Selective breeding programmes for medium-sized fish farms

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PREPARATION OF THIS DOCUMENT

This document has been prepared within the framework of the Regular Programme activities of the Inland Water Resources and Aquaculture Service of the Fishery Resources and Environment Division. The primary objective of this document is to outline selective breeding programmes that can be used to improve cultured populations of food fish on medium-sized farms. The document is directed to extension personnel and aquaculturists.

The original manuscript was prepared by Douglas Tave of Urania Unlimited, Oregon, USA. It was reviewed by Charles (Bo) Collins, Katherine Bruner Tave, and Devin M. Bartley. The figures were prepared by Sally Rader under the supervision of Douglas Tave.

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ABSTRACT

This manual, written for extension workers and aquaculturists, deals with methods for selective breeding programmes to improve cultured populations of food fish on medium-sized fish farms. The manual contains chapters on general principles, basic genetics, selection for qualitative phenotypes, selection for quantitative phenotypes, and how to conduct simple selective breeding programmes; a glossary and selected reading list are also included. The principles of quantitative and qualitative genetics are explained through examples of tila pia and carp breeding studies. The resources that are necessary for aquaculturists to possess in order to successfully implement selective breeding programmes are discussed and serve to help evaluate the prospects of success before starting a genetic improvement programme.

Distribution:

FAO Fisheries Department
Inland Waters - General
FAO Regional Fisheries Officers
Author

PREFACE

The purpose of this manual is to outline selective breeding programmes that can be used to improve cultured populations of food fish on medium-sized farms. This manual is not a complete genetics text book; it is designed to explain one topic--selective breeding as it relates to aquaculture on medium-sized fish farms.

There is no good definition of what a medium-sized fish farm is, but it was assumed to be a farm with about 2 ha of ponds. The same principles and ideas that are discussed in this manual also apply to selective breeding programmes that could be conducted on larger fish farms, although some breeding programmes that could be conducted on larger farms are not included in this manual. Some of the selective breeding programmes discussed in the manual could be conducted on smaller fish farms.

There is no magic farm size that allows or prohibits a selective breeding programme. The number of ponds on the farm is more important than the overall size of the fish farm. The selective breeding programmes outlined in this manual can be conducted in one to 150 ponds, depending on the type of breeding programme that is used and the culture system that is typically used to produce the fish. Additional ponds would be needed to hold and/or spawn brood fish. Holding tanks and other facilities might also be needed.

Most of the selective breeding programmes outlined in this manual are simple and inexpensive, although there is no such thing as a free breeding programme. Several of the breeding programmes that are presented can be conducted in only one to five ponds. Breeding programmes that require a large number of ponds are included to illustrate a particular type of selection and to contrast them with the simpler ones.

Even though selective breeding is a tried-and-true method of increasing yields, most farmers should not be encouraged to conduct one. The most important criteria that determine whether a farmer should conduct a selective breeding programme are his ability to conduct a breeding programme and his desire to conduct one. The farmer who conducts a selective breeding programme:

Must be a good manager.
- Must be able to record data and to manage information. If he cannot do this, the extension agent must be willing to do it for him.
- Must be willing to allocate ponds and other facilities for the breeding programme. Must be willing and able to allocate money to conduct the breeding programme. Must be willing to allocate the labour needed to conduct the breeding programme.
- Must accept the fact that the benefits are long-term benefits. Often, genetic gain is not transferred to the production ponds which are used to grow fish for market for one generation (the replacement of brood fish with their progeny). Annual gains made as a result of selective breeding are usually small, but they are cumulative, and over time they can significantly improve growth rate and yield.

The manual is divided into five chapters, a glossary, and a suggested reading list. Chapter 1 is a brief introduction that explains what the manual is about and discusses selection in relation to other types of breeding programmes. Chapter 2 is a brief discussion about

some aspects of basic genetics and presents background information that helps explain how selection works. Chapter 3 discusses selective breeding programmes that are needed to create true-breeding populations when working with qualitative phenotypes (phenotypes such as colour). Chapter 4 discusses selective breeding programmes that can be used to improve quantitative phenotypes (phenotypes such as length). Chapter 5 outlines simple selective breeding programmes that can be conducted to improve growth rate and other quantitative phenotypes, and provides examples of the types of data that must be recorded and data tables that can be used to record these data when conducting selective breeding programmes.

This manual was written to help educate extension specialists or university-trained aquaculturists understand the basic ideas and the basic work plans that are needed to conduct selective breeding programmes to improve growth rate and other phenotypes. As such, the manual contains information that does not need to be discussed in workshops that might be held for interested farmers. The information in Chapter 2 was presented only to provide some background information that helps explain the breeding programmes that are outlined in Chapters 3, 4, and 5. Those who have a good background in genetics can skip this chapter. When conducting a workshop for farmers, extension personnel should omit most of the material in Chapter 2. Nothing will destroy a farmer's interest in selective breeding faster than a long, boring technical lecture on genetics. Few farmers really need to know the basic genetics that was discussed in Chapter 2.

Some of the material discussed in Chapters 3, 4, and 5 should also be omitted when conducting a workshop for farmers. For example, some of the selective breeding programmes that were mentioned in Chapter 4 were discussed only for the sake of completeness, and especially because I wanted to discourage their use.

Chapter 3, which outlines selective breeding programmes that can be used to fix desirable qualitative phenotypes, such as body colour or scale pattern, was included in the manual because I wanted to make the mechanics of selective breeding more understandable. The selective breeding programmes outlined in Chapter 3 are simple and easy to understand. A reader who studies the breeding programmes that are outlined in Chapter 3 and who understands the processes that allow a farmer to fix qualitative phenotypes will find the information in Chapters 4 and 5 easier to understand.

Chapters 4 and 5 are the heart and soul of the manual. Chapter 4 outlines the basic types of selective breeding programmes that can be used to improve a quantitative phenotype, such as growth rate: individual selection, between-family selection, and within-family selection. It explains the type of information that must be gathered before a farmer conducts a breeding programme; it outlines how the different breeding programmes are conducted; it discusses how a farmer measures fish and decides which fish should be saved; and it shows how a farmer can evaluate the results of the breeding programme.

Chapter 5 outlines of how simple selective breeding programmes can be conducted to improve growth rate by individual selection, within-family selection, and between-family selection. Included are examples of selective breeding programmes that can be conducted using only one or two ponds. Techniques that can be used to transfer gain made from selection to the production ponds are also discussed.

The manual was written for extension personnel and for aquaculturists; it is not a genetics text book. It is written in a simple straightforward manner. I tried to use as little jargon

as possible, but some had to be used. Scientific terms are defined in the text when they are first used, and there is an extensive glossary that defines the terms used in the book.

Finally, citations were not included in the text or tables. The omission of citations is not intended to slight the contributions made by others. I simply wanted to produce an uncluttered readable manual. A list of suggested references is provided at the end of the manual for those who want to pursue the subject of selective breeding in fish in greater detail.

I thank Charles (Bo) Collins and Katherine Bruner Tave for critical review of the manuscript. I also thank Sally Rader for turning my preliminary figures into works of art.

This book is for Katherine and Kai, because they never stopped believing in me.

Douglas Tave
December, 1994

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Introduction

There are two ways a fish farmer can increase fish production: The first is to increase the the size of the fish farm. The second is to increase yield, which is the weight of fish produced in each pond. It is often impossible to increase the size of the farm, because either the land is unavailable, the land is prohibitively expensive, or the land that can be used or water supply associated with that land is so poor that the costs of production would exceed the value of the crop. Even when a farmer can increase his land holdings, it often makes sense to improve production efficiency and produce greater yields (kg/ha). There are two ways a fish farmer can increase yields: The first is by environmental manipulations, such as the increased use of lime, fertilizers, feeds, and/or improved water quality management. The second is by growing genetically improved fish. If both approaches are used, yields can increase dramatically.

There are a number of breeding programmes that can be used to improve a population of fish genetically. Selective breeding and crossbreeding (also called "hybridization") are the two traditional approaches that have been used for thousands of years, and they have been used to improve all major crops and livestock grown by farmers. Inbreeding is often combined with hybridization to improve the results of the crossbreeding programme. Three additional approaches have been developed recently: chromosomal manipulation, production of sex-reversed brood stock, and genetic engineering.

Although farmers have conducted breeding programmes on livestock for thousands of years, fish farmers are only beginning to use selection, hybridization, or other breeding programmes to improve aquacultured species of food fish. Although some progress has already been made, many fish farmers are culturing fish that are essentially wild and unimproved.

Selective breeding is a breeding programme that tries to improve the breeding value of the population by selecting and mating only the best fish (largest, heaviest, those with the desired colour, etc.) in the hope that the select brood fish will be able to transmit their superiority to their offspring. If this occurs, the next generation will be more valuable because the fish will grow faster, which will increase yields; the fish will grow more efficiently, which will lower feed costs; or all fish will have a more desired body colour, which will increase their market value.

Crossbreeding is a breeding programme that tries to find mating combinations between different populations of fish which produce superior offspring for grow-out, offspring that are said to exhibit hybrid vigour. Although crossbreeding is a tried-and-true method of increasing yields, the results of crossbreeding programmes are impossible to predict (unless the mating has been made previously), so the production of superior offspring is a hit-or-miss proposition. Many combinations often have to be evaluated before one is discovered that produces offspring with hybrid vigour. Crossbreeding programmes usually involve different strains within a species (intraspecific hybridization), but different species can also be hybridized (interspecific hybridization). To date, much of the breeding work in aquaculture has been devoted to hybridization among the different species of tilapia in an attempt to produce all-male hybrids for grow-out.

In general, crossbreeding is used to produce superior fish for grow-out (production fish), while selection is used to create superior brood fish. The hybrids that are created in a crossbreeding programme are usually grown and sold as food. A farmer rarely retains and spawns hybrids to produce a new generation of production fish. On the other hand, select brood fish that are created in a selective breeding programme are created for one purpose--to produce the next generation of fish for grow-out--and their offspring can, in turn, be retained and selected to continue the process.

In recent years, biotechnological research has led to the development of three additional breeding programmes that can be used to increase yields. One of the most common breeding programmes in aquaculture is the production of sex-reversed brood stock to produce monosex populations for grow-out. This is done either because one sex is superior or more desirable or to prevent reproduction during grow-out. For example: female sturgeon are more valuable than males because they produce caviar; female salmon are the more valuable sex, because sexually precocious males die before they can be harvested; male tilapia are more desired than females because they grow twice as fast. The major goal in tilapia farming is to prevent reproduction during grow-out; this can be best accomplished by producing a monosex male population.

The production of sex-reversed brood stock is usually accomplished by feeding either estrogens or androgens (sex hormones) to sexually undifferentiated fry to sex-reverse them. Sex-reversed fish are individuals that are one sex phenotypically but the other genetically. If sex reversal is done properly, sex-reversed fish are capable of producing monosex populations for grow-out. The type of hormone used--estrogens to produce sex-reversed females or androgens to produce sex-reversed males--depends on the sex-determining system of the species and whether you want to produce an all male or an all-female population.

