | 3868.9 | 12.8 | |
| | in this population the group of smalls | | $K_4$ | 65 | 238.4 | 3667.6 | 11.5 | |
| | " " " " " " averages | | $K_4$ | 130 | 504.6 | 3881.3 | 12.1 | |
| | " " " " " " larges | | $K_4$ | 33 | 140.0 | 4242.9 | 11.7 | |
| | to the wintering pond Bagna V | 15.X. 1965 | $K_4$ | 248 | 959.5 | 3868.9 | 12.8 | |
| 1966 | Fishing of the wintering pond Bagna V | 27.IV.1966 | $K_4$ | 247 | 900.6 | 3646.1 | 12.7 | Selection |
| | in this population the group of smalls | | $K_4$ | 62 | 213.9 | 3449.3 | 11.4 | of |
| | " " " " " " averages | | $K_4$ | 134 | 487.9 | 3640.8 | 12.5 | breeders |
| | " " " " " " larges | | $K_4$ | 33 | 135.0 | 4092.1 | 10.0 | |
| | Effects of selection and stocking of ponds Szpitale | 27.IV.1966 | $K_4$ | 78 | 308.2 | 3951.8 | 11.0 | |
| | in this population the group of smalls | | $K_4$ | 8 | 28.9 | 3613.7 | 4.9 | |
| | " " " " " " averages | | $K_4$ | 45 | 176.9 | 3930.7 | 10.2 | |
| | " " " " " " larges | | $K_4$ | 20 | 84.3 | 4217.6 | 9.2 | |
| | Fishing of all breeders in the stock. | 29.X. 1966 | $K_5$ | 76 | 385.3 | 5070.4 | 7.8 | |
| | in this population the group of smalls | | $K_5$ | 6 | 28.8 | 4800.0 | 4.2 | |
| | " " " " " " averages | | $K_5$ | 25 | 129.9 | 5196.0 | 7.6 | |
| | " " " " " " larges | | $K_5$ | 18 | 92.9 | 5219.4 | 5.6 | |
| | in this population the group which lost their marks | | $K_5$ | 27 | 132.7 | 4914.8 | 8.1 | |

place „at the dam", that is, neat the ponds while they were being emptied in Spring and Autumn. The data thus assembled were worked out statistically at the Laboratory in Cracow. Besides weighing, biometrical measurements were taken according to the scheme in use at the Laboratory. The result of these measurements are not included here. Before uniting the three different groups random samples were drawn from the populations (Table II) and after uniting the selected fishes 100% semples were weighed (Table III). In this way y received the individual record for every fish in the proper experiment. In this way also the growth of the initial groups could be watched and individual selection could be carried out after their reaching maturity in $K_4$ on the basis of their achievements.

## Experiment and discussion

The course of the experiment and its results are illustrated in Tables II and III. Table II shows the experiment before the selections (that is before the experiment proper), while Table III shows the course of the experiment

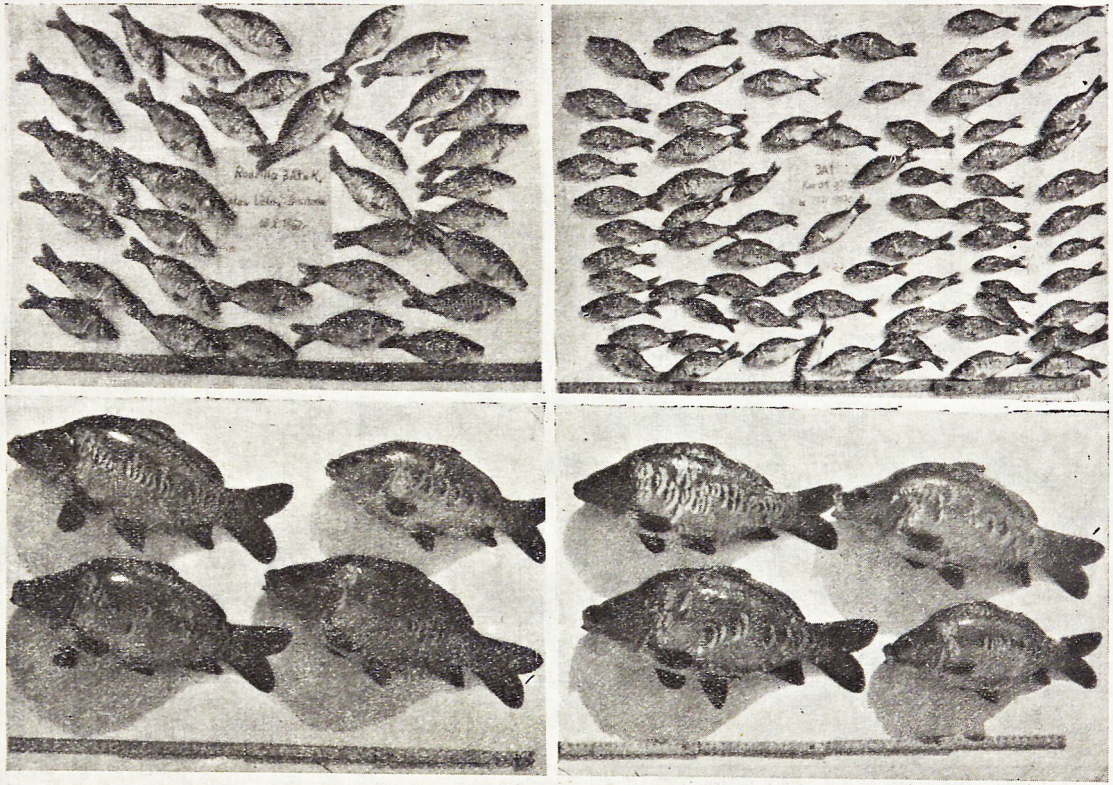

Fig.1. The selection only for growth for two preceding generations led to the formation in the experimental population of this scaliness

