## Chapter 15

# Selective Breeding of Walleye: Building Block for Closed-System Aquaculture

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## Introduction

This chapter begins with a brief introduction to some basic genetic concepts involved in selective breedmg, then illustrates these concepts with some data on walleye, and ends with general advice to aquaculturists who might be interested in conducting a breeding program. If you are looking for a quick fix to increase production or to reduce variability in yield, this chapter may disappoint you. In terrestrial agriculture, selective breedmg has been an effective method of improving production, but the improvements came from long-term commitments to breeding programs.

The ideas and recommendations in this chapter apply only to walleye breeding programs for aquaculture in contained systems; i.e. systems where fish have a negligible risk of escape into natural waters. Also, we strongly discourage aquaculturists from undertaking selective breeding or other genetic modifications of walleye that are destined for intentional stocking into natural waters. In any breeding program, there is a trade-off between improved performance in the selected environment and reduced performance in other environments. If you start with a wild-type or nearly wild-type broodstock and practice artificial selection for improved performance in an aquaculture environment, offspring of the selected parents will exhibit reduced performance in wild environments. Intentional, selective breeding of walleye in an aquaculture system selects for improved performance within that artificial, captive environment. This necessarily reduces the selectively bred strain's performance in environments of natural bodies of water.

We particularly caution the reader against stocking selectively bred walleye into waters containing wild walleye populations. This could adversely affect wild genetic diversity and, thus, jeopardize the long-term sustainability of walleye populations. It is in the best interest of aquaculturists to protect wild gene pools, because these are irreplaceable sources of future genetic material that may be needed to improve captive populations. For instance, if a new disease were to sweep through progressively inbred, domesticated walleye broodstocks, wild gene pools of walleye could be the source of a gene that confers disease resistance. Because all artificial breeding programs inevitably reduce the broodstock's genetic variation over time, a periodic infusion of wild walleye genetic material is one of the best ways to avoid problems such as inbreeding depression.

## Basic genetic concepts involved in selective breeding

### Quantitative traits

Many production traits of interest to aquaculturists are called quantitative traits. Quantitative traits are described by a measurement, such as grams of body weight, and are controlled by many genes. Figure 1 shows the frequency distribution of the quantitative trait, body weight at 247 days, in a captive walleye population which was raised in a series of indoor flow-through tanks. In any interbreeding population, quantitative traits vary among individuals due to the different genetic make-up of each fish and the different environmental conditions experienced by each fish over its
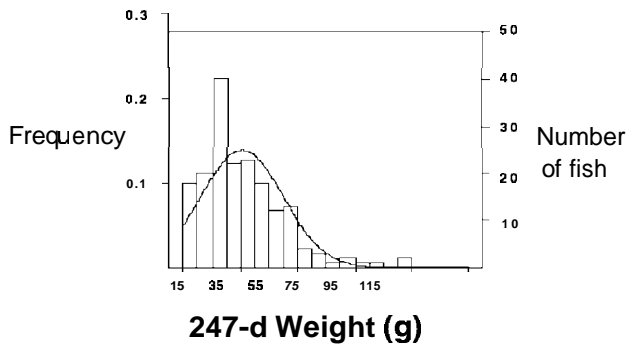
**247-d Weight (g)**

**Figure 1. Frequency distribution of individual weight (g) at age 247 days for the founder generation of a pedigreed walleye broodstock that was raised in flow-through indoor tanks at the University of Minnesota.**

lifetime. Data in Figure 1 represent fish belonging to 12 dfferent families; these families were propagated by crossing gametes collected from adults of one wild population. Each family was first raised in a separate tank, and then fish of each family were evenly distributed among two grow-out tanks. Although we tried to keep culture condtions similar in the entire facility, different fish still experienced different environments.

### *Heritability and artificial selection*

Heritability provides a way to measure the degree of genetic control over a particular quantitative trait. Heritability of a trait quantifies the degree to which the performance of offspring resembles the performance of their parents because of genetic control over the trait. The value of heritability, symbolized by $h^2$, can range from 0 to 1. If $h^2 = 0$, there is complete environmental control and no additive genetic control over the observed trait. If $h^2 = 1$, there is complete genetic control and no environmental control over the trait. The closer the value is to 1, the more offspring tend to predictably resemble their parents and the more easily can the trait be modified by artificial selection.