Another breeding programme that is becoming more commonplace is chromosomal manipulation. This is usually done to produce sterile fish. The most common form of chromosomal manipulation is to use temperature or pressure to shock newly fertilized eggs (chemicals can be used, but they are less effective). If this is done properly, the shock prevents the second polar body from leaving the egg, so the newly fertilized egg contains a haploid sperm nucleus, a haploid egg nucleus, and a haploid second polar body nucleus. These three haploid nuclei fuse and produce a triploid zygote which, in turn, produces a triploid fish. Triploids are sterile. This type of breeding programme is used to enable farmers to grow exotic species whose culture might otherwise be illegal or to induce sterility in species that become sexually mature before they reach market size. For example, grass carp culture in most of the United States is legal only if a farmer raises triploids. This technique can also be used to improve the results of interspecific hybridization.

Chromosomal manipulation can be used to produce animals that have only a mother (gynogens) or only a father (androgens). This is done by creating haploid zygotes and by then shocking the zygotes to produce diploid zygotes. Haploid zygotes are produced in one of two ways: a normal egg is fertilized by sperm whose DNA has been destroyed by UV irradiation (gynogenesis); a normal sperm is used to fertilize an egg whose DNA has been destroyed by UV irradiation (androgenesis). Gynogenesis and androgenesis are techniques that can be used to produce highly inbred lines for breeding purposes. It can also be used to produce supermales; such males are capable of producing all-male populations.

In recent years, a new, high-tech breeding programme has been developed: genetic engineering. This is a breeding programme that transfers a single gene or a set of genes from one individual into another. This transfer can be within a species, between two species, or even across kingdoms. Although genetic engineering has generated lots of publicity, to date it has not produced genetically superior fish for farmers. Furthermore, this type of breeding programme is very expensive, highly regulated, and requires highly trained scientists. This type of breeding programme should be conducted only by scientists working at universities, at governmental research stations, or at agribusinesses that are capable of supporting expensive research projects with secure containment facilities.

Although all breeding approaches that can be used to improve yields are important and although they can be used either singly or in combination to achieve specific goals, this manual will describe only those procedures that can be used to improve fish by selective breeding.

The decision to conduct a selective breeding programme is a decision that must be made for each farmer or each fry/fingerling production center on a case-by-case basis. The decision to incorporate selective breeding into a farmer's work plan should not be a general decision made at a regional level. If it is, most of the selective breeding programmes will be failures, because selective breeding programmes require dedication, a certain level of sophistication, record keeping, and the investment of extra labour. Additionally, selective breeding programmes are not free; they also require the investment of money. Finally, these programmes usually do not produce immediate improvements. Improvements are usually not seen for at least one growing season, so a farmer must be able to incorporate long-term planning into his farm management programme, and he must be patient. As a result, within a region, only a small percentage of farmers or fingerling production centers should or will ever conduct selective breeding programmes.

A final requirement that must be met before a farmer can conduct a selective breeding programme is the existence of proper facilities. This manual outlines selective breeding programmes that can be used to improve growth rate and other phenotypes on a medium-sized farm or fingerling production center, which was arbitrarily defined as a farm with about 2 ha of ponds. The breeding programmes outlined in this manual can be conducted in 1-150 ponds, depending on the type selection that will be used and the culture system that is typically used to grow the fish. Additional ponds will be needed to hold brood fish and to spawn them; other types of facilities, such as holding tanks, will also be needed.

Finally, common sense must prevail when choosing the most appropriate breeding programme. Even if a farmer has the ability and the desire to conduct a selective breeding programme, the biology of the species and the way it is grown should be carefully considered before the decision is made to conduct a selective breeding programme to improve growth rate. Even though most farmers would like to have faster-growing fish, in some cases greater yields can be achieved by improving other phenotypes via another type of breeding programme. For example, the biggest problem in tilapia culture is the fact that tilapia become sexually mature before they reach market size and, as a result, reproduce in the grow-out ponds. This uncontrolled reproduction means that a significant percentage of yield is unmarketable. Tilapia farmers may benefit from breeding programmes that can produce monosex male populations far more than from selective breeding programmes that might improve growth rate.

CHAPTER 2

Genetics

The ultimate goal of every selective breeding programme is to improve the breeding value of the population. The breeding value is determined by the fish's genes. A farmer hopes that when he improves the breeding value of his population he will also improve its monetary value, which is determined by the fish's phenotypes. To accomplish this goal, a breeder selects (saves) fish that possess certain phenotypes and culls (removes) those that do not, and hopes that his breeding programme will create a genetically improved population (breeding is the applied science of genetics; thus, a farmer who conducts a selective breeding programme is a breeder). If it does, the fish in the next generation will be more valuable because their genes will enable them to grow faster or to exhibit a more desirable colour.

Although the goal of a selective breeding programme is to manipulate a population's genes and thus produce better fish, it is impossible to examine and manipulate the genes directly. Instead, a fish's genes are examined indirectly by examining its phenotypes (also called "traits"), which are the physical expressions of the genes. Because the goal of a selective breeding programme is to manipulate a fish's genes, it is important to understand how the genes are transmitted from a parent to its offspring and how the genes produce the phenotypes. Understanding these processes helps explain how selection works. This is important, because if a farmer understands why he is doing something, he is more likely to do it correctly, and this ensures success. Additionally, an understanding of how the genes produce various phenotypes enables a breeder to choose the breeding programme that will allow him to achieve his goal quickly and efficiently.

This chapter is not an all-encompassing review of basic genetics. Only a few topics are covered: The first section discusses meiosis, which is the process by which a parent's genes are parcelled into its gametes (eggs and sperm). The second section describes the difference between phenotype and genotype. The remaining sections explain how phenotypes are inherited.

The information contained in this chapter is important because many of the terms introduced in this chapter will be used in Chapters 3 and 4 to explain how selective breeding programmes should be conducted and how they work. It is not necessary to become a geneticist in order to conduct a successful selective breeding programme, but a basic understanding of how phenotypes are inherited will make the rest of the manual easier to understand and will also enable a farmer to be a better breeder.

The material in this chapter is intended simply as background information for those who seek a better understanding of how selection alters phenotypes and improves a population. The material in this chapter, especially that dealing with quantitative phenotypes, is intended for extension agents and for highly educated aquaculturists. It is not intended for the vast majority of farmers or for those who are interested only in the nuts and bolts of how to conduct a selective breeding programme and who do not care how it works. It is hoped that extension agents will read this material, because it will provide a better

grounding in fish breeding, and an understanding of how selection works genetically may make them more comfortable with the design and implementation of a selective breeding programme.

Those who are not interested in this material or those who already understand basic genetics can skip this chapter and go directly to Chapters 3 or 4 which describe selective breeding programmes.

Meiosis

Genes are located on structures called "chromosomes," which are located in the nucleus of every cell. Although there are some exceptions, for the most part, chromosomes occur in pairs, which means that a gene is a paired entity. Throughout this manual, we will assume that chromosomes in cultured fishes occur in pairs. One chromosome of each pair comes from a fish's mother, while the other comes from its father. The number of chromosomes varies among species, but it is constant within a species.

Although every cell in a fish contains the entire genome (a fish's genetic make-up--every gene on every chromosome), the genes that exist in the primary gametocytes are those that are ultimately of greatest interest to a breeder. All genes in the various cells of a fish are, of course, important because they produce the various phenotypes that breeders work with and ultimately select. But those in the primary gametocytes are of greater importance because the primary gametocytes are the cells which develop into sperm and eggs--the gametes which carry the genes and which produce the next generation of fish.

Primary gametocytes are the cells that develop into eggs and sperm by a process called "meiosis." Meiosis is one of the most important of all biological processes, because it greatly increases genetic variability through crossing over and through independent assortment. In addition, mistakes that occur during the replication of chromosomes in meiosis are heritable, and this is how new alleles and genes are created. The end result of meiosis is the creation of haploid sperm and eggs. Were it not for meiosis, life would not have evolved past single-celled organisms.

During the initial part of meiosis, the chromosomes replicate, and the homologues of each pair come together (the homologs are the two chromosomes that form a pair; one homolog comes from the father, and one comes from the mother). The replication of the homologues is usually uneventful, in that they replicate themselves perfectly. Occasionally, however, a mistake is made during replication, and a gene is not replicated perfectly. Such mistakes are called "mutations." The mutation rate for individual genes is rare and ranges from 1 in 10,000 replications to 1 in 100,000 replications. Although rare, the fact that males are capable of producing several hundred million to over a billion sperm and that females can produce tens of thousands to hundreds of thousands of eggs all but guarantees that each fish will produce dozens of gametes which contain one or more mutations. The production of mutations is a very important biological process, because it increases genetic variability by creating new alleles and new genes which can, in turn, produce new phenotypes.

Because each homolog replicated before they paired, the bundles are composed of four chromosomes and are called "tetrads." The chromosomes in each tetrad are extremely elongated and drawn out rather than compact, and they twist around each other. As they

twist, the chromosomes break, and pieces from different homologues rejoin. The exchange of genes from one homolog to another is called "crossing over," and it is one of the most important genetic events, because this greatly increases genetic variability by creating new and different gene combinations every generation. These different gene combinations will, in turn, increase phenotypic variability, which helps breeders produce better fish.

The second important process that occurs during meiosis is reduction division. During this process, the chromosome number is reduced from the diploid (paired state) state to the haploid (unpaired) state. When chromosomes are paired, a cell or individual is said to be a diploid (2N). When a cell or individual contains only one chromosome from each pair, it is said to be a haploid (N).

During reduction division, the replicated homologues of each chromosome pair separate, and the primary gametocyte then divides and forms two cells. In males, these cells are the secondary spermatocytes; in females, they are the secondary oocyte and the first polar body. The separation of the replicated homologues of each chromosome pair and the direction in which the replicated homologues go is independent of that which occurs for all other chromosomes. Although each tetrad divides itself along parental lines (the replicated homolog that came from a fish's father separates from the replicated homolog that came from its mother), the division of the homologues of each chromosome pair is random and is independent of that which occurs in all other tetrads. The random division of the maternal and paternal chromosomes is called "independent assortment," and it is extremely important because it creates new chromosomal and new gene combinations, which greatly increase genetic variability; this ultimately increases phenotypic variability. The secondary spermatocytes and the secondary oocyte are haploid, since each contains only one homolog from each pair.

The final step in meiosis is the equational division, during which the replicated homologues of each chromosome separate and go into one of two sperm cells or into the egg or second polar body. As was the case during reduction division, the direction that a replicated homolog from each chromosome goes is random and independent of that which occurs in all other chromosomes. This final shuffling of the chromosomes and of the genes also increases genetic variability.

The end result of meiosis is the production of haploid sperm and eggs. Each gamete contains a single chromosome from each pair. Even though some fish can produce millions of gametes, few if any are identical because of mutations, crossing over, and the independent assortment of chromosomes that occurs during reduction division.

The reduction of the chromosome number from the diploid state in the primary oocytes and primary spermatocytes to the haploid state in the eggs and sperm is critical. If this did not occur, the number of chromosomes would double each generation. Because gametes are haploid, the normal diploid number for a species is restored when a sperm fertilizes an egg.

Phenotype and genotype

A gene or set of genes contains the blueprints or chemical instructions for the production of a protein. This protein either forms or helps produce various phenotypes, such as body

colour, sex, number of rays in the dorsal fin, length of a fin, body length, and weight. When a geneticist talks about this process, he says that a fish's genotype controls or produces its phenotype.