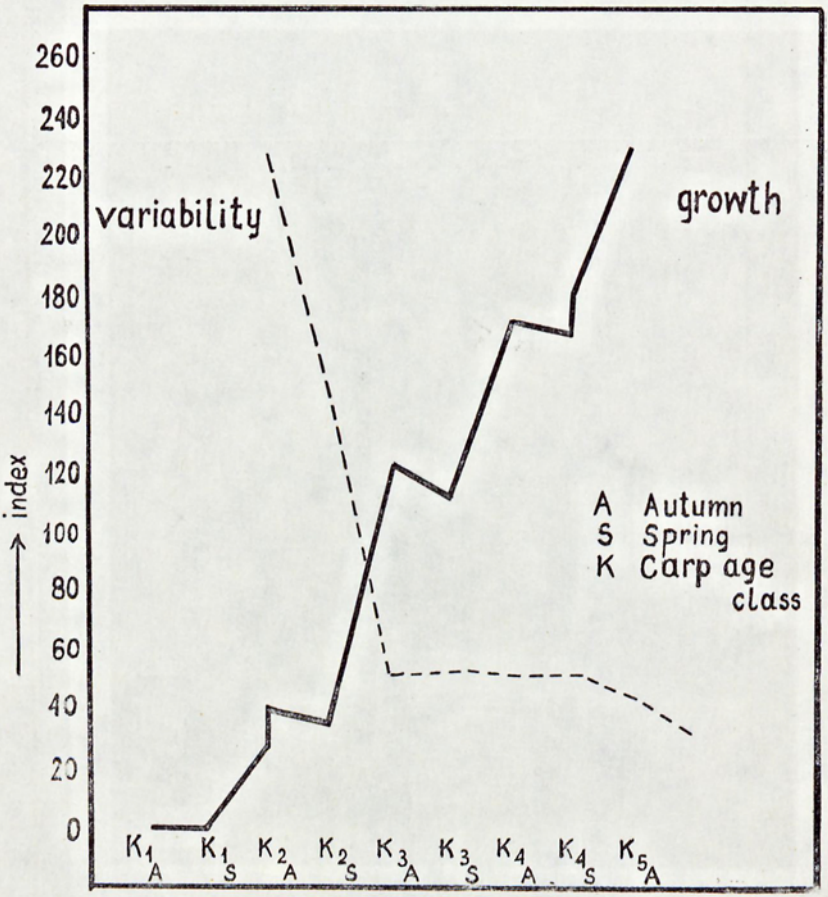


Fig. 2. Growth of the experimental population 3A1 and its relative variability (in indices). Experimental farm Ochaby 1962—1966

proper, i.e. the growth of the three selected groups. The same is illustrated graphically in figures 2 and 3. From the figures one can best follow the course of the entire experiment. The graphs presented in the figures were drawn on the basis of indices calculated from the data in Tables II and III. As the basis for the calculation of indices the total respective means were taken both for the features of weight and for the coefficients of variations.

The growth of the whole experimental population was typical. Fig. 2 shows that it had a similar course of growth as the curve of growth of carp calculated on a larger material (W ł o d e k 1968). This type of growth was also similar to the growth curve of a single carp specimen given by S c h ä p e r c l a u s (1961). This is a fast rising curve with characteristic breakdowns during winter. The accompanying relative variability calculated for the whole experiment also had a typical course: the index for

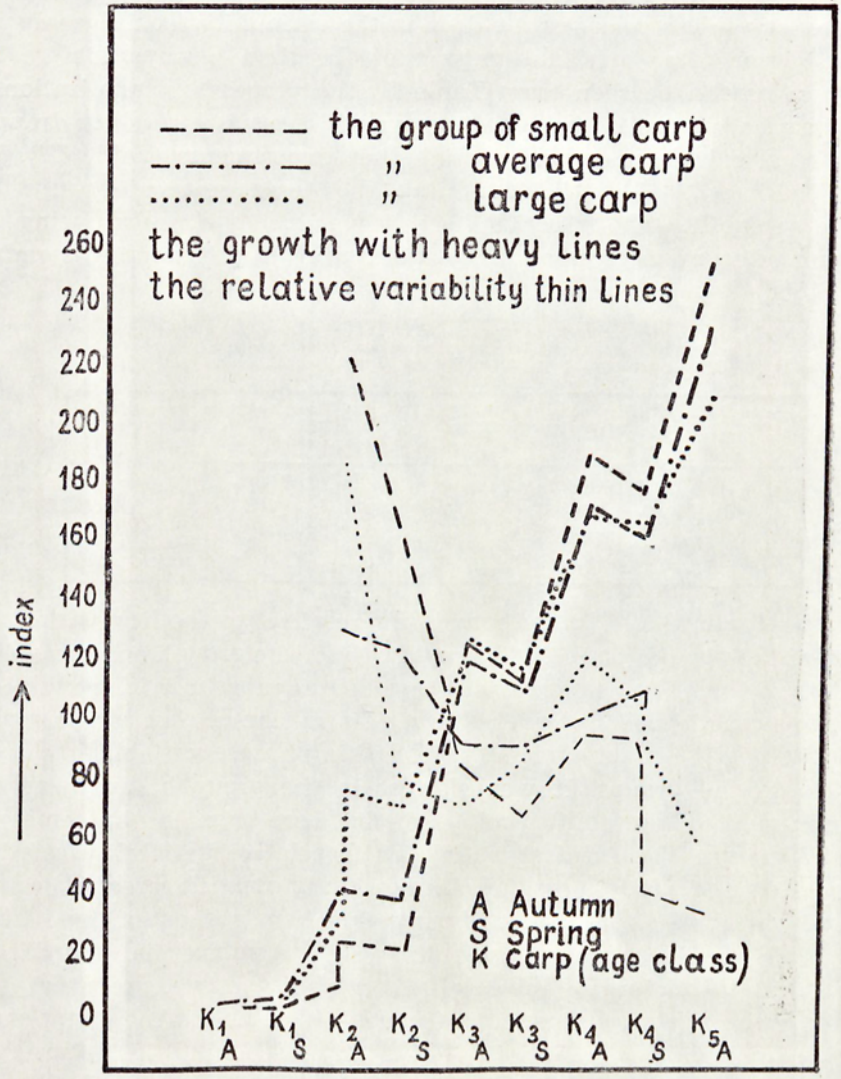


Fig. 3. Growth of the experimental groups and their relative variability (in indices). Experimental farm Ochaby 1962—1966

the coefficients of variations shows initially a sudden drop, but later on it becomes stabilized, this being a regular course in conformity with what was expected on the basis of previous works (Włodek 1968). The observed fall in the index curve in the last year of the experiment came into effect because of the last selection, while the relative variability dropped from the level of stabilization. The stabilization of variability in the whole population, i.e.after uniting the three groups, followed on the level given in a previous work (Włodek 1967 b). It is very

characteristic that a considerable drop in the variability took place during the first year after artificial uniting of the three groups. Before the selections, as can be seen from Table II, the process of equalization of variability had begun in the regular way: the relative variability dropped to the level calculated previously in other experiments (Table IV).