Even when there is no change in the genetic control of a trait, the measured heritability for a trait withn a broodstock will decrease if the fish experienced high environmental variability in their culture conditions. This is because heritability is a ratio that reflects both genetic and environmental variation that affect the trait:

$$h^2 = V_A / (V_G + V_E + V_{G-E}) \tag{1}$$

where:

V, = additive part of genetic variance affecting expression of the trait';

V, = total genetic variance affecting expression of the trait;

$V_E$ = environmental variance affecting expression of the trait;

$V_{G-E}$ = interaction of genetic and environmental variance affecting the trait

The terms in the denominator of equation (1) for heritability add up to the phenotypic variance (V,) of the trait in the population. Phenotype refers to the detectable property of a trait, for example, the measured wet weight of fish; so $V_P$ is the variance of wet weight among all fish measured in a given population. Thus,

$$V_P = V, + V, + V_{GxE} \tag{2}$$

and

$$h^2 = V, / V_P \tag{3}$$

### *Rearing environment influences heritability.*

An increase in environmental variability — for example, increased differences in fish stochng or in feeding rates among tanks at one fish farm — will likely increase the value of the denominator of the ratio in equation (1) and, therefore, will decrease the $h^2$.

Aquaculturists must also beware that different rearing environments may change the value of heritability of
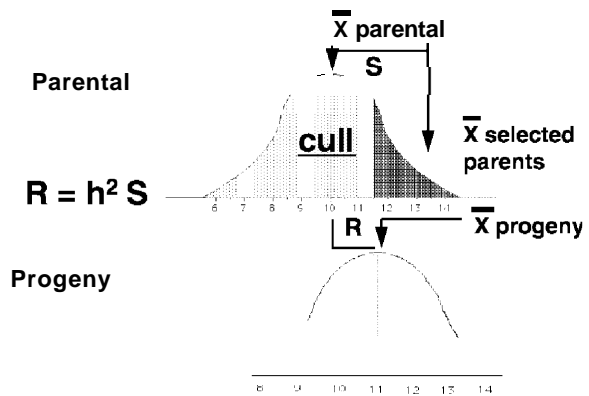


**Figure 2. An illustrative example of response to mass selection. S is the selection differential imposed in the parent generation, $h^2$ is the heritability of the selected trait, and R is the response to selection in the progeny generation.**

the same trait, so that heritabilities estimated at one facility may not be directly transferable to a population cultured at another facility. For example, studies have shown that heritabilities of fish survival and growth differed under different rearing temperatures and in different rearing facilities (reviewed by Tave 1993:131 and 148).

*Importance of heritability in application of selection.* To understand the central role of heritability in selective breeding, consider the simplest form of selection, called "mass selection" (Figure 2). The upper curve shows the normal distribution of trait X in a population being raised at a fish farm. The selection differential, **(S)** is the difference between the mean phenotypic value of the entire parental population **(X**parental) and the mean phenotypic value of the select broodstock ($\overline{X}$ selected). The select parents, whose values for trait **X** are denoted by the shaded portion of the distribution, are the only parents that are mated to produce the next generation. The lower curve shows the altered distribution of trait **X** in the progeny generation. The response to selection (R) is the difference between the mean of the progeny and parental generations.

Breeders can estimate heritability at one of two points in a selective breeding program:

(1) *In the parent generation, before actually imposing selection.*
This approach involves actually estimating the values of the variances in Equation *(3)*. It allows breeders to determine whether a breeding program is likely to be worthwhile. If selection appears worthwhile, it allows breeders to plan the most effective way to apply artificial selection on one or more traits and to obtain the desired response in the next generation. It also permits improved forecasting of costs and benefits of the breeding program. But it requires greater up-front costs of producing the parental population through a specific mating scheme and keeping performance records on individually marked fish.

(2) *After imposition of selection.*
This approach involves actually measuring **S**, R, and then estimating heritability as:

$$h^2 = R / S \qquad\qquad (4)$$

This approach is cheaper at the outset. It precludes, however, good forecasting of costs and benefits because one lacks the information to predict the response to selection. It also involves taking the risk that the breeding program will be a waste of effort due to low heritabilities for your population or in your rearing environment. For a review of two real cases where this happened, see Tave (1993: 148-149).