The genotype is the genetic make-up of the fish. It is the gene or genes that controls a particular phenotype. Because chromosomes occur in pairs, genes also occur as pairs (there are some exceptions, but they will not be discussed in this manual), so the genotype is a paired entity.

A gene can occur in more than one form. Alternate forms of a gene are called "alleles." In a population, a gene may exist in only one form, which means that there is only one allele at a given locus (locus = gene), or there may be up to a dozen alleles at a locus.

Because chromosomes occur in pairs, an individual can possess either one or two alleles at a given locus. Even if there are ten alleles for a specific gene in a population, an individual can possess no more than two (in this manual, we will assume that all fish are diploids). If the pair of alleles at a given locus is identical, the fish is said to be "homozygous" at that locus. If the pair is not identical, the fish is said to be "heterozygous" at that locus. The terms homozygous and heterozygous (the genotype) refer to specific genes, not the fish's entire genome. A fish's genome is composed of tens of thousands of genes, which is a mixture of homozygous and heterozygous loci.

The reason why it is important to make a distinction between individuals that are homozygous or heterozygous, is that different forms of a gene (alleles) produce different forms of that gene's protein. This means that the various alleles at a locus are responsible for the production of various body colours or of different rates of growth. And it is these differences that interest geneticists, because they can be exploited by selection to produce faster-growing or more attractive fish.

The phenotype is the physical expression of what the gene or set of genes produce, and this is what we describe (for example, colour or sex) or measure (for example, length or weight). Breeders divide phenotypes into two major categories: qualitative phenotypes and quantitative phenotypes.

Genetics of qualitative phenotypes

Qualitative phenotypes are the phenotypes that are described, such as colour, sex, or scale pattern. Qualitative phenotypes are those that are the easiest to observe simply because an individual falls either into one discrete, descriptive, non-overlapping category or it falls into another. For example, if there are blue and yellow fish in a population, individual fish fall either into the blue or into the yellow categories.

The genetics of qualitative phenotypes is simple and is often called "Mendelian genetics" in honour of Gregor Mendel who discovered it. These phenotypes are usually controlled by one or two genes. The alternate forms of a phenotype (for example, blue vs yellow) are produced by the alternate forms of a gene (alleles). Often, the normal phenotype is called the "common" or "wild-type" phenotype, while the others are referred to as "mutant" phenotypes.

Qualitative phenotypes are often called "cosmetic" because they primarily affect an individual's appearance. But this does not mean that they are unimportant. These phenotypes can improve health or make the product more acceptable to consumers. For example: dwarf is a desired phenotype in many varieties of wheat because short stalks are stronger than the normal tall stalks, and they do not bend or break while the plant is growing; polled (hornless) is a desired phenotype in many varieties of cattle for safety and health reasons; white feathers is a desired phenotype in poultry because dark feathers leave dark, unattractive spots on the skin when they are removed. Qualitative phenotypes can also greatly increase the value of farmed fish. For example, in the United States, body colour of fathead minnow has a major effect on its market price: normally pigmented (dark) ones are worth $6.05/kg, while rosy red ones are worth $8.25/kg. Fish farmers need only look at the ornamental fish farming industry to see the importance of qualitative phenotypes. The value of an ornamental fish is determined by its colour, colour pattern, fin shape, eye shape, etc.

Qualitative phenotypes can be divided into two major categories: autosomal and sex-linked. Autosomal phenotypes are those that are controlled by genes located on an autosome (a chromosome other than a sex chromosome). Sex-linked phenotypes are controlled by genes located on the pair of chromosomes that determines sex. (There are some exceptions; some fish have more than one pair of sex chromosomes, while other species have an odd number--either one or three sex chromosomes. All important aquacultured food fish have a single pair of sex chromosomes.)

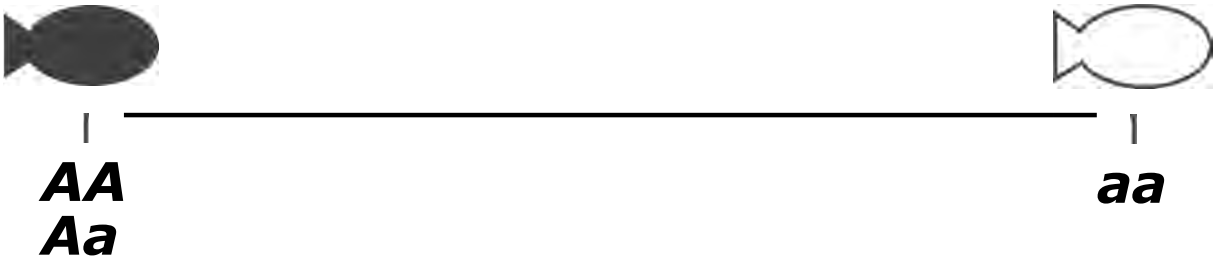
Autosomal genes are inherited and expressed identically in males and females (unless a sex hormone is needed for phenotypic expression). Sex-linked genes are inherited and expressed differently in males and females. To date, all qualitative phenotypes that have been deciphered in food fish are autosomal. Sex-linked genes are known only in ornamental fish, and most information about this type of inheritance comes from the guppy and platyfish. Because all qualitative phenotypes that have been discovered in cultured food fish are autosomal, this section will describe only the genetics of autosomal phenotypes. Sex-linked phenotypes will not be discussed.

For the sake of simplicity, all examples that will be used in this section are genes that have two alleles. In reality, in a population, a gene may have a dozen alleles. Tail spot pattern in the platyfish is an example of a gene that has nine alleles. When there are more than two alleles, the number of qualitative phenotypes that a gene can produce can increase tremendously, depending on the mode of gene action. It is a bit more complicated to work with such phenotypes, and although it only requires an extension of what is discussed in this section, it does require far more effort and record keeping. Fortunately, such genes are rare. The few that are known are in ornamental fish.

Qualitative phenotypes produced by single autosomal genes

Most qualitative phenotypes that have been deciphered genetically in food fish are controlled by single autosomal genes with two alleles per locus. In general, genes express themselves either in an additive or in a non-additive manner. In additive gene action, each allele contributes equally to the production of the phenotypes in a stepwise unidirectional manner, and the heterozygous phenotype is intermediate between the two homozygous phenotypes. In non-additive gene action, one allele (the dominant allele) is expressed more strongly than the other (the recessive allele), and it has a greater influence on the production of the phenotypes (Figure 1).

COMPLETE DOMINANT GENE ACTION



INCOMPLETE DOMINANT GENE ACTION

ADDITIVE GENE ACTION

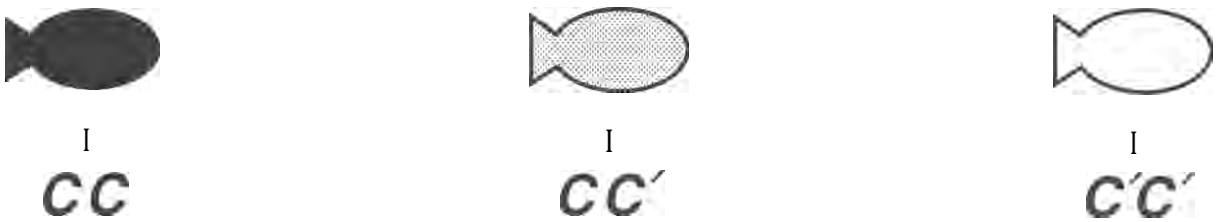


Figure 1. Schematic diagram of qualitative phenotypes that are controlled by a single autosomal gene with either complete dominant gene action, incomplete dominant gene action, or additive gene action. Genotypes are given below the phenotypes. Gene A produces black and white colours by complete dominance, so there only two phenotypes. Black is the dominant phenotype, and it is produced by both the homozygous dominant (AA) and heterozygous (Aa) genotypes. White is the recessive phenotype, and it is produced by the homozygous recessive (aa) genotype. Gene B produces black and white colours by incomplete dominance. Because the mode of gene action is incomplete dominance, the heterozygous (Bb) genotype produces a unique phenotype (light-black), one that resembles but that is slightly different than the dominant phenotype (black), which is produced by the homozygous dominant (BB) genotype; white is the recessive phenotype, and it is produced by the recessive genotype (bb). Gene C produces black and white colours by additive gene action. Because neither allele is dominant, the heterozygous (CC') genotype produces a unique phenotype (gray) that is intermediate between the phenotypes (black and white) produced by the two homozygous genotypes (CC produces black and and C'C' produces white). When the mode of gene action is additive, there is no dominant or recessive allele or phenotype.

Complete dominant gene action: Complete dominant gene action occurs when the dominant allele is so strong that it produces its phenotype, regardless of the genotype. Only a single dominant allele is needed to produce the dominant phenotype. This means the homozygous dominant and heterozygous genotypes both produce the dominant phenotype; thus, the phenotypes produced by these genotypes are identical. The recessive allele can produce the recessive phenotype only when no dominant allele is present, which means it can produce the recessive phenotype only when a fish is homozygous recessive. Consequently, with this mode of inheritance, there are three genotypes but only two phenotypes (Figure 1):

Phenotype	**Genotype**
Dominant	Homozygous dominant
Dominant	Heterozygous
Recessive	Homozygous recessive

For example, light-coloured (pink) and normal pigmentation phenotypes in Nile tilapia are controlled by the B gene. The dominant B allele produces the dominant normally pigmented phenotype, while the recessive b allele produces the recessive pink phenotype. Because the B gene exhibits complete dominance, normal pigmentation is produced by both the homozygous dominant genotype (BB) and by the heterozygous genotype (Bb), while pink is produced only by the homozygous recessive genotype (bb) (Figure 2). Table 1 lists some qualitative phenotypes in important cultured food fishes that are produced by single autosomal genes with complete dominance.

Table 1. Examples of phenotypes in cultured food fishes that are controlled by single autosomal genes with complete dominant gene action. All phenotypes in this table are body colours except caudal deformity syndrome, which is a tail deformity.