As the result of artificial uniting the three selected groups the relative variability should have risen; nevertheless already during the first year of common growth, the variability fell to the expected standard (Table IV).

Table IV. A comparison of the course of relative variability v % in the experimental population with standards calculated previously. Experimental population No 3A1. Experimental farm Ochaby 1964–1966

| Age of population | Expected standard for relative variability (from Włodek 1967-b) | | Observed relative variability for the whole of experimental population No 3A1 v % |
|---|---|---|---|
| $K_2$ Spring | 14.4 | | 35.0 |
| $K_3$ Autumn | 12.5 | 12 % is the standard level of stabilization | 12.5 |
| $K_4$ Autumn | 13.5 | | 12.8 |
| $K_5$ Autumn | 10.5 | | 7.8 (after selection) |

Figure 3 shows the growth and the relative variability within the groups of the population 3A1. The regularity of the growth and variability is on the whole the same as in the entire experimental population, although a certain rise in the relative variability can be observed in groups after reaching the maximum fall. The fall in relative variability was not identical in the groups. It was slowest in the group of averages, the rising in relative variability being smaller here than in the remaining extreme groups. The greatest initial fall in relative variability could be observed in the group of smalls, in which group the greatest rise in relative variability took place during the fourth year of life. These increases in the $K_4$ relative variability were not substantial and did not affect the total picture of the relative variability curve, probably being caused by the uneven maturation of males and females. The effect of the last selection can be seen in the fall of relative variability in $K_4$ Spring — the selection always favoured the larges individuals, thus leading to the decrease in the relative variability.

Comparing the slopes of the growth curves in fig. 3, it can be seen that the smalls overtook the rest in growth only in the second year of the experiment proper, i.e. in the growing season $K_3$-$K_4$. In other words, they recovered from the stress of crowding only in the second year after artificial uniting of the groups. The good quality of swift growth for which the stock had been previously selected for two generations, came into effect. In the first year of the experiment proper, i.e. in the growing season $K_2$-$K_3$, the group of larges showed the fastest growth. In the third year, i.e. in the selected stock of spawners, the group of smalls still showed the fastest growth.

Table V. Indices of equalization of average weights in the 3 groups of the growth experiment. Indices based on the averages of the whole population in a given season. Experimental farm Ochaby 1964–1966

| Group | $K_2$ Autumn selects | $K_2$ Spring | $K_3$ Autumn | $K_3$ Spring | $K_4$ Autumn | $K_4$ Spring | $K_4$ Spring selects | $K_5$ Autumn selects | Remarks |
|---|---|---|---|---|---|---|---|---|---|
| small | 52.4 | 52.9 | 91.2 | 89.4 | 94.8 | 94.6 | 91.4 | 94.6 | the index increases |
| average | 110.3 | 110.0 | 100.4 | 101.0 | 100.3 | 99.8 | 99.4 | 102.5 | |
| large | 153.0 | 153.4 | 117.5 | 118.0 | 109.7 | 112.2 | 106.7 | 102.9 | the index diminishes |
| all | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | |

During the course of growth the differences within the experimental populations decreased. If we take the average weight for the entire population in each year as 100%, we can compare with it the averages in the groups. In this way Table V was prepared, the same being illustrated graphically in fig. 4.

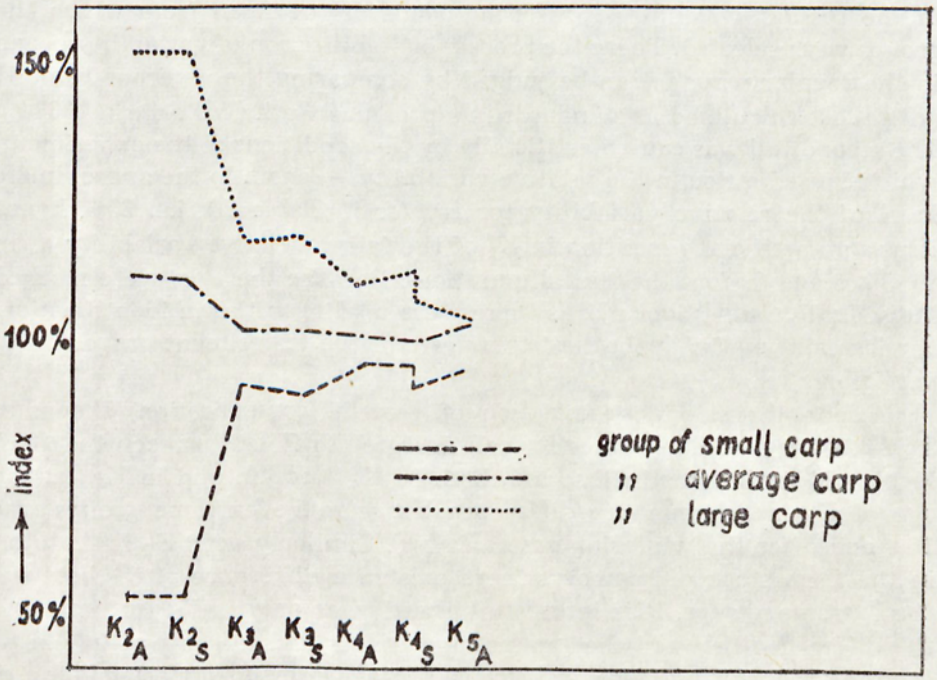


Fig. 4. The compensation of individual average weight of the three experimental groups expressed in indices. The total average individual weight for a season = 100%. Experimental Farm Ochaby 1963—1966

By comparing the indices in rows of Table V from each Spring to each Autumn, it can be seen how the differences between the groups diminished during growth. It is very characteristic that the greatest equalization of

differences took place in the first year of united growth, i.e. in $K_2$-$K_3$. It seems that the population loses the artificially caused differences in ist composition. The averages of both extreme groups approached the total average of the population by about 37%, the group of smalls by 39% and the group of larges by 35%; this means that though they had an uneven number of specimens, the two groups equalized their growth at approximately the same rate. From this same Table it can be seen, that the successive wintering did not affect substantially the indices reached in the Autumn. The relations between the averages reached in Autumn were not affected by wintering of the population. This shows that the carp lose weight proportionately during the winter. This was observed earlier by the present author (W ł o d e k 1959 b). After wintering the process of equalization of differences continued, but not so violently as in the first year.

