Genetic Improvement of Wild Fish Populations

Harvested wild organisms can be preserved by hybridization with "tailor-made" selected breeds.

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In this article we present a plan for the genetic improvement of commercially exploited natural populations. It is based on the creation, on breeding farms, of "tailor-made" domestic breeds for the specific objective of crossing them with indigenous populations in order to produce, in uncontrolled environments, hybrids of improved economic value. The plan is potentially applicable to any wild organisms—fish, beneficial insects, wild grazing animals, or even pasture plants. It is discussed here in terms of fish, since this application is most important in view of the long-term needs for research and development in world food production (*1*).

Summary. A plan for the genetic improvement of commercially exploited wild animals is presented. It consists of crossing wild with domesticated breeds to produce heterotic hybrids and to upgrade the wild stocks. Empirical evidence is presented from experiments with the carp. Procedures for monitoring the manipulated populations are outlined. The suggested plan is ecologically reasonable and would counteract the negative genetic changes caused by excessive commercial exploitation of many species.

More than 90 percent of all fish used for human consumption are harvested from natural bodies of water, where conventional methods of selective breeding are not applicable and where intensive fishing for many generations has caused a continuous selective removal of individuals that are larger and easier to catch. Under these circumstances, fish that grow slowly, mature early, and evade nets are likely to have a strong selective advantage, resulting in genetic changes with effects unfavorable to humans—that is, a gradual decrease of economic quality in fisheries throughout the world. Changes have also been observed in migratory behavior, spawning site and time, habitat preference, food preference, and feeding behavior (*2*).

A dramatic example of this process was provided by Gwahaba (*3*), who showed that since the intensification of commercial fishing for *Tilapia nilotica* in Lake George, Africa, in 1950, the mean size of the landed catch decreased from 900 to 400 grams, while the length range at maturity decreased from 29 to 18 centimeters (*4*).

Most fisheries harvest simultaneously a number of sympatric species. Frequently, these fisheries have progressed from large to small mesh sizes as the composition of the catch has shifted from large- to small-sized species (*2, 5, 6*). Two recent conferences (*6*) documented the drastic reduction in the abundance of commercial salmon and percid fisheries. In many cases there was no recovery after fishing had virtually ceased, which suggested that negative selective genetic changes or environmental deterioration, or both, had occurred. Attempts to remedy the situation by restocking and placing restrictions on fishing often seemed to be ineffective. We believe that genetic deterioration is a major factor that is neglected in considerations of these failures. Also, solutions to problems posed by the pollution of natural waters, another major cause of fishery collapse, should have a genetic component, namely, the breeding of pollution-resistant genotypes.

Expected large genetic changes in size, sexual maturation, and behavioral patterns due to intensive fishing probably have further disturbing effects on whole ecological systems. All these negative processes create a strong incentive for genetic "correction" of the damage done by fishing. Furthermore, it should be possible to improve the overall economic value of harvested fish in their natural (wild) environments (*7*).

Releasing hatchery-raised fry of domesticated breeds is widely practiced with trout and common carp, but their performance in the wild has usually been inferior, in spite of the fact that they were superior to their wild relatives in the protected environments for which they were selected (*8, 9*). This shortcoming of domesticated breeds can probably be partially overcome by selecting under harsh conditions that simulate those in the wild. However, we prefer the alternative of selecting fast-growing breeds (henceforth designated D) under protected environments with high feed inputs, and hybridizing them with wild indigenous relatives (henceforth W) to produce F_1 hybrids combining the high productivity of the D parents with the adaptability to wild conditions of the W parents. This alternative approach, namely, specific selection of compensatory traits in a domesticated breed followed by its mating to a wild indigenous population, is the essence of our proposition.

The heterosis (hybrid vigor) of D×W hybrids in wild environments has been demonstrated by several investigators working with trout and carp. In one experiment (*9*), 2-year-old D×W trout had superior viability and had an average weight of 572 g, compared to the parental weights of 349 and 358 g. On the basis of this difference, the yield of the hybrid was approximately 1.5 times higher than that of either parent.