Species	Recessive phenotype	Dominant phenotype
Common carp	blue	normal pigmentation
	gold	normal pigmentation
	grey	normal pigmentation
	normal pigmentation	light yellow band on dorsal fin; yellow on head
Nile tilapia	blond	normal pigmentation
	syrup	normal pigmentation
	light-coloured (pink)	normal pigmentation
	caudal deformity syndrome	normal tail
	normal pigmentation	red
Grass carp	albino	normal pigmentation
Channel catfish	albino	normal pigmentation
Rainbow trout	albino	normal pigmentation
	iridescent metallic blue	normal pigmentation

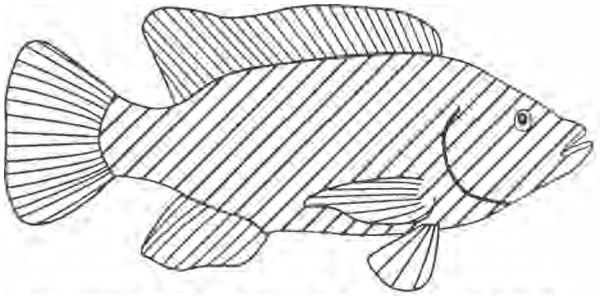
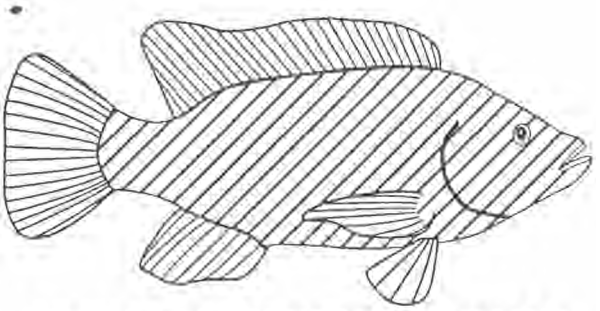
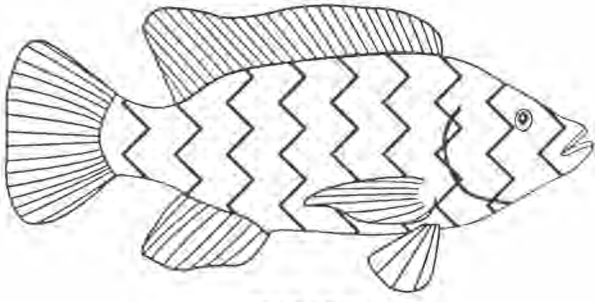
PHENOTYPE	GENOTYPE
 NORMAL PIGMENTATION	***BB***
 NORMAL PIGMENTATION	***Bb***
 PINK	***bb***

Figure 2. Inheritance of normally pigmented and pink body colours in Nile tilapia. These phenotypes are controlled by a single autosomal gene with complete dominant gene action called the B gene: tbe dominant B allele produces normal pigmentation, while the recessive b allele produces pink. Because the B allele is completely dominant over the b allele, the BB and Bb genotypes both produce the dominant normally pigmented phenotype. The recessive pink phenotype is produced only when a fish is homozygous recessive (bb). The pictorial representations of body colour used in this figure will also be used in Figures 3 and 9.

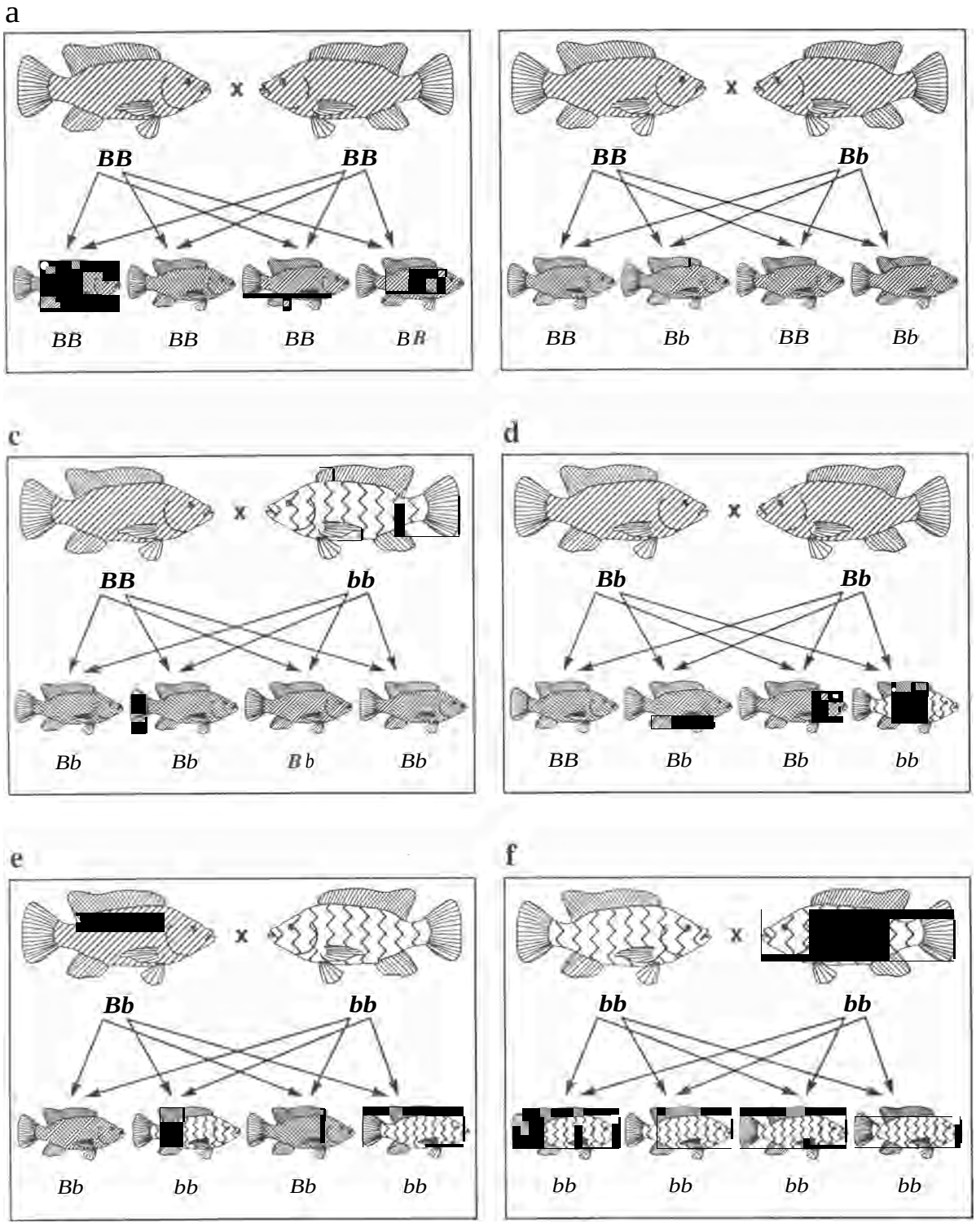


Figure 3. All possible mating combinations between normally pigmented and pink Nile tilapia, and the phenotypes of the offspring produced by each mating. Pictorial representations of the phenotypes are the same as those used in Figure 2. Genotypes are given below the fish. The arrows represent gametes. Mating combinations a and f are examples of true-breeding populations, the goal of a selective breeding programme.

Figure 3 illustrates all possible mating combinations between pink and normally pigmented Nile tilapia and the phenotypes of the offspring produced by each mating. The mating combinations and the phenotypic ratio of the offspring produced by each mating in Figure 3 (for example, 3 normally pigmented:1 pink in mating 3d) are typical for all qualitative phenotypes that are controlled by a single autosomal *gene* with complete dominant gene action (provided no genotype is lethal).

The phenotypic ratios of the offspring that are produced by different mating combinations are used to decipher the genetics that controls the phenotypes. Different modes of gene action produce different phenotypic ratios. In a genetics experiment, mating 3c is one of the first matings made. Offspring from mating 3c are called "F_1 offspring." When mature, these fish are mated (mating 3d) to produce what are called "F_2 offspring." The phenotypic ratio of **F2** offspring is the key ratio that is used to decipher most forms of inheritance.

In Figure 3, matings 3a and 3f are examples of true-breeding populations. The goal of all selective breeding programmes is to produce a true-breeding population. Breeding programmes that can be used to produce true-breeding populations are outlined in Chapter 3.

Incomplete dominant gene action: Incomplete dominant gene action occurs when the dominant allele expresses itself more strongly than the recessive allele, but it is not strong enough to completely suppress the recessive allele in the heterozygous genotype. Because of this, the dominant phenotype can be produced only when a fish has two copies of the dominant allele (homozygous dominant). Since the recessive allele is not completely suppressed by the dominant allele, the heterozygous genotype produces a phenotype that resembles, but is not identical to, the dominant phenotype. As was the case with complete dominance, the recessive phenotype is produced only when a fish is homozygous recessive. Because the heterozygous genotype produces a phenotype that is similar to but is different from the dominant phenotype, when the mode of gene action is incomplete dominance, there are three genotypes and three phenotypes, a unique phenotype for each genotype (Figure 1):

Phenotype	**Genotype**
Dominant	Homozygous dominant
Heterozygous	Heterozygous
Recessive	Homozygous recessive

For example, black (normal pigmentation), bronze, and gold body colours in Mozambique tilapia are controlled by the G gene. The dominant G allele produces melanistic (dark-coloured) fish, but because the G gene exhibits incomplete dominance, the G allele does not completely suppress the expression of the recessive g allele in the heterozygous state. The homozygous dominant and heterozygous genotypes produce unique phenotypes: GG fish are black, while Gg fish are bronze. Gold fish are produced by the homozygous recessive genotype (gg) (Figure 4). Table 2 provides examples of qualitative phenotypes in important cultured food fishes that are produced by single autosomal genes with incomplete dominance.

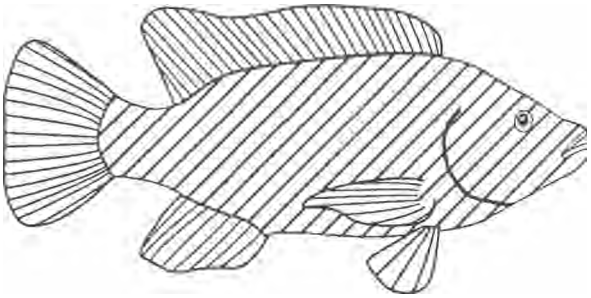
Figure 5 illustrates all possible mating combinations among black, bronze, and gold Mozambique tilapia and the phenotypes of the offspring produced by each mating. The mating combinations and the phenotypic ratio of the offspring produced by each mating in Figure 5 (for example, 1 black:2 bronze:1 gold in mating 5d) are typical for all qualitative phenotypes that are controlled by a single autosomal gene with incomplete dominant gene action (provided no genotype is lethal). In Figure 5, matings 5a and 5f are examples of true-breeding populations, and the phenotypic ratio of the offspring produced by mating 5d is the key that is used to unlock the mode of inheritance.

Additive gene action: With only one exception, all qualitative phenotypes controlled by a single autosomal gene that have been discovered in cultured food fish are controlled either by complete or by incomplete dominance. The lone exception is a gene that controls golden, palomino (the heterozygous phenotype) and normal body colours by additive gene action in rainbow trout. When phenotypes are controlled by additive gene action, there is no dominant or recessive allele. Both alleles contribute equally to the production of the phenotypes, so the heterozygous genotype produces a phenotype that is intermediate between those produced by the two homozygous genotypes. Consequently, when the mode of inheritance is additive gene action, there are three genotypes and three phenotypes, a unique phenotype for each genotype.

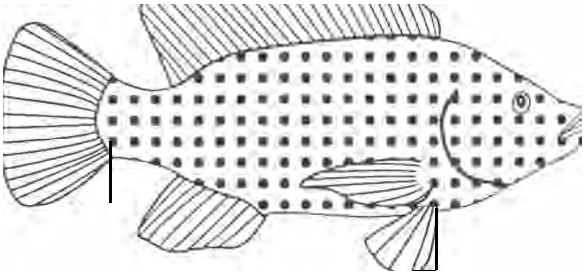
The difference between additive gene action and incomplete dominance is that when the mode of gene action is incomplete dominance, the heterozygous phenotype approximates one of the homozygous phenotypes (the dominant one), while it is intermediate between the two homozygous phenotypes when the mode of gene action is additive (Figure 1). Because qualitative phenotypes are descriptive and are not measured, it is possible to mis-classify incomplete dominance and additive gene action. Even if the mode of gene action is mis-classified, it is of no practical importance for a breeding programme. Because both types of gene action have three genotypes and each produces a unique phenotype, the breeding programmes that are used to control phenotypes produced either by incomplete dominance or by additive gene action are identical.