It is worth noting that this was the second serious fall in relative variability during the life of this generation of carp, the first fall occuring in the regular way in the different ponds of the farm from which the groups were selected. There the process of stabilization of variability began in the regular way, as can be judged by comparing the v% from Table II with those calculated as standards in a previous work (W ł o d e k 1967 b). The second fall was caused artificially by the conditions of the experiment, which caused a rise in the relative variability — again to the approximate level of the relative variability for fry (as in Table II), i.e. 35%, hence it was an artificial repetition in $K_2$ of the fall in relative variability as in the $K_1$ stage (before the first diminution). Because the carp were marked individually with silver marks there were no difficulties in identification, the losses in marks in the first two years of the experiment proper being negligible.

Despite the strong equalization of growth (compensation) shown in Table V and fig. 4, the lines for relative growth failed to reach the 100% level, where they distinctly tend, both in $K_4$ Autumn and in $K_5$. At the age of $K_4$ in Autumn the difference between the extreme groups was 15% and after the wintering rose a few %. Similarly with $K_5$ in Autumn in the farm stock of spawners there existed a difference of 8% between the extreme groups. It is interesting that it was only in $K_5$ Autumn that the difference between the groups of averages and larges was 0.4%.

The group of averages showed an average growth, differing initially by only 10% from the total average, this difference being effaced in the first year of the experiment. The group of averages caught up the group of larges only at age $K_5$, the difference proving to be non-significant and amounted to only 23 g. (= 0,4%). This fact shows the importance of the genotype of carp. In the group of averages, as in the group which was selected for the first time from the entire population, there was the greatest probability of finding true jumpers.

If we take into consideration only the differences in the indices between the extreme groups (from Table V) and if we call them the indices of diminution of the differences, then we obtain an interesting picture of the equalization of growth. These differences were calculated from Table V and are given in Table VI.

Table VI. Indices of diminution of differences between the average individual weights of extreme groups in the growth experiment with population No 3A1.

| Age of experimental population 3A1 | Differences in indices and in kg | | | |
|---|---|---|---|---|
| | Differences in the indices for the whole population 3A1 | | The same specimens as in $K_5$ | |
| | Index | The same in kg | Index | The same in kg |
| $K_2$ Autumn 1963 | 88.8 | 0.60 | | |
| $K_2$ Autumn after selection | 100.6 | 0.89 | | |
| $K_2$ Spring 1964 | 100.5 | 0.82 | 84.1 | 0.86 |
| $K_3$ Autumn 1964 | 26.3 | 0.70 | 24.5 | 0.72 |
| $K_3$ Spring 1965 | 28.7 | 0.70 | 26.6 | 0.72 |
| $K_4$ Autumn 1965 | 14.9 | 0.58 | 15.2 | 0.64 |
| $K_4$ Spring 1966 spawners, all, | 17.6 | 0.64 | | |
| $K_4$ Spring 1966 spawners after selection | 15.3 | 0.60 | 16.2 | 0.65 |
| $K_5$ Autumn 1966 " " " | 8.3 | 0.42 | 7.7 | 0.40 |

In Table VI is also given the difference between the extreme groups at age $K_5$, i.e. for the stock of spawners selected from the experimental population. Table VI shows how the process of equalization of weights between the extreme groups continues uninterruptedly in such a population. Only one pair of groups showed non-significance of the difference between their means. This shows that the initial weights of the groups were decisive in maintaining for such a long time (three years at least) the differences between the groups on a significant level in the presence of a strong compensation growth and the stabilizing effect of variability. This phenomenon of significance is especially interesting from the point of view of the economics of pond farming practice.

Żarnecki et al. (1961) showed that the initial weight is a decisive factor in the better growth of jumpers in the first two years of life. This experiment shows that the initial weight is the deciding factor for better growth not only for the first two years but also from the third year on.

Tables V and VI show clearly that the average individual weights in a carp population equalize their growht. In this experiment the greatest equalization occurred during the first year of common growth of the groups. The population had already gone through the process of diminution of variability in the different ponds in which it was reared before the start of the experiment proper. Nevertheless, it was induced by the conditions of the experiment to repeat the phenomenon.

During the first year of the experiment proper the differences decreased by 75%. This is shown in Tables V and VI which show that there

exists an equalization of growth around the means of weights for each season.

This equalization, or in other words, the levelling of growth around the means of weight in the course of time is called by Zamachajev (1967) the phenomenon of compensation growth in fishes. Korotkevič (1965) after her experiments came to the conclusion that this phenomenon exists in carp populations. The results of the present experiment fully confirm this opinion.