The D×W hybrids may be produced either by releasing D spawners of a single sex into the wild populations or by introducing W individuals into breeding farms, hybridizing them with D, and releasing D×W into the wild. The choice of method depends on specific circumstances related to each species and the environment.

When a commercially valuable species is being harvested simultaneously with a related smaller and hence less valuable

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species (*2, 5*), a reverse strategy may be used to preserve the larger species. That is, a recessive dwarf mutant may be introduced and established in the natural environment to serve as W stock while the original large stock is maintained and protected in breeding farms to serve as D stock.

We note that the pest control method of releasing sterile individuals of a single sex (males) specifically treated to interfere with the pest's reproduction (*10*) is essentially identical to our proposed procedure; however, in our plan the animals released are selected to produce hybrids with superior performance in wild environments.

Homing fish are a very important group that can be bred by conventional methods. Saltwater salmonids, for example, are selected and bred in hatcheries, and the juveniles are sent to pasture the rich oceans and return for breeding to their home farms. It has been demonstrated that selective breeding can modify economic characteristics that express themselves during the grow-out phase in the ocean—that is, the rate of growth and time of return (*11, 12*).

Genetic Differences Between Wild and Domesticated Breeds of Fish

To determine which traits should be incorporated into a hybrid to upgrade wild populations, a comparative assessment of selective adaptation under the conditions of wild and protected habitats is necessary. We have done this, taking the common carp (*Cyprinus carpio* L.) as a model (*13*).

Natural environments, as a rule, offer fish relatively little protection, low feed inputs, a continuous strong pressure of selective harvesting, and strong intra- and intergroup competition. These features dictate evolution toward overall hardiness, competitiveness, efficient utilization of limited amounts of natural feed resources (*14*), and the ability to evade the fisherman's nets by jumping over them, digging into the mud, and so on. For example, in one experiment where Chinese carp (W), European carp (D), and their hybrids were stocked together in the same ponds, the percentages of fish caught by seines were 1.5, 25.7, and 7.7 percent, respectively (*15*). Another way in which some W fish, such as carp and tilapias, evade harvesting is to reach sexual maturity at a smaller body weight—preferably below minimal fishing weight—and to attain high fecundity (*3, 16*).

Typically, the environment of domesticated fish (as well as most other farm livestock) offers protection from predators, adequate feeding regimes, veterinary care, and artificial selection for rapid growth. A typical D fish responds to this environment with an increased growth rate and efficient utilization of the inputs. At the same time it is expected to lose (as correlative genetic changes) its specific adaptation to the wild environment—that is, its hardiness and ability to escape the fisherman's nets (*14, 16, 17*).

An evolutionary adaptation of some commercially exploited wild fish in the struggle with their major predator—man—is to start with fast larval growth, which improves juvenile viability, to sustain it until a size just below minimum fishing weight is reached, and then to stop somatic growth in favor of gonadal growth, which ensures maximum fecundity (*3*). Figure 1 shows growth curves of