The mating combinations and phenotypic ratio of the offspring produced by the matings that are shown in Figure 5 can also be used to illustrate what occurs for phenotypes that are controlled by a single autosomal gene with additive gene action. The phenotypic ratios for phenotypes controlled by incomplete dominance and by additive gene action are identical. The only difference is the appearance of the heterozygous phenotype--does it resemble the dominant phenotype (incomplete dominance), or is it intermediate between the two homozygous phenotypes (additive)?

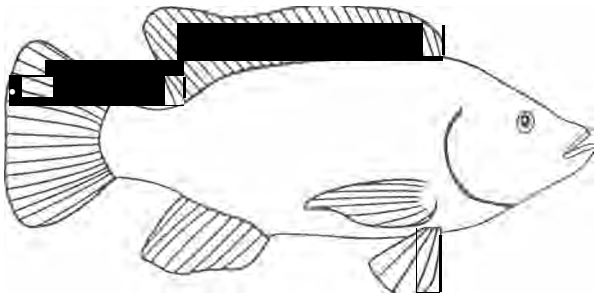
PHENOTYPE GENOTYPE



BLACK *GG*



BRONZE *Gg*



GOLD *gg*

Figure 4. Inheritance of black, bronze, and gold body colours in Mozambique tilapia. These phenotypes are controlled by a single autosomal gene with incomplete dominant gene action called the G gene. Because the dominant G allele is not completely dominant over the recessive g allele, the heterozygous genotype produces a phenotype that is similar to but distinct from that produced by the homozygous dominant genotype. Homozygous dominant fish (GG) are black (the dominant phenotype); heterozygous fish (ag) are bronze (the heterozygous phenotype); homozygous recessive fish (gg) are gold (the recessive phenotype). Pictorial representations of body colour used in this figure will also be used in Figures 5, 10, 11, 17, and 18.

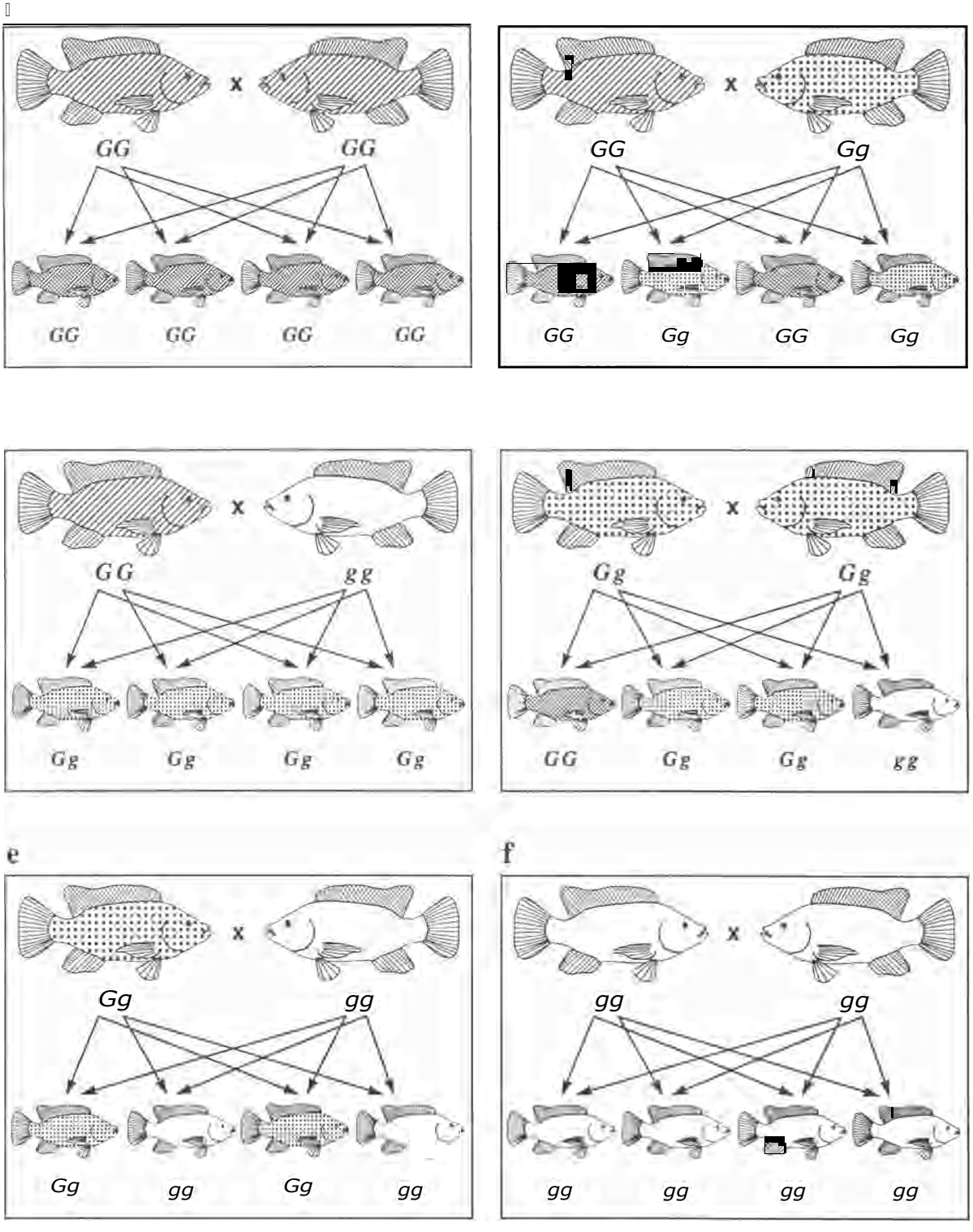


Figure 5. All possible mating combinations among black, bronze, and gold Mozambique tilapia, and the phenotypes of the offspring produced by each mating. Pictorial representations of the phenotypes are the same as those used in Figure 4. Genotypes are given below the fish. The arrows represent gametes. Mating combinations a and f are examples of true-breeding populations, the goal of a selective breeding programme.

Table 2. Examples of phenotypes in cultured food fishes that are controlled by single autosomal genes with incomplete dominant gene action.

Species	Dominant phenotype	Heterozygous phenotype	Recessive phenotype
Common carp	**death**	**light coloured**	**normal pigmentation**
Blue tilapia	**death**	**saddleback (abnormal dorsal fin)**	**normal**
Mozambique tilapia	**black (normal pigmentation)**	**bronze**	**gold**

Qualitative phenotypes controlled by two autosomal genes

Some qualitative phenotypes are controlled by two autosomal genes. When two genes control the production of a set of phenotypes, there is usually some sort of interaction, and one gene influences the expression of the other. This means one gene alters the production of the phenotypes that are produced by the second gene. This gene interaction is called "epistasis."

Most of the examples of epistasis that have been found in fish were discovered in ornamental fish, but several have been found in important cultured food fishes. The two most important are scale pattern in common carp and flesh colour in chinook salmon. Because common carp is one of the most important cultured food fishes in Asia and Europe, it is arguable that scale pattern in common carp is the most important set of qualitative phenotypes that have been found in any aquacultured species. Scale pattern also helps determine colour pattern, and thus the value, of ornamental common carp (koi).

The four scale pattern phenotypes in common carp--scaled (normal scale pattern), mirror, line, and leather--are controlled by two genes (S and N) with what is called "dominant epistasis." The S gene determines the basic scale pattern via complete dominance. The dominant S allele produces the scaled phenotype (SS and Ss genotypes), while the recessive s allele produces the reduced scale phenotype called "mirror" (ss genotype). The N gene modifies the phenotypes produced by the S gene. There are two alleles at the N locus. The dominant N allele modifies the phenotypes as follows: in the homozygous state (NN), the N allele kills the embryo; in the heterozygous (Nn) state, the N allele changes the scaled phenotype into the line phenotype and changes the mirror phenotype into the leather phenotype. The recessive n allele has no effect on the phenotypes produced by the S gene. The five phenotypes (one is death) and the underlying genetics are illustrated in Figure 6.

A set of qualitative phenotypes may be controlled by more than two genes. Body colour in the Siamese fighting fish is an example of a set of phenotypes that is controlled by the epistatic interaction among four genes. Working with these phenotypes is far more complicated because of the number of genes involved. Fortunately, in food fish, no qualitative phenotype controlled by more than two genes has been discovered.