The compensation growth appeared in this experiment despite the severe selection of the populations before the experiment proper. The carp did not grow proportionately after selection but in a compensative way. Zamachajev (1964, 1967) draws attention to the fact that compensation growth appears in different species of fishes and can last for a long period of time in a fish population. Compensation growth is closely connected with relative variability diminution. This experiment shows that the carp grow unevenly in the ponds, some showing greater increments, while the growth of others is retarded (Stegman 1965 a, b) shows that the old opinion that the rate of growth of carp in ponds is the same throughout life is not correct; in his experiments transitions of carp from one class of magnitude to another were observed during the first two years of life. His experiments confirm the results of the present work, though not by exactly the same method. If there were no transitions of carp during their growth from one class to another there would be no

Table VII. The significance of differences between the experimental groups

| Age of the population | Differences between groups | | Significance for 5 % level |
|---|---|---|---|
| | Groups | Difference in index | |
| $K_2$ Spring 1964 (after selection) | small - average | 57.9 | + |
| | small - large | 100.6 | + |
| | average - large | 42.7 | + |
| $K_3$ Autumn | small - average | 9.2 | + |
| | small - large | 26.3 | + |
| | average - large | 17.1 | + |
| $K_3$ Spring | small - average | 11.4 | + |
| | small - large | 28.6 | + |
| | average - large | 17.0 | + |
| $K_4$ Autumn | small - average | 5.5 | + |
| | small - large | 14.9 | + |
| | average - large | 9.4 | + |
| $K_4$ Spring | small - average | 5.2 | + |
| | small - large | 17.6 | + |
| | average - large | 12.4 | + |
| $K_4$ Spring (after selection) | small - average | 8.0 | + |
| | small - large | 15.3 | + |
| | average - large | 7.3 | + |
| $K_5$ Autumn | small - average | 7.9 | + |
| | small - large | 8.3 | + |
| | average - large | 0.4 | - |

phenomenon of compensation growth nor equalization of variability. Despite the fact that the compensation growth and the parallel stabilization of variability appeared very clearly in the investigated population, they did not lead to definite equalization or compensation of the experi-

mental groups within this population. The criterion of compensation between the groups is understood to be a statistical non-significance of the differences between them. The initial difference between the extreme groups was 1 : 3, while after the third year of common growth is was only 8%, though the groups were significant throughout the experiment with only one exception. This is shown in Table VII.

It would seem that the selection is primarly responsible for this state of affairs since it created large initial differences which persisted throughout the experiment on the statistical significance level. From this fact comes the important conclusion that the selection of carp populations is a useful tool for raising pond productivity. It can also be concluded that the production of heavy fry destined for selection is useful. The significance was calculated by a method given by Snedecor (1959) for testing differences between groups with an uneven number of observations. The only non-significant difference between the means of groups in Table VII is that at age $K_5$ between the average and the large group from which it may be concluded that the group of averages caught up the group of larges in growth. It is achieved only in $K_5$. All other combinations of differences between the groups show characteristic significance. The selection of experimental population was responsible for this, but one must also remember that the experimental population came from a stock which had previously been selected for two preceding generations according to the same principle of selection. This must have influenced the selection in the population and gave a greater possibility of getting greater differences. One might also expect that groups of carp from such selected populations would grow proportionally more quickly because they were always genetically uniform. The experiment showed otherwise. Dorfner (1962) draws attention to the fact that carp from good strains do not lose their ability for good growth inspite of unfavorable environmental conditions. In the present experiment the group of smalls was in unfavorable environmental conditions because of crowding. This group strongly compensates ist growth, accelerating it in comparison with the other groups (Table VI). Despite this acceleration, the group of smalls could not in the first year overtake the others, only in the second year of experiment proper did it catch up.

When investigating the differences in the average weights before and after the selections, i.e. between the average in the initial populations and that of the selected one, an interesting regularity can be observed: the differences decrease constantly during the growth of the population. This means that, if it is selected, the older the population, the smaller the difference we may get. The selection difference is expressed in %% of weight of the average weight in g. of the initial population. This means also that the greatest effect of the selection can be observed in the

youngest population. This is shown in respect to the experimental population in Table VIII.

The absolute data in Table VIII do not show this regularity but only the relative data. The selection difference in %% decreases parallelly to the rise in the average individual weight. The diminution of relative selection difference is not strictly correlated with time, but is, as can be

Table VIII. The selection differences in the growth experiment

| Date of selection | Age and class of population | The selection difference | |
|---|---|---|---|
| | | in grams | in %% to the average (= 100 %) of initial population |
| 1. 23.IV.1963 | $K_1$ fry | 29.9 | 297.0 |
| 2. 31.X. 1963 | $K_2$ two-yearlings | 236.8 | 103.8 |
| 11.X. 1963 | $K_2$ market size | 525.3 | 63.1 |
| 3. 27.IV.1966 | $K_4$ spawners | 305.6 | 8.4 |
| spawners from the group of smalls | | 164.4 | 4.8 |
| " " " " " averages | | 289.8 | 7.9 |
| " " " " " larges | | 125.4 | 3.1 |

seen from Table VIII, with weight. This can be observed from data in Table VIII for the selection in $K_2$. In this year a larger selection difference was obtained from the small carp than from those of average size. The two-yearling carp showed in 1963 a selection difference 40% higher than that from the same period in market size carp, which are always larger than the two-yearlings. The diminution of selection difference with growth is in accordance with the compensation growth. The differences between the carp are effaced in the course of growth, so that the selection difference decreases. This demonstrates once more that the production of heavy fry for selection purposes favours in this sense the process of selection. Heavy fry falicitate the finding of those specimens from such a population which will not surrender to the general tendency for compensation within it. By providing conditions of abundance of feed in a pond, greater possibilities are made for finding through selection better growing individuals. This in usually done by thinning the stocking of a pond.

Analysis of increments during the experiment proper shows that the individual increments in the entire experimental population as well as in the three groups decreased constantly, in time parallelly to the growth of the carp. This is a common phenomenon in growth and could be expected to occur in the investigated population. The relative variability of these increments was also investigated and an interesting regularity was found. The increments were observed individually during the three years of the experiment proper. The increments were investigated during those three years always on the same fishes. The individual marking of fishes made this analysis possible. It is shown in Table IX.