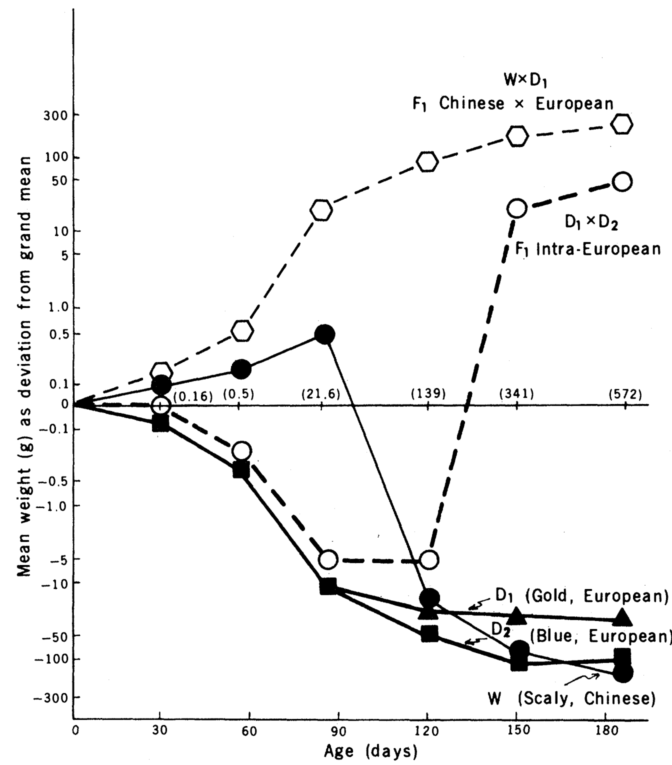

Fig. 1. Differences in growth characteristics of European domesticated carp (D), the Chinese big-belly carp (W), and their F_1 hybrid, when all were raised together in the same crowded pond. Curves labeled D_1 and D_2 represent two European inbreds marked, respectively, by the gold (*gg*) and blue (*bb*) recessive body coloration genes. Both were also marked by another recessive gene (*ss*), which produced a scale pattern called mirror that distinguished all three European groups (D_1, D_2, and $D_1 \times D_2$) from the Chinese (W) and the interrace $D_1 \times W$ hybrid, which had the wild-type scale cover. The $D_1 \times W$ hybrid was distinguished from its W parent by the recessive gold marker (*gg*). The ordinate is a logarithmic scale to present the wide range of mean weights from 0.16 g on the first to 572 g on the last sampling date. The numbers in parentheses are unweighted mean body weights, in grams, of all five groups at each sampling date.

Table 1. Expected genetic differences between W and D breeds of fish and their F_1 ($D \times W$) hybrids, following the carp model, and additional characteristics desired in D breeds selected for upgrading wild populations and in their offspring.

Characteristic	Group		
	D	W	F_1
	Expected differences between D and W		
Viability under wild conditions	Low	High	High
Seine catchability	High	Low	Intermediate
Sexual maturity*	Late	Early	Intermediate to late
Carcass quality	High	Low	Intermediate to very high†
Growth characteristics			
In wild environments	Low	High	High to very high
In cultivation	High	Low	Intermediate
	Additional characteristics desired		
Seine catchability	Increased		
Sexual maturity	Later		
Time of spawning in season	Earlier		
Egg size of a typical mother	Larger		
Morphological distinction	Conspicuous		
Electrophoretic genetic markers	$A_dA_dB_dB_d$	$A_wA_wB_wB_w$	$A_wA_dB_wB_d$
Fecundity			Sterile or one sex†

*When D breeds are selected specifically for earlier sexual maturity, these relations may be reversed.
†Sterile interspecific hybrids may have meatier carcasses and superior growth characteristics (*24*).

Table. 2. Expected segregation ratios of genotypes of two independent electrophoretic markers in hybrid derivatives between D and W fish breeds. The subscripts w and d designate, respectively, the origin of the alleles at the A and B loci. See Fig. 2 for designations of the six groups of fish.

Genotype	Group of fish					
	W	BC_{W_1}	F_2	F_1	BC_{D_1}	D
$A_wA_wB_wB_w$	1.00	0.25	1/16 = 0.0625			
$A_wB_wB_wB_d + A_dA_wB_wB_w$		0.50	4/16 = 0.25			
$A_wA_dB_wB_d$		0.25	4/16 = 0.25	1.00	0.25	
$A_wA_dB_dB_d + A_dA_dB_dB_w$			4/16 = 0.25		0.50	
$A_dA_dB_dB_d$			1/16 = 0.625		0.25	1.00
$A_wA_wB_dB_d + A_dA_dB_wB_w$			2/16 = 0.1250			

the Chinese big-belly carp (W), two genetically marked European inbreds (D_1 and D_2), their hybrid ($D_1 \times D_2$), and an interrace hybrid ($W \times D_1$). All five groups were raised in a single crowded pond and were distinguishable by morphological mutations in body coloration and scale pattern. The big-belly started faster than the three European groups (D types). After the third sampling date, at the age of 84 days, it began to fall behind, and 100 days later even the two poor European inbreds surpassed it. The most striking feature of Fig. 1 is the strong heterosis of the $W \times D_1$ hybrid, whose superiority results from its ability to surpass its W parent during the first 3 months and then switch to resembling its D_1 parent as performance drops in W, probably triggered by the earlier sexual maturation.