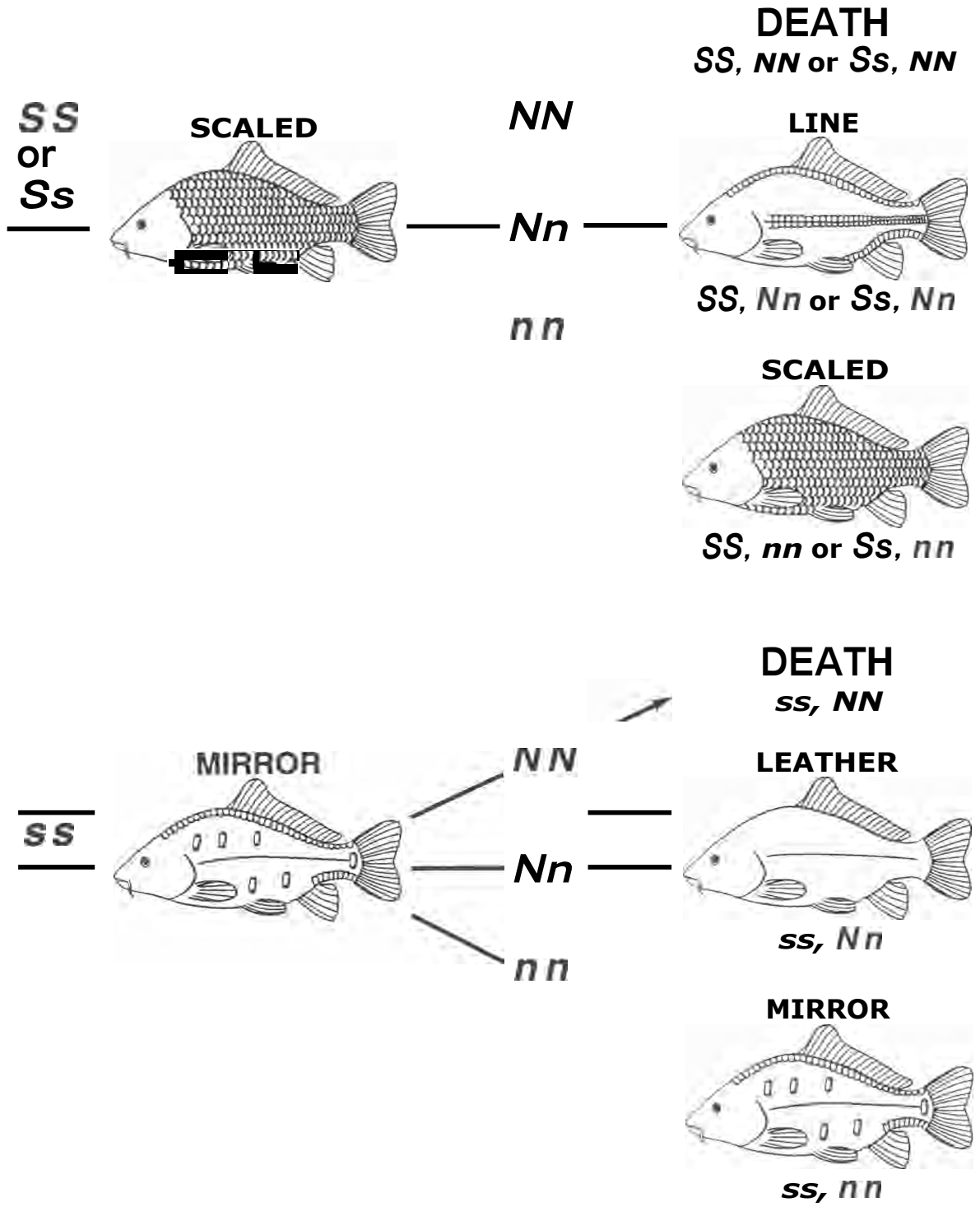


Figure 6. Inheritance of scale pattern in common carp. Scale pattern is determined by the epistatic interaction between the S and N genes. The S gene determines whether the fish has the scaled phenotype (SS and Ss genotypes) or the mirror phenotype (ss genotype). The N gene modifies those phenotypes. The NN genotype kills the fish (SS,NN, Ss,NN, and ss,NN genotypes); the Nn genotype changes the scaled phenotype into the line phenotype (SS,Nn and Ss,Nn genotypes) and changes the mirror phenotype into the leather phenotype (ss,Nn). The nn genotype does not alter the phenotypes produced by the S gene, so scaled fish have the SS,nn or Ss,nn genotypes, while mirror fish have the ss,nn genotype.

Genetics of quantitative phenotypes

Quantitative phenotypes are the phenotypes that are measured, such as length, weight, eggs/kg female, or feed conversion. Quantitative phenotypes differ from qualitative phenotypes in that individuals do not fall into discrete, non-overlapping categories. When a geneticist describes a quantitative phenotype, he creates only a single category, such as weight. Fish are not grouped into discrete categories such as "light" or "heavy." Instead, individuals are arranged along a continuum, and an individual's phenotypic value is determined by the unit of measurement that the farmer uses (millimeters, centimeters, grams, kilograms, etc.).

Because an individual's phenotypic value is determined by measurement (for example, length in millimeters) rather than by descriptive category (for example, colour), the differences between two individuals is a matter of degree (millimeter) rather than of kind (colour). Because the differences among individuals are matters of degree, in a population quantitative phenotypes form what are called continuous distributions, which can be described graphically, as is illustrated in Figure 7.

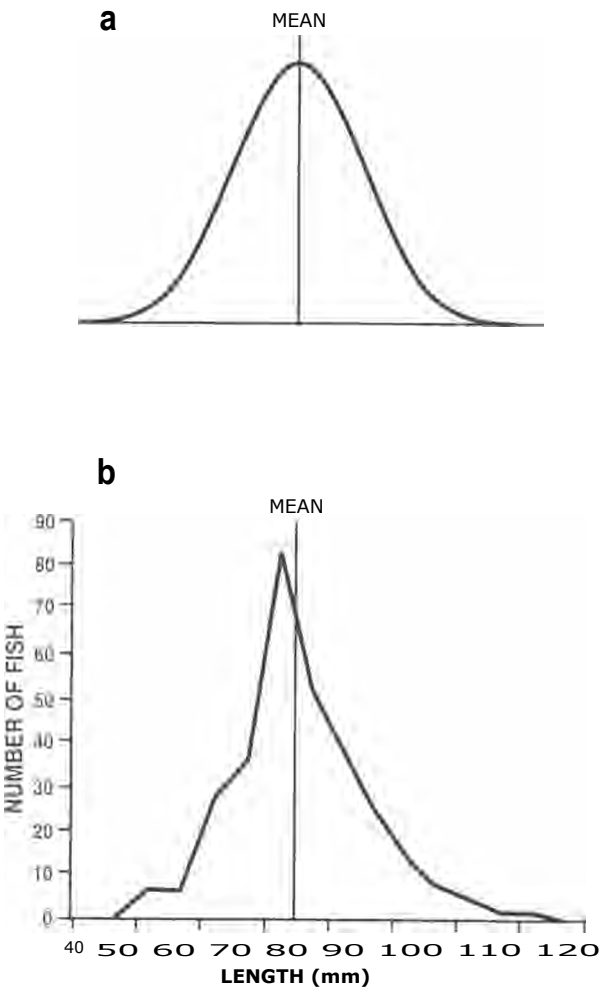


Figure 7. Distribution exhibited by a quantitative phenotype in a population. Graph a illustrates a perfect distribution, which creates what is called a "bell-shaped curve" with the mean bisecting the curve at its peak. Graph b is the distribution of 7-month length in a population of common carp.

The reason why quantitative phenotypes do not segregate individuals into neat and precise categories, as was the case with qualitative phenotypes, is that they are much more complicated genetically. In general, qualitative phenotypes are controlled by one or two genes. They can be controlled by more, but few are. Quantitative phenotypes are controlled by dozens to hundreds of genes. The exact number is usually never known. Additionally, the genes are shuffled like a deck of cards during meiosis due to crossing over and the independent assortment of chromosomes; the combination of these events ensures that each offspring will receive a slightly different genetic message.

Quantitative phenotypes are also strongly influenced by environmental variables, and this helps produce a continuous distribution. These variables range from the obvious ones, such as stocking density, to ones not often considered, such as size and age of the mother. Some of these variables are felt at the family level (for example, date of birth and age of mother), while others are felt at the individual level (for example, access to food).

The simultaneous actions of these genetic and environmental factors results in the creation of single phenotypic categories where the only way an individual can be described is by measuring it. Because quantitative phenotypes are single categories with continuous distributions, you cannot analyze ratios or determine what percent of the population has a specific phenotype, as is the case with qualitative phenotypes. Instead, you calculate populational values and compare individual or family phenotypic values to the population's values. In a population, quantitative phenotypes are described by the mean, which is the arithmetic average, and by the standard deviation, which is the square root of the variance. The mean describes the central tendency and the standard deviation describes how the values in the population are distributed about the mean.

For practical breeding work on medium-sized fish farms, it is important to know how to calculate the mean, so that a farmer can assess the effect of his selective breeding programme. A farmer really does not need to know how to determine the standard deviation; scientists and researchers, on the other hand, must know how to determine the standard deviation. Table 3 illustrates how the mean is determined.

Because quantitative phenotypes are controlled by dozens to hundreds of genes, the simultaneous and/or sequential expression of these genes makes it impossible to identify individual genes and to decipher their modes of inheritance. Consequently, a different approach is needed to work with and to understand these phenotypes. Because quantitative phenotypes are more complicated genetically, it is more difficult to work with these phenotypes, but quantitative phenotypes are the most important phenotypes in agriculture or aquaculture--weight, fecundity, etc.--so the breeding value of a farmed population of food fish is mainly determined by the genes that control quantitative phenotypes. Their importance is underscored by the fact that quantitative phenotypes are often called "production phenotypes."

Table 3. How to calculate the mean for a quantitative phenotype. In this example, we will calculate mean length. In general, you determine the mean from a random sample of 30-200 fish.

Step 1. **Obtain individual lengths to the nearest millimeter. Thirty fish are measured.**

98	103	106	111	104	91	87	114	103	107
101	104	97	105	108	100	110	104	113	105
95	97	107	108	99	111	112	105	113	103

Step 2. **Determine the sum of the measurements; that is, add the phenotypic values.**

98 + 103 + 106 + 111 + 104 + 91 + 87 + 114 + 103 + 107 + 101 + 104 + 97 + 105 + 108 + 100 + 103 + 113 + 105 + 95 + 97 + 107 + 108 + 99 + 111 + 112 + 105 + 113 + 103 = 3,120

Step 3. **Divide the total value derived in Step 2 by the number of fish that were measured. In this case, 30 fish were measured, so you divide by 30.**

$$\frac{3{,}120}{30} = 104$$

The mean length in this population is 104 mm.

Phenotypic variance

Because quantitative phenotypes exhibit continuous distributions in a population, the only way to work with and to improve these traits is to analyze their variance and to divide it into the heritable and the non-heritable components. Phenotypic variance is the variability that a phenotype exhibits in a population; the mean describes the average phenotypic value, while the variance describes how individuals are distributed around the mean (the standard deviation, which was mentioned earlier, is the square root of the variance). Phenotypic variance (V_P) is the sum of three components: genetic variance (V_G), environmental variance (V_E), and genetic-environmental interaction variance ($V_{G\cdot E}$). This can be represented by the following formula:

$$V_P = V_G + V_E + V_{G\cdot E}$$

Genetic variance

Obviously, genetic variance is the component that breeders try to manipulate during a breeding programme. Genetic variance is itself the sum of three components, and different breeding programmes are needed to exploit these sub-components.

Genetic variance (V_G) is the sum of additive genetic variance (V_A), dominance genetic variance (V_D), and epistatic genetic variance (V_I). As before, this can be represented by a formula:

$$V_G = V_A + V_D + V_I$$

The words "additive," "dominance," and "epistatic" do not refer to specific types of gene action as they do when discussing the modes of inheritance for qualitative phenotypes. The correct terms are "additive genetic variance," "dominance genetic variance," and "epistatic genetic variance" (not gene action), and they refer to specific components of variance that are produced by the entire genome, not by one or two genes.

Additive genetic variance is the genetic component that is due to the additive effects of all the fish's alleles. One way of thinking about this is that additive genetic variance is the sum of the values that each allele makes to the production of the phenotype. Some alleles will make a large contribution; some will make a small contribution; some will make no contribution; and some may even make a negative contribution. The contribution made by every allele is added, and the sum is the additive genetic variance component for each fish.

Dominance genetic variance is the genetic component that is due to the interaction that exists between the pair of alleles at every locus. Because of this, dominance genetic variance cannot be inherited.

The idea that some form of genetics cannot be inherited usually causes confusion, but it is a simple concept. Dominance genetic variance is due to the interaction of the pair of alleles at each locus, which means that dominance genetic variance is a function of the diploid state (2N). The reason that dominance genetic variance is not heritable is that each parent contributes a haploid (N) gamete to the production of each offspring. Gametes do not contain pairs of alleles (2N); the diploid state is reduced to the haploid state during meiosis. During reduction division, all allelic pairs are separated when the chromosomes undergo independent assortment, which means that a parent's dominance genetic effects are destroyed during meiosis. Since an individual's dominance genetic variance is destroyed during reduction division, it cannot be transmitted via a gamete to an offspring--thus, it is not heritable. Dominance genetic variance effects are recreated at fertilization when a haploid sperm fertilizes a haploid egg to produce a diploid zygote. At fertilization, genes once again exist in the paired state, which means that an interaction exists between the pairs of alleles at each locus which, in turn, means that dominance genetic variance exists. Consequently, dominance genetic variance effects are destroyed and then recreated in new and in different combinations each generation.