In the walleye genetics research done at the University of Minnesota, we chose the first approach and measured $h^2$ for many traits in the parental generation. Our original goal was to obtain the best planning information for a long-term breedmg program.

Using the first approach, we estimated the heritability of wet weight at age 247 days to be 0.93. This was based on data collected from indwidually marked fish belonging to 12 families of a parental generation and raised in a flow-through indoor tank system. This high heritability value is a welcome result because the closer the value is to 1, the more offspring tend to predictably resemble their parents and the more easily can we modify the trait by artificial selection.

Now that we know the heritability value for this trait, we can predict the average weight of progeny from select parents for any **S** that we might consider imposing in the parental generation. Figure 3 illustrates this point for the following example: By relying on our individual performance records and the fact that parental generation fish are indwidually marked with passive integrated transponder (PIT) tags, we could choose to mate only those fish which weighed more than *53* g at age 247 days. According to the calculations shown below, we predict the average weight of offspring at 247 days to be 64.1 g, **an** increase of 35.5 g:

*Response to selection for* **wet** *weight at 247 days*
- **S** = 66.3 g - *35.5 g* = *30.8* g
- $h^2$ = 0.93 (estimated from University of Minnesota parental data)
- R = S x $h^2$ = 30.8 g x 0.93 = 28.6 g
- Progeny average weight: $\overline{X}$ progeny = $\overline{X}$ parental **+** R = 64.1 g.

These calculations predict a gain of *80.5%* per generation, which is very large. If we were to actually impose the selection differential of this example, the realized response will likely be lower[2], but these results show
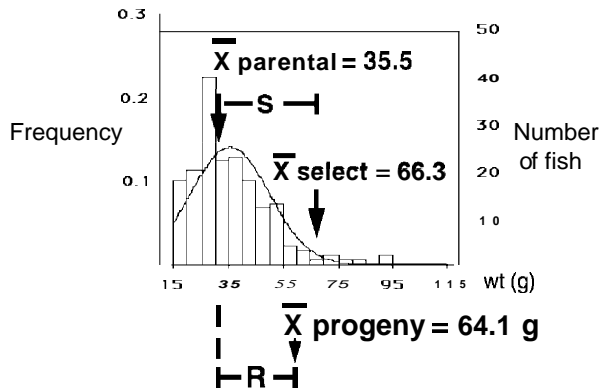
**Figure 3. Example of how breeders can use a measured trait heritability to predict the response to selection for any selection differential, S, that they might consider imposing in the parental generation. If a breeder mates only those fish which weighed more than 53 g at age 247 days, predicted average weight of progeny is 64.1 g based on the following calculations: Selection differential, S = 66.3 g - 35.5 g = 30.8 g. Heritability, $h^2$ = 0.93 (estimated from data on parental fish raised at the University of Minnesota). Response, R = S x $h^2$ = 30.8 g x 0.93 = 28.6 g. Progeny average weight: X progeny = X parental + R = 64.1 g.**

the potential for rapid gains through selective breedmg of walleye for food fish aquaculture.

## Potential for selective breeding of walleye

Collective experience of animal breeders leads to the following general recommendations about the effectiveness of artificial selection depending on a trait's value of $h^2$. Traits with $h^2 > 0.25$ respond well to selection, while traits with $h^2 < 0.15$ are hard to change by selection, although certain selection strategies more complex than mass selection can improve response in such cases. Traits with $h^2$ between 0.15 and 0.25 will respond to selection, but may require more generations of selection to reach desired values for the modified trait.