Expected genetic differences between typical D and W breeds of fish based on the carp model are summarized in Table 1. Also shown are a set of characteristics to be selected into a D fish bred specifically to produce superior D×W hybrids in the wild.

Population Dynamics

When D×W hybrids reach minimum fishing weight before sexual maturation, higher seine catchability and faster growth are expected to result in the removal of most of them before they reproduce. Hybrids that escape fishing may join the spawning population, adding three groups of fish that contribute to the yield and gametes of subsequent generations, as shown in Fig. 2. To estimate the overall economic value of the resulting mixed fish population, the relative value of each group and its proportion in the harvested population have to be evaluated. The F_1 hybrids, being heterozygous at all loci differentiating between their D and W parents, benefit from maximum heterosis (*H max* in Fig. 3A). The three second-generation hybrids, F_2, BC_{W_1}, and BC_{D_1}, lose half the heterozygosity of F_1, and in each subsequent generation heterozygosity is further reudced by half. This is shown in Fig. 3A, where the hypothetical heterotic component of overall economic value is plotted as a function of the relative degree of heterozygosity. The mean performance of each hybrid generation is the sum of its mean heterotic and mean additive genetic components. To clarify this point, Fig. 3B shows the effect on the curve in Fig. 3A of adding an additive component that is a hypothetical function of the proportion of D genes in the mean genotype (*18*). A stepwise degradation of performance is expected in consecutive hybrid generations (F_1, F_2, F_3, . . .), and crosses of successive BC_W generations with D rapidly approach the level of performance of the F_1 generation.

We obtained some empirical support

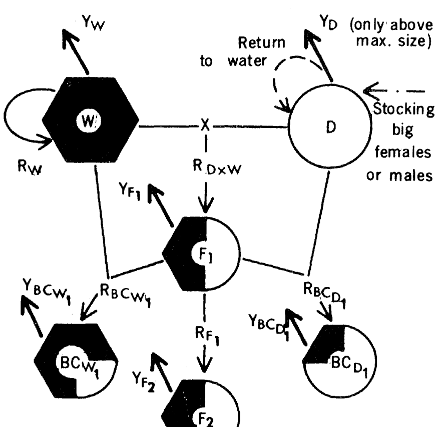

Fig. 2. Flow chart showing the components of the total yield (*Y*) and total reproduction (*R* = proportion of all fish fry in a season) after the first participation of D×W hybrids (F_1) in reproduction. Heavy arrows pointing up represent contributions to the harvest (output of the system). Lighter arrows pointing down represent recruitment of new fish into the population. Backcross of F_1 with the W parent results in BC_{W_1} and with the D parent results in BC_{D_1}. In this model, relatively large D breeders of a single sex are released into the natural environment. When captured, they may be returned to the water if they are under a predetermined size. The dark areas correspond to the proportion of W genes in each group.

of these relations when we tested the growth rates of several groups of the domesticated European carp, the Chinese big-belly carp, their F_1 hybrids, the first backcross with the European parent (BC_{D_1}), and the offspring of a mating between the first backcross and the Chinese parent (BC_{W_1}). All these groups were stocked together in polyculture ponds that received different management (*19*). Figure 4A shows the average weight gains, plotted against the proportion of D genes, of two selected European lines (D_a and D_b), the big-belly (W), and their various hybrids when grown in duplicate ponds receiving daily rations of liquid manure without any extra feeding. The heterosis of the W×D hybrids is conspicuous (*20*). In contrast, in a similar experiment where the fish were given a high feed input, the D breeds were decidedly superior (Fig. 4B). These results show the importance of genotype-husbandry interactions, and should serve as a warning against ranking genotypes in wild environments on the basis of data obtained under conditions of domestication.

Cost Considerations

Cost considerations dictate that each unit of released D parents should produce a relatively large weight of harvested offspring. Because of the great fecundity of most fish species, a small number of parents are able to produce vast numbers of offspring. For example, a single 5-kilogram female carp may produce about a half-million eggs. Most fish larvae die during a relatively short period after hatching, when mortality is strongly density-dependent since a limited number of growing fish can be supported by a particular niche. Therefore, a genotype with greater competitive ability may have a greatly increased chance of survival. We found that when a spawn of carp fry hatched a single day earlier in a crowded pond, their relative survival was increased as much as tenfold. Similar increased survival was found among offspring of 2-year-old carp mothers compared to offspring hatched in the same ponds from the much smaller eggs of 1-year-old mothers (*21*).