Epistatic genetic variance is the genetic component that is due to the interaction(s) of alleles between or among loci; in other words, it is the interaction(s) that an allele has with alleles other than its own pair. Epistatic genetic variance is a mixture of heritable and non-heritable variance. The portion of the interaction that is between and among the alleles that were included in a gamete is heritable, but the portion that is between or among alleles that were parcelled to other sperm or to the polar bodies is not heritable. The percentage of epistatic genetic variance that is heritable varies from gamete to gamete because of crossing over and independent assortment. Independent assortment and crossing over tends to disrupt most epistatic genetic variance during meiosis, so only a small random sample is transmitted from a parent to its offspring; consequently, only a small random portion of epistatic genetic variance is heritable.

The differences among additive genetic variance, dominance genetic variance, and epistatic genetic variance and how they are transmitted is important on a practical level because different kinds of breeding programmes are needed to exploit these components of genetic

variance. Furthermore, the relative amount of phenotypic variance that can be attributed to these components of genetic variance determines the type of breeding programme that can be used and how effective it will be in improving the phenotype.

The two important genetic components are additive genetic variance and dominance genetic variance. Most breeders assume that epistatic genetic variance is not important. This assumption is made because it is difficult to try and select for combinations of alleles when you do not know what combinations are desirable. Additionally, the improvement that can be gained by selection for epistatic effects is rather small, and it plateaus quickly.

Additive genetic variance and dominance genetic variance are essentially opposites. Additive genetic variance is a function of the alleles, so it is function of the haploid state; dominance genetic variance is a function of allelic pairs, so it is a function of the diploid state. A parent produces haploid gametes, so it can transmit its additive genetic effects to its offspring, but it cannot transmit its dominance effects, which are destroyed during meiosis. Dominance effects are created in each zygote after fertilization. Thus, the additive effects are a function of each parent, while the dominance effects are a function of specific matings. Because the additive effects are transmitted from a parent to its offspring, additive genetic variance is often called the "variance of breeding values."

Because additive genetic variance is transmitted from a parent to its offspring, selection is the breeding programme that is used to exploit this component of variance and to improve the population. Because dominance genetic variance is not heritable but a function of the mating, hybridization is the breeding programme that is used to exploit this component of variance and to improve the population.

Heritability: Because additive genetic variance is transmitted from a parent to its offspring in a predictable and reliable manner, if the percentage of phenotypic variance that is due to additive genetic variance is known, a farmer can predict the amount of improvement that can be made as a result of selection, and he can even customize selection to achieve a pre-determined amount of improvement per generation.

The proportionate amount of additive genetic variance is called "heritability," and it can be represented by the following formula:

$$h^2 = V_A/Vp$$

where: h^2 is the symbol for heritability, **VA** is additive genetic variance, and V_p is phenotypic variance. Heritability is expressed as a percentage (0-100% or 0.0-1.0). Thus, heritability quantifies the percentage of phenotypic variance that is inherited in a predictable and reliable manner.

The major reason for determining the heritability of a quantitative phenotype is that it can be used to predict the results of a selective breeding programme by using the following formula:

$$R = Sh2$$

where: R is the response to selection (gain per generation), S is the selection differential (the superiority of the select brood fish over that of the population average; to determine this, you simply subtract the population average from the average of the select brood fish), and h^2 is heritability. Table 4 shows how a heritability can be used to predict response to selection.

Table 4. How to predict the response to selection if the heritability (h^2) of the phenotype is known. In this example, we will predict response to selection for increased length and then calculate the predicted mean length of the next generation.

Given:	h^2 for length at 12 months = 0.26 mean length at 12 months of the population = 146 mm mean length at 12 months of the select brood fish = 162 mm
Step 1.	Calculate the selection differential (S). S = mean length of the select brood fish mean length of the population S = 162 mm - 146 mm = 16 mm
Step 2.	Calculate the predicted response to selection (R). $R = Sh^2$ R = (16 mm)(0.26) R = 4.16 mm
Step 3.	Calculate the mean of the F_1 generation of select fish. mean of the F_1 generation = mean of the population + R mean of the F_1 generation = 146 mm + 4.16 mm = 150.16 mm

The preceding formula clearly demonstrates that heritability is the factor that determines the percentage of selection differential that can be gained via selection; in other words, how much gain is possible. In general, heritabilities > 0.25 indicate that selection will produce good gains, while those <0.15 indicate that selection will be ineffective. Heritabilities >0.3 are considered to be large.

Although it is advantageous to know the heritability of a quantitative phenotype before conducting a selective breeding programme, it is not necessary. If one exists, it can be used to predict the gains, to customize the selection differential that is needed to achieve a desired response to selection, or to indicate that selection will be so ineffective that the programme should be scrapped. Table 5 shows how a heritability can be used to customize the selection differential in order to achieve a desired response to selection.

It is often unnecessary to determine a heritability, because published information already exists. Several hundred heritabilities have already been determined for phenotypes such as growth rate, food conversion, disease resistance, fecundity, egg size, egg number, dressing percentage, body conformation, and pesticide tolerance in many important aquacultured species of food fish. The heritabilities that are published may not be the same as those in a farmer's population, because heritabilities are specific for the population that was evaluated and for the culture conditions that were used in the experiment, but the published values should be similar to those that exist in most populations. Table 6 lists some of the heritabilities that have been determined in common carp and tilapia.

Table 5. How to use the heritability (h^2) of the phenotype to customize the selection differential in order to produce the desired response to selection.

Given: h^2 for length at 12 months = 0.26
mean length at 12 months of the population = 146 mm
desired response to selection = 6 mm

Step 1. Calculate the selection differential (S) needed to produce a response of 6 mm:

$R = Sh^2$
6 mm = (S)(0.26)
6 mm/0.26 = S
23.08 mm = S

Step 2. Calculate the mean of the select brood fish that will be needed to produce a selection differential of 23.08 mm.

S = mean length of the select brood fish - mean length of the population
23.08 mm = mean length of the select brood fish - 146 mm
mean length of the select brood fish = 146 mm + 23.08 mm
mean length of the select brood fish = 169.08 mm

Role of environment in phenotypic expression

Although the genes are the blueprints that are used to produce the phenotypes, they produce these phenotypes in conjunction with the environment. The environment influences the production of all phenotypes, but quantitative phenotypes are more affected by environmental variables than qualitative phenotypes. If a fish cannot eat the necessary nutrients, it will be unable to produce certain proteins, which means the fish will be unable to produce specific phenotypes. This is especially true for qualitative phenotypes which depend on pigments which cannot be synthesized by fish. For example, tropical fish farmers add various plant pigments to fish feed in order to enhance the body colours of ornamental fish, and salmon farmers add pigments to salmon feed so the flesh will be pink rather than white. Environmental factors that influence quantitative phenotypes range from obvious ones, such as stocking density and feed quality, to those which are subtle and usually not considered; these factors include: female age, female size, spawning date, feed particle size, and feeding practices. Even if the environment plays a large role in the production of a quantitative phenotype, the role it plays is not critical to the success of a breeding programme if it is the same for all fish. When conducting a selective breeding programme to improve a quantitative phenotype, it is crucial to be able to control environmental variables and to prevent them from varying among individuals, families, and ponds. If they are not controlled, they will differentially influence phenotypic expression, and a farmer will not know if the select fish are best because they are genetically superior or because they had the better environment. The difference is crucial, because only fish that are superior genetically will be able to transmit this superiority to their offspring, which is the goal of all selective breeding programmes.

Table 6. Heritabilities (h^2) for some phenotypes in common carp, Nile tilapia, blue tilapia, and Mozambique tilapia. The existence of different heritability values for a phenotype (for example, 1-year weight in common carp) is because they were determined either by different researchers or in different populations or under different growing conditions. **A** realized heritability is one that was determined from a selective breeding programme.

Species	Phenotype	
Common carp	1-year weight	0.0
	1-year weight	0.34
	1-year weight	0.49
	2-year weight	0.15
	2-year weight	0.50
	3-year weight	0.24
	4-year weight	0.21
	weight gain (realized)	0.0
	weight gain	0.25
	1-year length	0.04
	1-year length	0.34
	2-year length	0.55
	1-year body depth	0.42
	2-year body depth	0.69
	3-year body depth	0.47
	body shape (length:weight) (realized)	0.47
	fat content	0.14
Nile tilapia	4-week weight	0.0
	4-week weight	0.06
	45-day weight	0.04
	8-week weight	0.0
	8-week weight	0.21
	10-week weight	0.0
	10-week weight	0.46
	90-day weight	0.04
	136-day weight, female	0.71
	136-day weight, female	0.37
	136-day weight, male	0.71
	136-day weight, male	0.30
	7-month weight (realized)	0.05
	45-day length	0.10
	90-day length	0.06
	fecundity at first spawning	0.0
	fecundity at first spawning	0.09
Blue tilapia	40-week weight gain, female (realized)	0.38
	40-week weight gain, male (realized)	0.20
	49-week weight gain, female (realized)	0.10
	49-week weight gain, male (realized)	0.27
	40-week length gain, female (realized)	0.87
	40-week length gain, male (realized)	0.40
Mozambique tilapia	5-month weight, female (realized)	0.01
	5-month weight, male (realized)	0.10

CHAPTER 3

Selection for qualitative phenotypes

Qualitative phenotypes are usually less important than quantitative phenotypes for food fish farmers, but an understanding of how they can be controlled and exploited by selective breeding programmes is important for two reasons: First, and most important, is the fact that qualitative phenotypes can affect the value of the crop or the cost of production. If a farmer can produce a more attractive product, consumers are often willing to pay more for it, which increases his profits. On the other hand, some qualitative phenotypes, such as deformities, can decrease the value of the population, either by increasing the cost of production or by producing fish so unattractive that consumers will not buy them. In both cases, farmers can use selection to improve their populations. Secondly, an understanding of how selective breeding programmes can be used to fix (frequency = 100%) the desired qualitative phenotypes and eliminate (frequency = 0%) the undesired ones and thus produce true-breeding populations may make it easier to understand how selection can be used to improve quantitative phenotypes.

Those who already have a good grasp of Mendelian genetics and understand how breeding programmes can be used to fix or to eliminate qualitative phenotypes, or those who only wish to work with quantitative phenotypes, may skip this chapter and go directly to Chapter 4.

Factors that must be considered before conducting selective breeding programmes

Before conducting a selective breeding programme, a farmer must realize that he can use selection to accomplish only those goals which are achievable biologically. Selection is a breeding programme that exploits heritable phenotypic variance; consequently, the two prerequisites for a successful selective breeding programme are: one, the phenotype that the farmer wants to change must exhibit variance; two, the variance must be heritable. Breeders are able to accomplish only what the fish and the fish's genes allow them to accomplish. Breeders cannot custom-design fish by removing undesirable phenotypes, such as sharp pectoral spines, unless individuals without these spines are discovered, and even if such individuals are discovered, the phenotype must be heritable or selection will be an expensive, futile, and frustrating waste of effort. If the phenotypes in question are heritable, the genetics should be known before a breeding programme is conducted. This information will enable the breeder to use the most appropriate breeding programme. Finally, the farmer must know the relative costs of the traits (production costs) and what they are worth (market value) before he initiates a selective breeding programme.