### Table 1. Examples of walleye fry traits amenable to selection, based on pedigreed families raised at Iowa State University (Summerfelt and Bristow 1994).

| Trait | Sire $h^2$ |
| --- | --- |
| Hatching length | 0.47 |
| Gas bladder inflation **(14** d) | 0.83 |
| Gas bladder inflation (21 d) | 0.60 |
| Cannibalism | 0.55 |

### Examples of juvenile traits amenable to selection

Following these general guidelines, a number of juvenile walleye traits should be amenable to selection. Table 1 shows some of the trait heritabilities which were estimated using 12 families of fry raised at Iowa State University (Summerfelt and Bristow 1994). Table 2 shows some of the growth-related heritabilities which were estimated using a different set of 12 families reared at the University of Minnesota. The families raised at Iowa and Minnesota were founded from the same source population — gametes collected from wild fish caught in the Mississippi River near Genoa, Wisconsin. In Table 1, the relatively high $h^2$ for gas bladder inflation and cannibalism indicate that these traits should respond well to selection. This is good news because tank-reared walleye have shown poor performance in these traits. In Table 2, the high heritabilities indicate that a selective breeding program should be able to improve growth in walleye with good to excellent rates of gain per generation. Note that these heritabilities of weight and length increase as age increases.

### Other traits potentially amenable to selection

A growing body of data indicates that many production traits show sufficiently high heritabilities across various fish species, which means that they can be modified by artificial selection (Chevassus and Dorson 1990; Tave 1993: 132-147). So far, we have mentioned the potential for selection on fry traits, weight-at-age, and length-at-age. Other traits may show adequate heritabilities in walleye. Traits worthy of future genetic investigation in walleye include:
• carcass traits — gutted weight, dressing percentage, belly thickness, percent fat;
• reproductive traits — age at sexual maturity, age at spawning, egg size, egg number;
• disease resistance traits — survival from exposure to specific pathogens; and
• physiological traits — oxygen consumption, food conversion, tolerance of sub-optimal temperatures,

Through proper planning and appropriate application of systematic selective breeding, fish breeders have

experienced good to excellent rates of change in average values of traits per generation. To get a sense of the rates of change per generation obtained from selective breedmg of other fish species, Table **3** presents reported gains in weight or growth rate for four selective breeding programs. Gains can be expected for many generations of continuous selection in the same direction on a given trait. However, selection will likely reach a plateau possibly after 30 to 100 generations of selection. The number of generations it takes to reach the selection plateau depends, in **part,** on the amounts of $V_A$ for the trait. Thus, it is desirable to start a breeding program with a population that has good overall levels of genetic variability. This was one criterion used to choose the Genoa, Wisconsin wild population, compared to other candidates, as the source of founders for the walleye families raised at Iowa State University and University of Minnesota (NCRAC 1993:31).

**Table 2. Examples of growth-related traits amenable to selection, based on pedigreed walleye families raised at the University of Minnesota.**

| Trait | Sire $h^2$ |
| --- | --- |
| 25-d length | 0.30 |
| 47-d weight | 0.41 |
| 115-d length | 0.42 |
| 115-d weight | 0.62 |
| 247-d length | 0.74 |
| 247-d weight | 0.93 |
| 270-d weight | 0.90 |

**Table 3. Reported gains in fish weight or growth rate from different selective breeding programs.**

| Species | Gain/Generation | Reference |
| --- | --- | --- |
| Rainbow trout | 10% | Kincaid et al. 1977 |
| Atlantic salmon | 30% | Gjedrem 1979 |
| Atlantic salmon | 10-14% | Kinghorn 1983 |
| Coho salmon | 10% | Hershberger et al. 1990 |

of yield due to genetic causes. Genetic variation decreases over time through a process geneticists call "random drift" or "genetic drift." This leads to loss of some alleles that have beneficial effects on economically important production traits. Also, inbreeding accumulates over generations. If inbreeding levels get too high, it can cause inbreeding depression, whch might cause reductions in survival, growth, or disease resistance or detrimental changes in other traits. The second lowest curve depicts the case where genetic factors have no effect on yield. The number of parents per generation is sufficient to keep levels of genetic drift and inbreeding low enough to avoid adverse effects on yields. This independence from genetic factors, however, cannot go on forever. Broodstock will need periodic infusions of new genetic material to avoid detrimental levels of inbreeding and genetic drift.

## What do different breeding programs offer?

If you are contemplating embarking on a breeding program, it is important to understand the different opportunities and constraints offered by different types of breeding programs[3]. Figure 4 compares the effects on yields of no breeding, systematically choosing the best strain, selective breeding, hybridization, and certain combinations among these options.