These and similar findings point to a general method of increasing the proportion of F_1 hybrids while maintaining a low biomass of the released D mothers. That is, larger and older D mothers (or fathers, when paternal size is the major determinant of the relative reproduction rate) may ensure high fecundity and fry survival. Also, the use of hormone injec-

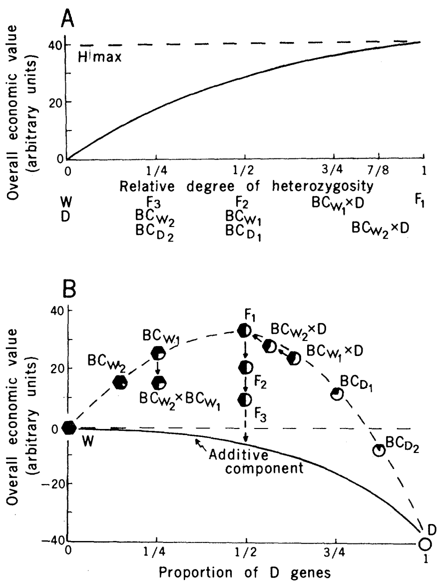

Fig. 3. Hypothetical distribution of overall economic value of W and D breeds of fish and various hybrid generations grown in a wild environment. The symbol BC_{W_1} denotes the first backcross with the W parent ($W \times F_1$), and BC_{W_2} denotes the second backcross with the W parent ($W \times BC_{W_1}$). Similarly, BC_{D_1} and BC_{D_2} represent the first and second backcrosses with the D parent. The second ($F_1 \times F_1$) and third ($F_2 \times F_2$) hybrid generations are F_2 and F_3, respectively. (A) Heterotic component (*H*) of overall economic value, presented as a function of relative degree of heterozygosity. (B) Total overall economic value (additive and heterotic components) presented as a function of the proportion of D genes in a W×D hybrid. The heterotic component is that of (A). Small arrows indicate consecutive generations.

tions, maintenance in hothouses before stocking, and other artificial methods may force D mothers to spawn somewhat earlier than their W competitors, and thus ensure relatively high survival of the F_1 hybrids.

For species that require vast numbers of breeders—too many for economic production in breeding farms—we should consider release of the grandparent generation. This is common practice with farm livestock, particularly chickens. In this case the F_1 hybrids should produce (by $F_1 \times F_1$ or $F_1 \times W$ matings) the majority of the harvested individuals. Thus, the scheme is feasible when the weight of recruits into the fishery is higher than the weight at onset of reproduction, and it requires fertile and reproductively competitive F_1 hybrids.

Ecological Considerations

A prime consideration in planning genetic manipulations of wild populations is the potential danger of damaging the populations themselves or their environment. In this respect, an attractive feature of the present plan is its ecological safety. When single-sex D breeders that produce only sterile W×D hybrids are released, the natural gene pool cannot be contaminated or harmed. Interference with other organisms sharing the same environment can be easily corrected by discontinuing the release of D parents. But even with fertile D×W hybrids, the number of gene substitutions that can take place is very limited and consequently the likelihood of damage appears to be extremely low. The higher catchability and lower viability in wild environments of qualified D genotypes should lead to strong natural selection against hybrids having a high proportion of D genes, and therefore they should be relatively rare. On the other hand, backcrosses in the W direction may lead to a slow introgression of D genes into W. This process would upgrade the economic value of W and counteract the damaging effects of fishing. For maximum safety, the manipulated populations should be monitored by genetic markers, as outlined in the following section.