The coefficients of individual increments constantly increase with time and growth of the fishes. The same is observed in the entire experimental population and in the three groups. The decrease in the average weight of increments and the parallel increase in the relative variability were negatively correlated. From Table IX and from other works by the present author (W ł o d e k 1967 a, 1968) it can be inferred that in the same carp sib-population there exist two opposing variability phenomena. On the one hand, the phenotypical variability decreases and stabilizes, and on the

Table IX. Average individual increment in groups and its relative variability. The same fishes during the experiment as in $K_5$

| Year | Age in the growth season | Group | Average individual increment in grams | Number of observed fishes | Relative variability of increments in v % |
|---|---|---|---|---|---|
| 1964 | $K_2 - K_3$ | small | 2066 | 5 | 5.1 |
| | $K_2 - K_3$ | average | 1912 | 25 | 9.6 |
| | $K_2 - K_3$ | large | 1930 | 18 | 9.6 |
| | $K_2 - K_3$ | all | 1935 | 48 | 9.4 |
| 1965 | $K_3 - K_4$ | small | 1486 | 5 | 8.4 |
| | $K_3 - K_4$ | average | 1524 | 25 | 19.4 |
| | $K_3 - K_4$ | large | 1398 | 18 | 21.6 |
| | $K_3 - K_4$ | all | 1473 | 48 | 25.3 |
| 1966 | $K_4 - K_5$ | small | 1258 | 5 | 11.9 |
| | $K_4 - K_5$ | average | 1273 | 25 | 30.2 |
| | $K_4 - K_5$ | large | 1003 | 18 | 28.6 |
| | $K_4 - K_5$ | all | 1170 | 48 | 30.6 |

other the relative variability of increments as shown in Table IX increases in the same time. It should be stressed that the increment variability concerns only the achievement of growth during only a given growing season. The phenotypical relative variability shows the state of variability in a carp population as the total result of past and present achievements in growth, i.e. all past and present variabilities of increments are included. This gives the total phenotypical picture of relative variability in a carp population and is the fundamental difference between the two, so that they are only apparently contradictory. Table IX shows that during growth in time the individual differences between carp become greater and greater. This demonstrates that the carp have individual possibilities for growth which was accentuated by the fact that the carp were always together in the same environment. The greatest differences were found between the third and fourth year of life. The analysis of absolute increments from Table IX shows that during the first year of common growth of the three groups, the group of smalls showed the greatest individual average increment. The line of growth from fig. 3 shows that the group of larges held the first place as to rate of growth. In the second year of common growth the greatest increments were shown by the group of averages but in the line of growth from fig 3 the smalls took the first position and maintained it in the third year. In the last year

of common growth the averages showed the greatest individual absolute average increment.

The wintering losses in the experiment were regular. They can be seen in Tables V and X. They were similar to the losses through wintering found in a previous work (W ł o d e k 1959 b).

Table X. Average winter decreases in weight of experimental population No 3A1

| A g e | Date | Decrease in % |
|---|---|---|
| wintering $K_2$ | 1963/1964 | 8.1 % |
| " $K_3$ | 1964/1965 | 8.3 % |
| " $K_4$ | 1965/1966 | 5.8 % |

## Conclusions

The experiment demonstrates that selection influences the growth of a carp population to a high degree. In this experiment the influence of the selection could still be seen in the third year of the experiment proper, i.e. in the fifth year of the growth of the population 3A1 from the farm Ochaby. On the other hand, the compensation growth, as measured by the stabilizing effect of variability and the indices of equalization, also exerted an important influence on the population, as can be seen from Table V and VI. The compensation or equalization growth can, in the author's opinion be encountered in every carp population living in ponds. Selection in an artificial factor influencing the life of a carp population. The interference of these two factors, i.e. of selection and compensation growth, was demonstrated by the experiment. Only in $K_5$ did the experimental group of average size carp (average size for the experiment) equalize their growth statistically with the group of large carp. During the three years of common growth of the three experimental groups the factor of selection prevailed over compensation growth. This observation is of importance for the economics of pond farm management because it shows that during the age of production, and even after it, one can artificially promote better growth in a carp population, by means of selection for growth, before the factor of compensation growth is shown in it. The deciding factors for achieving such a status in a carp population are, according to K i r p i t c h n i k o w (1968) the severity of the selection and its intensity. The experiment shows the factor of selection as the opposing factor of compensation growth and the stabilizing effect of variability.

The compensation growth of a carp population and the diminution and stabilization of variability are a growth regularity. If one artificially makes groups differing in their mean weights, the population later compensates the weights and stabilizes its variability, although these pheno-