Walleye farming with no deliberate breeding program might follow one of two trajectories depicted by the two lowest curves in Figure 4. The lowest curve depicts the situation where the number of parents used to propagate each generation of offspring is too low, leading to loss
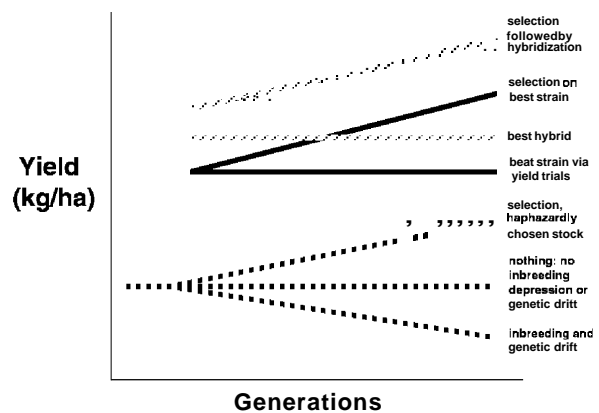


**Figure 4. Comparison of different breeding programs in terms of genetic gains possible over future generations (adapted from Tave 1993).**

Compared to these two cases, selective breeding of the same broodstock brings about some increase in yields over time. However, the broodstock may not have a desirable genetic make-up, compared to other possible sources of founders. From a breeder's perspective, this broodstock is a haphazard choice for launching a breeding program. It may seriously limit the gains obtained from the breedmg program.

Compared to doing nothing, a better option for increasing yields is to establish a captive broodstock from the best strain. To identify the best strain, breeders conduct carefully designed and monitored comparisons of a number of candidate strains under the same aquaculture environment(s). This approach essentially involves taking advantage of nature's past work by finding the pre-existing gene pool that is already fairly well adapted to a particular aquaculture environment. For example, Figure 5 shows the differences in body weight among 19 different strains of Atlantic salmon cultured in the same aquaculture environment. As explained more fully below, a breeding program aiming to increase size at harvest might involve application of selection, hybridization, or both. The number of generations of breeding needed to reach a specific goal for increased size, as well as the associated costs, would be reduced if breeders began with 1, the best performing strain, rather than with strain **19.** Additionally, different strains may naturally perform better in dfferent aquaculture systems. Thus, systematic identification of the best strain for a given aquaculture environment is essential for having an effective breeding program. The limitation of a breeding program based solely on identification of the best strain is that it precludes additional genetic gain in future generations. This is depicted by the horizontal line in Figure 4.
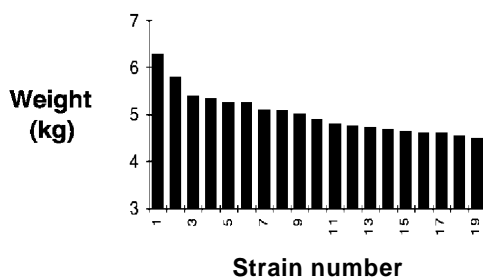


**Figure 5. Ranking of strains of Atlantic salmon for body weight after two years in sea cages (adapted from Refstie 1990).**

Building on identification of the best strain, breeders have three options for getting additional genetic gain. A one-time increase in genetic gain is possible by propagating the best hybrid. In this context, hybridization can be between different species (interspecific hybrid), such as the crossing of walleye and sauger to produce "hybrid walleye," or between genetically different strains or lines of the same species (intraspecific hybrid). In either case, there is no way to predict a *priori* which hybrid will yield the greatest genetic gain. Note that this option is also limited by lack of additional genetic gain in future generations, as depicted by the correspondmg horizontal line in Figure 4.

The two remaining types of breeding programs permit additional genetic gain in future generations and rely on the genetic concepts presented above. The simplest breedmg program is to practice selection on the best strain. Finally, a combined approach is to practice selection on separate strains and then cross them through hybridization. The two strains could be from the same species or two different species. Compared to simple hybridization, combined selection and hybridization will generate offspring exhibiting less variability in their performance traits; for instance, it could decrease size variability. This could measurably reduce production costs and increase yields.

## Small producers and breeding programs

It will be difficult for most small-scale producers to conduct a breeding program as a peripheral activity of a farm primarily focused on grow-out of fish to marketable size. There are three feasible strategies for involvement of small producers in genetic improvement of walleye for indoor aquaculture. The order in which these are presented below does not imply any ranlung.