Monitoring with Genetic Markers

The D stocks can be made distinguishable from W by genetic marking with morphological mutations that affect body coloration or scale pattern or produce minor fin abnormalities (*7*). However, most morphological mutants have recessive expressions that make them inadequate for monitoring the composition of hybrid generations, a disadvantage not shared by electrophoretic genetic markers, which are, as a rule, codominant (*22*). Two properly chosen electrophoretic loci can provide a sufficient tool for estimating the proportion of each group in the harvest at the second hybrid generation stage. Table 2 shows the expected segregation ratios in the first and second hybrid generations of two independent electrophoretic loci, each having alternative alleles in the D and W populations. The two alleles of one locus are designated A_w and A_d, while those of the second are B_w and B_d. Hence, the purebreds in W and D are $A_wA_wB_wB_w$ and $A_dA_dB_dB_d$, respectively; the F_1 hybrids are $A_wA_dB_wB_d$; and the second generation hybrids, F_2, BC_{W_1}, and BC_{D_1}, segregate as shown in Table 2. The two "mixed" homozygotes, $A_wA_wB_dB_d$ and $A_dA_dB_wB_w$, may be found only in the F_2 generation (Table 2). Assuming that the two loci are subjected to only very mild selection and are uncorrelated with catchability, the expected proportion of

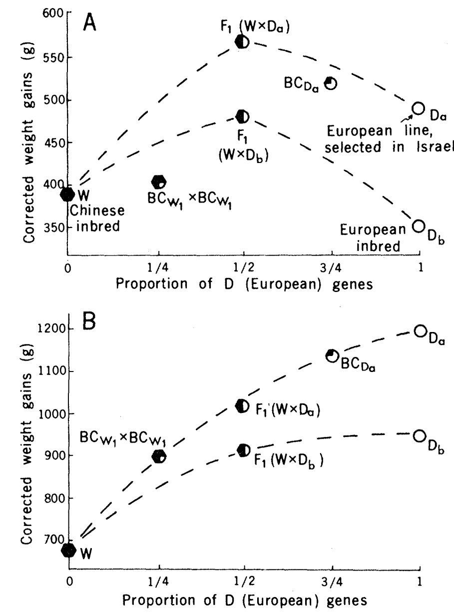

Fig. 4. Mean weight gains (corrected for differences in initial weights) presented as functions of the proportion of European genes in hybrids between the Chinese and European races of the common carp. (A) Results from ponds where the only feed supply was liquid cow manure. (B). Results from ponds where the fish were fed with abundant, protein-rich pellets. Note the difference in scale between (A) and (B).

these mixed homozygotes among caught F_2 individuals is $1/8 = 0.125$, so that eight times this value is an estimate of the total frequency of F_2 in the caught population, and the frequencies of the remaining five groups (W, D, F_1, BC_{W_1}, and BC_{D_1}) can be estimated easily by similar computations (*23*).

By studying the segregation ratios in seined samples at appropriate time intervals, one would be able to estimate relative mortality as a function of age and construct growth curves for each group of fish (*23*).

Timetable for Application

To adopt this plan on a large scale would require overcoming many constraints, primarily related to our inability to control the complete life cycle of most saltwater fish. Consequently, we foresee gradual implementation in a stepwise fashion. The plan could be applied with freshwater cultivated species (carp, trout, tilapia, and so on) in confined bodies of fresh water such as undrainable ponds, artificial reservoirs, and small lakes almost immediately (*7*). It could then be extended to larger lakes and rivers with more species. Next, it might be extended to coastal marine species that reproduce in captivity. Application to species of the open seas would be considerably more difficult, and some species may never be amenable to such breeding schemes.

This general breeding plan opens up new opportunities for applied geneticists. It can be modified in imaginative and useful ways to contribute to world food resources by means of the genetic preservation and improvement of economically important wild stocks. The improvement of breeding stocks for catch fisheries is an important and as yet unfulfilled role of aquaculture. We believe that the time lag to successful application of the plan with many commercially important aquatic and marine species is primarily a function of investment in problem-oriented research and development.