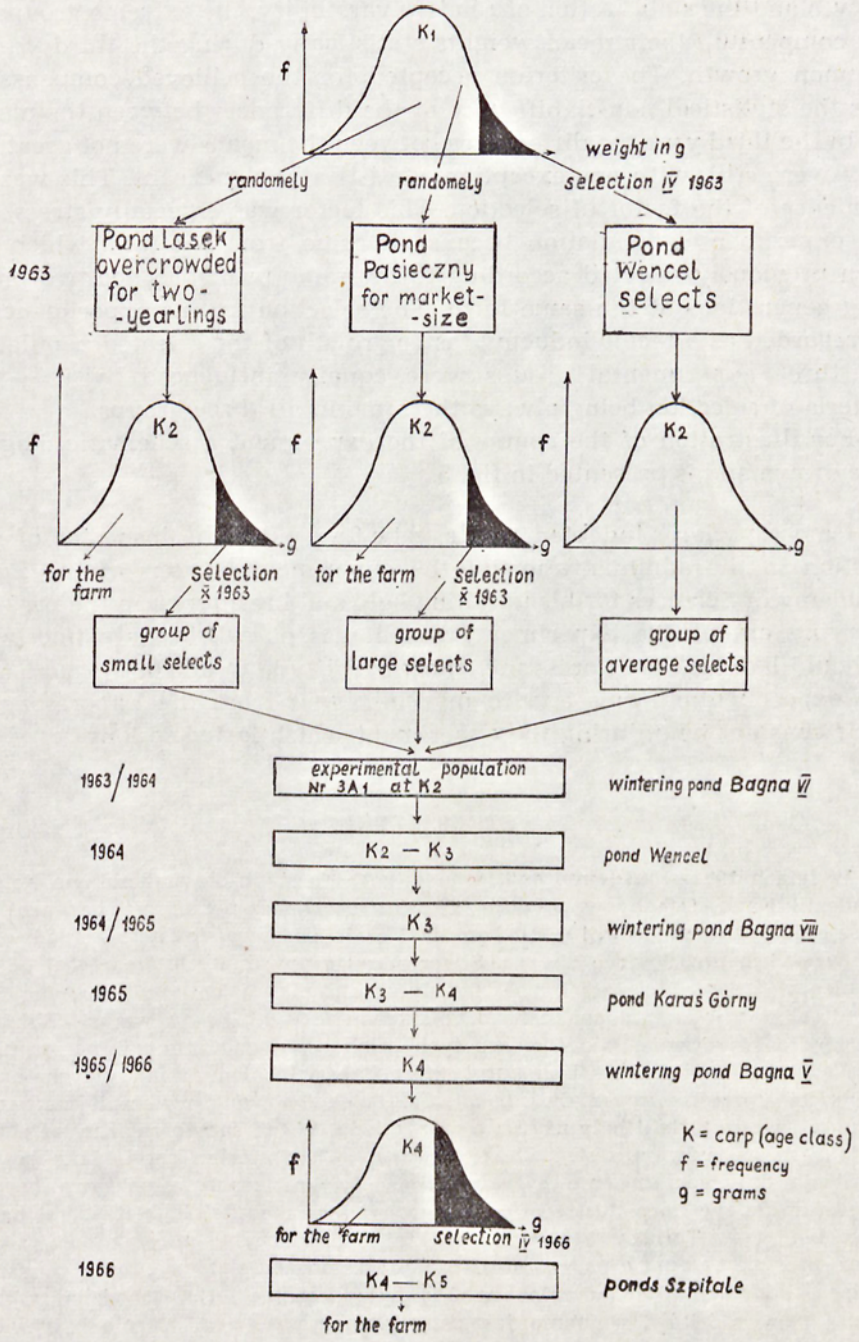


Fig. 5. Schematic diagram showing the growth experiment at the experimental farm Ochaby 1963—1966

mena occurred earlier in the regular way. Despite the compensation growth and the stabilization of relative variability, the extreme groups did not compensate their mean weights statistically during the third year of common growth. The criterion accepted for the achieved compensation was the statistical non-significance of the differences between the means.

In the third year the differences between the means were not great, but they were still, with one exception, statistically significant. This was the influence of the factor of selection. This factor was especially stressed in the experimental population because it came from a strain, which had been previously selected according to the same principles for two preceding generations at the same farm. The selection in this experiment can be regarded as a factor inducing faster growth of the selected population. All three experimental groups were equally influenced by it — the criteria of selection being always the same in all three groups.

For illustration of the course of the experiment a schematic diagram was drawn and is presented in fig. 5.

I am especially indebted to Mr S t e f a n R e c h, inspector of production in the administration of the experimental farms of the Polish Academy of Sciences for his unfailing help and his interest in the practical carrying out of the experiment, which was of substantial importance. I should like also to express my sincere gratitude to all the workers from the experimental farms and to my colleagues from the Laboratory for their constant help during the experiment which lasted so long.

## STRESZCZENIE

W latach 1962—1966 przeprowadzono w gospodarstwie doświadczalnym Polskiej Akademii Nauk, Ochaby w powiecie Cieszyn, doświadczenie odrostowe karpi. Populację doświadczalną karpi podzielono na 3 części różniące się istotnie między sobą pod względem przeciętnego ciężaru. Stworzono 3 grupy: małych, średnich i dużych. Różnice w średnich ciężarach pozostawały w stosunku jak 1 : 2 : 3. Populacja doświadczalna została poddana ostrym selekcjom ze względu na wzrost. Wszystkie 3 grupy doświadczalne pochodziły z tych selekcji. Równocześnie sama populacja doświadczalna pochodziła z linii karpi, która była selekcjonowana wg tych samych kryteriów uprzednio przez dwa pokolenia. Selekcjonowano wyłącznie na wzrost, tylko najcięższe tarlaki były używane do rozpłodu. W ten sposób chciano też zbadać, w jaki sposób uformuje się w takich warunkach eksterier karpi. Jako rezultat populacja doświadczalna nie była wyjątkowo wygrzbiecona, a pokrywa łuskowa przedstawiała typ karpi lustrzeni z rozrzuconymi, w niedużej ilości łuskami na powierzchni ciała. Tarlakami wyjściowymi tej hodowli były: mleczak sprowadzony przez prof. S t a r m a c h a z gosp. Montowo, pow. Działdowo, oraz miejscowa ikrzyca. Populacja doświadczalna nr 3A1 była „rodziną", tj. pochodziła tylko od jednej pary rodziców, podobnie jak poprzednie 2 pokolenia. Karpie były bardzo zdrowe.

Z narybku wyselekcjonowano grupę najcięższych karpi, które zwano później średnimi, gdyż ciężarowo zajmowały pośrednie miejsce między średnimi grup. Ze