First, one or a few farmers could decide to specialize in broodstock improvement. This would be the primary goal of their aquaculture operations and they would sell genetically improved eggs, fry, or fingerlings to farmers focused on grow-out. Second, a number of farmers could form a breeding cooperative. Members would pool their resources to develop 2-3 selectively bred strains. Offspring from the improved strains would be shared among cooperators. Such a cooperative could even coordinate multiple farm trials to identify best strains or to compare genetically modified strains propagated by selection, hybridization, or combined

selection and hybridization. The third option is to have a public research institution carry out the bulk of the time-consuming and expensive steps in a breeding program, followed by participation of different producers in on-farm trials and eventual public release of one or more improved strains. Obviously, variations of and combinations among these three options are possible. Each option has short-term and long-term benefits and disadvantages.

A strategy relevant to any of the three options laid out above for the institutional structure of a breeding program is to integrate pedigreed, tagged families into a larger grow-out stock of fish (Figure *6*). Selection is practiced only on the tagged fish in the pedigreed families and disruption of the grow-out operation is minimized. This approach has shown promise in coho salmon selection programs (Hershberger 1988). Tagged families and control fish are raised with production fish in a number of the production units. As selection is imposed, culled fish or families are placed in grow-out units (depicted by the arrows pointing away from the breeding circle in Figure 6). Currently, aquaculturists rely on artificial tags, inserted internally or affixed externally on individual fish. Recent research results, however, on characterization of naturally existing, genetic marks will eventually make it economically feasible for farmers to tag and track pedigreed families integrated into grow-out operations. One simple example of this idea is that fish have DNA fingerprints similar to human DNA fingerprints used in forensic investigations.

## Conclusion

Ultimately, it is the collective responsibility of diverse parties concerned with walleye aquaculture to decide the role of breedmg programs in food fish walleye aquaculture. In this chapter, we have tried to introduce some essential concepts and illustrate them with examples of genetic data on walleye and other fish species. Coming full circle to the beginning of this essay, we close by reminding prospective breeders that they also bear the responsibility to foster environmentally safe breeding programs.

## Acknowledgments
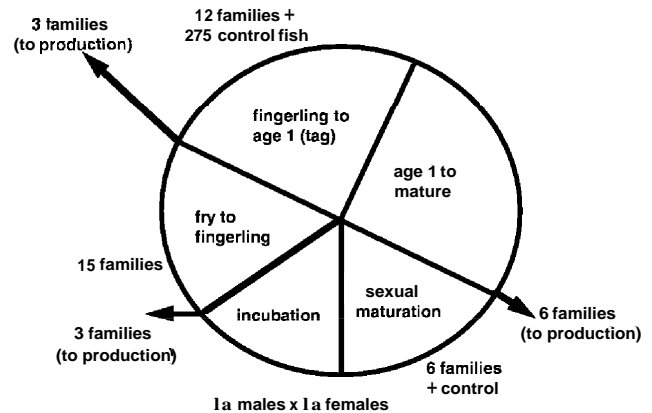
**Figure 6. Schematic of a selective breeding program integrated into a grow-out operation (adapted from Hershberger 1990). The cycle depicts combined selection on pedigreed walleye families, in which the best performing individuals from the best performing families are crossed each generation. These families bear individual marks, such as passive integrated transponder (PIT) tags. Fish culled during application of selection become part of the grow-out stock. Each revolution around the circle is equivalent to one generation. Number of males and females crossed to propagate the families involved in the breeding program and size of control line keep the inbreeding rate less than 2% per generation.**

## Footnotes

[1] Additive genetic variance is one component of the total genetic variance affecting the trait. It appears in the numerator of this ratio, because it is the portion of genetic variance that responds to selection from one generation to the next in a predictable manner.

[2] This is due to a fairly high standard error for our estimate for $h^2$.

[3] The following forms of genetic manipulation are beyond the scope of this chapter: ploidy manipulations (e.g., production of triploid walleye); gene transfer; and genetic modifications for sex control (e.g., production of monosex fish). One or more of these types of manipulations could be integrated with selective breeding, hybridization, or both.

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