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13. The carp was chosen as an example because (i) more is known about genetic control of the growth of carp than of any other fish species and (ii) the carp has been the subject of our intensive genetic research for 20 years, and for the last 7 years we have been studying genetic differences between the cultivated European and Chinese big-belly races of the carp in relation to their evolution and use in breeding programs. These studies provide the only documented empirical evidence that we know of concerning the present subject of fish domestication. The cultivated European carp has been selected by European fish breeders for hundreds of years and it may be considered a truly domesticated breed. The Chinese big-belly carp has been grown in ponds even longer than its European relative, but it has not been selected for improved economic value and it continuously absorbed immigrants caught in rivers and stocked in ponds for cultivation. Also, traditional reproduction and harvesting techniques used with the big-belly carp, as a rule, did not differ in major features between farms and rivers. Consequently, we feel justified in considering the big-belly a wild organism (*16*).
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18. The curvilinearity of the additive component may result from its nonlinear relation to traits such as growth rate, viability, and seine catchability [see R. Moav, *Anim. Prod.* **8**, 193 (1966)].
19. Here, polyculture implies the mixing together in one pond of several species of fish. For full details of this experiment, see R. Moav, G. Wohlfarth, G. L. Schroeder, G. Hulata, H. Barash [*Aquaculture* **10**, 25 (1977)].
20. When comparing the results presented in Fig. 4A with the equivalent hypothetical example in Fig. 3B, the following points should be borne to mind. (i) The $BC_{W_1} \times BC_{W_1}$ group of Fig. 4A had lost half of the heterosis of its parental generation BC_{W_1}. (ii) Weight gain is only one of the major components of overall economic value. A second major component is viability, which would favor **W** over D. (iii) The correction for differences in initial weights in Fig. 4A eliminated a major effect of competition that would have favored the **W** side of the diagram. For a detailed discussion of the last point, see G. Wohlfarth and R. Moav [*Aquaculture* **1**, 7 (1972)].
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23. The two genotypes with three **W** alleles may be found in both BC_{W_1} and F_2 at expected intragroup frequencies of 0.5 and 0.25, respectively (Table 2), so the frequency of BC_{W_1} may also be estimated.

$$(BC_{W_1}) = 2[A_wA_wB_wB_d + A_wA_dB_wB_w - {}^1/_4(F_2)]$$

Similarly

$$(BC_{D_1}) = 2[A_dA_dB_dB_w + A_wA_dB_dB_d - {}^1/_4(F_2)]$$

$$(F_1) = A_wA_dB_wB_d - {}^1/_4(BC_{W_1}) - {}^1/_4(BC_{D_1})$$

$$(W) = A_wA_wB_wB_w - {}^1/_4(BC_{W_1}) - {}^1/_{16}(F_2)$$

$$(D) = A_dA_dB_dB_d - {}^1/_4(BC_{D_1}) - {}^1/_{16}(F_2)$$

Note that the equations above provide estimates of the proportions of these groups among the caught fish. To calculate the equivalent proportions in the water, these estimates have to be multiplied by the appropriate relative catchability coefficients.
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25. We acknowledge the help of G. Wohlfarth, J. Bardach, and S. Malecha in the preparation of this manuscript. This research was supported by a grant from the United States–Israel Binational Science Foundation, Jerusalem, Israel. Contribution from the Agricultural Research Organization, Volcani Center, Bet Dagan, Israel: 1977 series, No. 204-E.

Research Involving Human Subjects

The performance of institutional review boards is assessed in this empirical study.

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Research involving human subjects raises ethical and legal issues of sufficiently serious and widespread concern that an increasingly comprehensive mechanism has been developed through which the judgments of researchers are reviewed. Institutions seeking funds under the Public Health Service Act for research involving human subjects are required under the National Research Act of 1974 to establish committees (called "institutional review boards" in the Act and commonly referred to as IRB's) to review such research conducted at or sponsored by the institution. However, such committees existed at most institutions prior to this statutory requirement, because of Public Health Service and Department of Health, Education, and Welfare (HEW) requirements dating back to 1966, and many institutions had review committees even earlier (*1, 2*). Under HEW regulations (*3*), IRB's are supposed to review research proposals to determine whether subjects will be placed at risk and, if so, whether the risks to the subjects are outweighed by the sum of the benefits to subjects and the importance of the knowledge sought, whether the rights and welfare of subjects are protected, and whether "legally effective informed consent" will be obtained by adequate and appropriate means. Institutional review boards also

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