stawu kroczkowego Lasek wyselekcjonowano grupę najcięższych zwaną małymi, a ze stawu Pasieczny wyselekcjonowano grupę najcięższych dwulatków, których przeciętny ciężar wynosił 1357 g. Grupę tę uzyskano ze względu na to, że na stawie tym wystąpiła silnie posocznica karpi niszcząc więcej niż połowę obsady. Jako skutek, karpie w tym stawie przyrosły znacznie ponad plan, gdyż przebywały w warunkach nie przewidzianej dla nich obfitości pokarmowej. Grupy te złączono po selekcji w jedną populację doświadczalną i od wiosny 1964 roku, hodowano zawsze razem w tym samym stawie przez następne trzy lata. W czasie wzrostu średnie ciężary indywidualne poszczególnych grup zmniejszały różnice między sobą (Tabele V i VI). Zjawisko to nazywamy kompensacją wzrostu lub wyrównywaniem się. Kompensacji towarzyszyło również zmniejszanie się względnej zmienności i jej stabilizacja. Jako kryterium kompensacji przyjęto osiągnięcie nieistotności statystycznej różnic pomiędzy średnimi grup. Przez cały czas trwania właściwego doświadczenia, tj. od czasu złączenia 3 grup i ich wspólnego odrastania zachodziła kompensacja, jednak pod koniec trzeciego roku średnie grup ekstremalnych nie były wyrównane statystycznie. Jedynie różnica między grupą przeciętnych a grupą dużych wyrównała się. Wszystkie inne różnice przez cały okres trwania właściwego doświadczenia wykazywały istotność statystyczną. Wyrównywanie się zmienności względnej zachodziło standardowo, podobnie jak w innej pracy autora. Populacja przeszła przed właściwym doświadczeniem zwykłą kompensację i zmniejszenie się względnej zmienności w stawach w gosp. Ochaby, w których przeprowadzono następnie selekcję. Przez wyselekcjonowanie trzech różniących się grup i złączenie ich wzmożono sztucznie zmienność; była ona mniej więcej taka sama jak u narybku, już w pierwszym roku wspólnego odrostu spadła do normy, czyli populacja bardzo szybko zaczęła odrabiać zaległości; widać to też z tabeli IX, analizującej przyrosty indywidualne karpi w grupach. Największe przyrosty indywidualne — bo ponad 2 kg — obserwowano w grupie małych. Okazało się, że zmienność przyrostów wzrasta w miarę wzrostu populacji, we wszystkich trzech grupach zmienność przyrostów wzrastała. Ponieważ populacja doświadczalna była oznaczona indywidualnie srebrnymi znaczkami, można było prześledzić przez trzy lata indywidualne przyrosty tych samych ryb. Podczas gdy indywidualny przyrost zmniejsza się z roku na rok, co można było przewidzieć, to zmienność przyrostów zwiększa się; uwidacznia się moim zdaniem w tym indywidualność poszczególnych osobników do lepszego wzrostu. Zimowanie doświadczalnej populacji zachodziło standardowo, zimowania nie wpływały na wzajemne ustosunkowanie się średnich grup po odroście. Potwierza to fakt wykazany przez autora gdzie indziej, że populacje karpi chudną proporcjonalnie, a nie indywidualnie.

W doświadczeniu wykazano oddziaływanie 2 czynników na odrost karpi w populacji doświadczalnej: czynnika selekcji, który jest czynnikiem sztucznym, oraz czynnika kompensacji wzrostu, który zwykle zachodzi — zdaniem autora — w każdej populacji karpiowej. Ponieważ początkowe różnice pomiędzy średnimi grup były duże, utrzymały się one początkowo w swej większości aż do trzeciego roku właściwego doświadczenia, tj. do piątego roku życia ryb. Na osiągnięcie tych różnic wpłynęła prawdopodobnie długotrwała uprzednia selekcja wg tych samych kryteriów populacji doświadczalnej 3A1. Doświadczenie więc wskazuje na znaczenie selekcji w zwiększaniu produkcji stawowej z ha stawu. Początkowe różnice okazały się tu decydującymi, co potwierdza wyniki Żarneckiego, z tą tylko różnicą, że doświadczenia Żarneckiego dotyczyły odrostu w $K_1$ oraz $K_2$, a w doświadczeniu ochabskim dotyczyły roczników od $K_3$ począwszy. Wskazuje to na to, że selekcja ma też znaczenie w dalszych stadiach rozwojowych karpi. Doświadczenie przeprowadzono w warunkach gospodarczych, karpie po selekcjach oddano do dyspozycji gospodarstwa Ochaby.

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## REFERENCES

Dorfner D., 1962. Lehren aus der Gewichtszunahme vorwüchsiger und zurückgehaltener Karpfen. Allg. Fisch. Ztg. 87, 593.

Kirpitschnikow V. S., 1968. Efficiency of mass selection and selection for relatives in fish culture. Proceedings of the World symposium on warm water pond fish culture. FAO Fisheries Reports, 44, 179—194.

Korotkevič G., 1965. Rost prudovogo karpa. Rybovodstvo i Rybolostvo, 1, 1—5.

Schäperclaus W., 1961. Lehrbuch der Teichwirtschaft. Berlin, Paul Parey.

Stegman K., 1965a. Zmienność zdolności przyrostowej karpi w pierwszym i drugim roku życia. Zeszyty Naukowe SGGW, Zootechnika, 5, Rybactwo, 2, 67—92.

Stegman K., 1965b. Wzrost karpi w drugim i trzecim roku życia. Zeszyty Naukowe SGGW, Zootechnika, 5 Rybactwo, 2, 93—110.

Snedecor G. W., 1959. Statistical Methods. Ames, Iowa.

Włodek J. M., 1959a. Cechy morfologiczne karpi z Gołysza. — Die morphologischen Merkmale der Karpfen aus Gołysz. Acta Hydrobiologica, 1, 1,5—16.

Włodek J. M., 1959b. Badania biometryczne nad zimującymi karpiami. — Biometrische Untersuchungen an den überwinternden Karpfen. Acta Hydrobiologica, 1, 3—4, 215—220.

Włodek J. M., 1967a. Studies on the variability of carp populations in ponds. Verh. Int. Ver. Limnol., 16, 3, 162—166.

Włodek J. M., 1967b. Hodowlane aspekty zjawiska działania wyrównującego. Roczniki Nauk Rolniczych, 90—H, 1, 146—169.

Włodek J. M., 1968. Studies on the breeding or carp (*Cyprinus carpio* L.) at the experimental pond farms of the Polish Academy of Sciences in southern Silesia, Poland. Proceedings of the FAO world symposium on warm water pond fisch culture. FAO Fisheries Reports, 44, 4, 93—116.

Zamachajev D. F., 1964. K voprosu vlijania rosta pervych let žizni ryb na posledujuščyj jejo rost. Tr. vsesojuz. n. issl. Inst. morsk. rybn. choz. i okenogr. 50, 109—141.

Zamachajev D. F., 1967. O kompensacionnom roste. Voprosy icht., 7, 2(43), 303—325.

Żarnecki S., Karbowski W., Rychlicki E., 1955. Wpływ selekcji narybku w okresie przysadkowania na późniejszy wzrost karpi. Roczniki Nauk Rolniczych, 70—B, 2, 207—220.

Żarnecki S., Rychlicka J., Rychlicki Z., Karbowski W., 1961. Przyrosty „pośpiechów" karpia w obsadach mieszanych z przeciętnymi. Roczniki Nauk Rolniczych, 78—B, 2, 344—355.

Żarnecki S., 1964. Das Problem der Vorwüchse in den Karpfenteichen. Zeitschrift für Fischerei, 12, NF 8/9/10, 685—707.

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