Qualitative phenotypes can be described as "either/or" phenotypes. A fish either has one phenotype or it has another; in other words, the fish in a population fall into discrete, non-overlapping phenotypic categories. Because selection exploits phenotypic variance, at least two phenotypes must exist in the population, and one must be the phenotype that the farmer wants. If there is only one phenotype, there is no phenotypic variance, which means that selection cannot be used to alter the phenotype. For example, if all fish in a

population are black, there is no phenotypic variance for body colour; consequently, selection cannot be used to change body colour.

Not only must variance exist, but the variance that is observed must be heritable, or selection will not be able to alter phenotypic frequencies. The distinction between heritable and non-heritable variance is important, because many qualitative phenotypes that are observed at fish farms and at fish hatcheries are non-heritable deformities. Some deformities have a genetic basis, but most are caused by nutritional deficiencies, environmental disturbances, toxins, disease, or injury or they are developmental mistakes. The deformities that are produced by non-genetic factors cannot be eliminated by selection. The only way to eliminate a non-heritable deformity is to discover the environmental factor that causes it and to eliminate the factor or modify the culture environment. It is often difficult, if not impossible, to identify the cause of a non-heritable deformity, so unless the frequency approaches 0.5% it probably should be ignored.

Before selection is used to fix or to eliminate qualitative phenotypes and produce true-breeding populations, the way the phenotypes are inherited should be determined. If a previous experiment has already determined the mode of inheritance, that information can be used to design the breeding programme. If the mode of inheritance is known, the correct breeding programme can be chosen, and this will enable the farmer to achieve his goal quickly and efficiently. If the mode of inheritance is not known prior to the breeding programme, the farmer may choose the wrong programme, which means he will not accomplish his goal and will waste effort, facilities, and money.

The research programmes that are needed to determine the modes of inheritance for qualitative phenotypes are not that complicated. In general, the inheritance is deciphered by conducting paired matings across two generations and by determining the phenotypic ratios produced by these matings (some of these matings and the ratios that are used are illustrated in Figures 3 and 5). Even though this type of research is not that complicated, it requires effort, facilities, and the ability to analyze the results statistically. Such research should be left to scientists at universities or governmental research stations.

Before conducting a selective breeding programme, a farmer should conduct an assessment to determine if a selective breeding programme is needed. The assessment can be conducted by a farmer (such studies are not cheap, and they require a high level of sophistication), or they can be conducted by fisheries cooperatives or a local fish farming research station. The farmer needs to determine if his customers want fish with a different body colour, or if they will pay extra for a prettier fish. His assessment will also tell him if the proposed breeding programme could open new markets. A farmer should only conduct a selective breeding programme when it is necessary or when it will increase his profits. Changing body colour or other phenotypes might produce a prettier fish, but if the assessment reveals that consumers do not want a different body colour, the breeding programme should not be conducted.

Finally, the farmer must know the costs of producing the alternate phenotypes before conducting a selective breeding programme. The values of some phenotypes are so obvious that no formal scientific study is needed. If a farmer wants to use selection to eliminate a heritable deformity which lowers growth rate or viability, formal studies to determine the relative values of the phenotypes are unnecessary, because he already knows that the deformity costs him money.

On the other hand, the relative production costs of some phenotypes are more difficult to determine and require evaluation in a scientific experiment. The relative production costs are determined by assessing the effects that the phenotypes have on growth rate, survival, egg production, etc. These secondary effects are called "pleiotropic effects," and in agriculture and aquaculture they can be more important than the phenotype itself--especially if growth, survival, or fecundity are affected. Almost all mutant body colours that have been investigated in fish have exhibited negative pleiotropic effects, in that they adversely affected growth rate or survival. Figure 8 illustrates the negative pleiotropic effect that red body colour has on viability in Nile tilapia.

If there are no negative pleiotropic effects or if the extra costs of production (slower growth rate and/or lower viability) are offset by the increased market value of the crop (extra money consumers are willing to pay), selection is worthwhile. On the other hand, if the increased costs of production exceed the extra market value of the crop, it would be foolish to conduct a selective breeding programme because the farmer will earn less money.

Selective breeding programmes to produce true-breeding populations

When working with qualitative phenotypes, the goal of all selective breeding programmes is to produce a true-breeding population. A true-breeding population is one that contains only one allele for the locus in question because it was fixed; selection eliminated the other allele. This means that every gamete produced by the select brood fish will contain only the desired allele, which means that every offspring produced by the select brood fish will have the desired phenotype. The only way the undesired phenotype can be produced after selection has been used to create a true-breeding population is by the accidental (or intentional) stocking of fish from another population or by mutation.

The undesired phenotype and the allele that produces it are eliminated by a process called "culling." Culled fish are not allowed to reproduce. They do not have to be killed; they can be grown and then sold as food, but they must not be allowed to spawn.

There are three basic rules that govern the selection of qualitative phenotypes:

1. If the desired phenotype is controlled only by a homozygous genotype, a single act of selection will create a true-breeding population.

2. If the desired phenotype is controlled by two or more genotypes, selection cannot create a true-breeding population. Progeny testing must be used to fix the desired allele and produce a true-breeding population.

3. If the desired phenotype is controlled by the heterozygous genotype, no breeding programme can create a true-breeding population. A population in which every fish has the desired phenotype can be produced by crossing the two homozygous phenotypes, but this procedure must be repeated every breeding season.

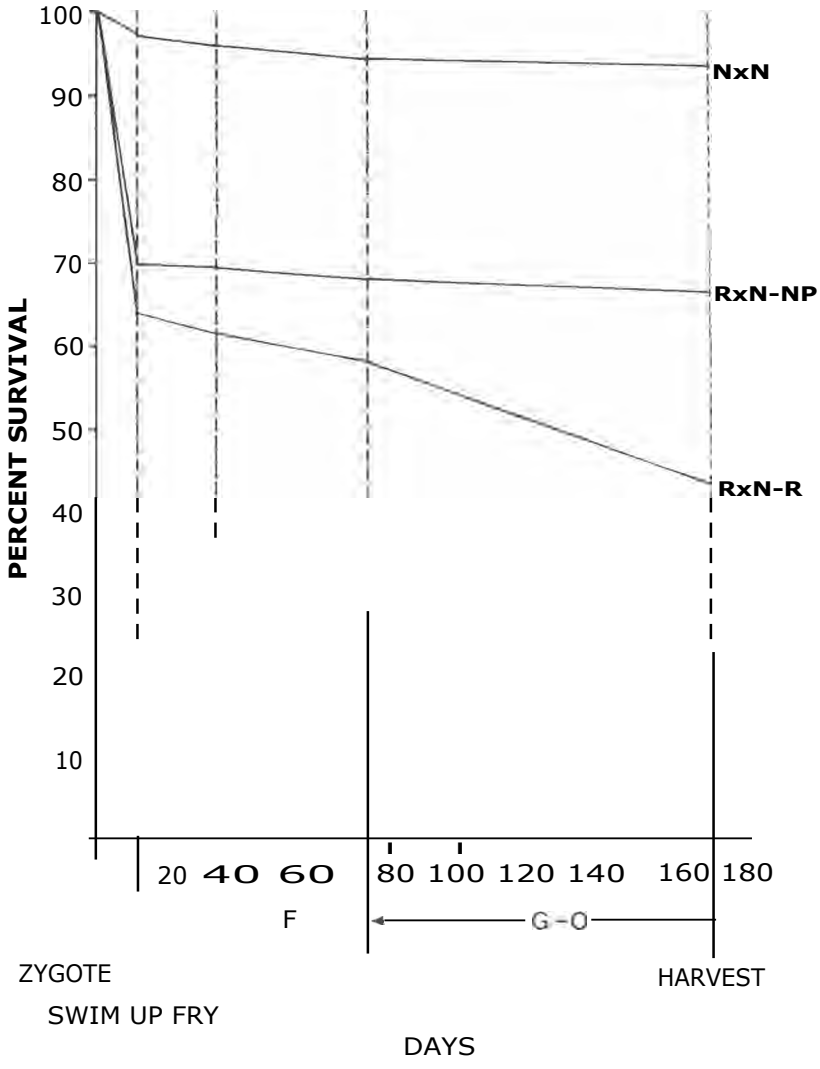


Figure 8. Effect of red body colour on viability in Nile tilapia. This is an example of a negative pleiotropic effect. Viability or red fish (R x N-R) is compared to that of their normally pigmented sibs (R x N-NP) and a control population which had no red fish (N x N). Viabilities during artificial incubation of eggs (I), sex reversal (SR), fingerling production (F), and grow-out (G-O) are shown. At harvest, fish averaged 250 g.

Source: After El Gamal, A.R.A.L. 1987. Reproductive performance, sex ratios, gonadal development, cold tolerance, viability and growth of red and normally pigmented hybrids of Tilapia aurea and T. nilotica. Doctoral dissertation, Auburn University, Alabama, USA.

Selection for homozygous phenotypes

When this type of selection is used, it is usually done because a farmer wants to fix the recessive phenotype and eliminate the dominant phenotype, and the phenotypes are produced by an autosomal gene that exhibits complete dominance. The term "recessive" does not imply inferiority; similarly, the term "dominant" does not imply superiority. The terms simply refer to the way the alleles express themselves and to the phenotypes that are produced by those alleles. Many recessive phenotypes have been shown to be quite valuable in various farmed plants and animals, and breeding programmes have been conducted to fix them. The terms "inferior" and "superior" should be applied to phenotypes only after biological and economic evaluations have been conducted.

If the desired trait is the recessive phenotype that is produced by a gene that exhibits complete dominance, the selective breeding programme that is needed to fix the trait and to produce a true-breeding population is simple, and this goal can be achieved by a single act of selection. To accomplish this, fish with the recessive phenotype will be saved, and fish with the dominant phenotype will be culled.

Genetically, fish with the undesired dominant phenotype are either homozygous dominant or heterozygous. Because every fish that has at least one dominant allele expresses the undesired dominant phenotype, a simple one-step culling of all fish with the dominant phenotype will eliminate all copies of the dominant allele. Conversely, every fish that expresses the desired recessive phenotype is homozygous recessive, which means that when these fish are selected, none will possess a copy of the undesired dominant allele. Thus, the recessive allele will be the only allele that exists in the select population, which means that it will breed true.

For example, say a tilapia farmer has both normally pigmented and pink Nile tilapia, and decides to grow only pink tilapia. He can create a true-breeding pink population by a simple one-step selective breeding programme during which he will cull all normally pigmented fish. Pink body colour is the recessive phenotype, and it is produced by the recessive b allele (bb genotype); normal body colour is the dominant phenotype, and it is produced by the dominant B allele (BB and Bb genotypes).

The culling of all normally pigmented tilapia will remove all B alleles from the population. The only fish that remain will be pink and, since they are homozygous recessive bb, the b allele will be the only allele that will remain in the population of select brood fish. Consequently, a single act of selection will create a true-breeding pink population (Figure 9).

This type of selective breeding programme can also be used to fix either the recessive or the dominant phenotypes when the mode of gene action is incomplete dominance, and it can also be used to fix either homozygous phenotype when the mode of gene action is additive. In both cases, there are two homozygous genotypes that can be identified and isolated. By culling the undesired phenotypes, true-breeding populations can be created by a single act of selection.

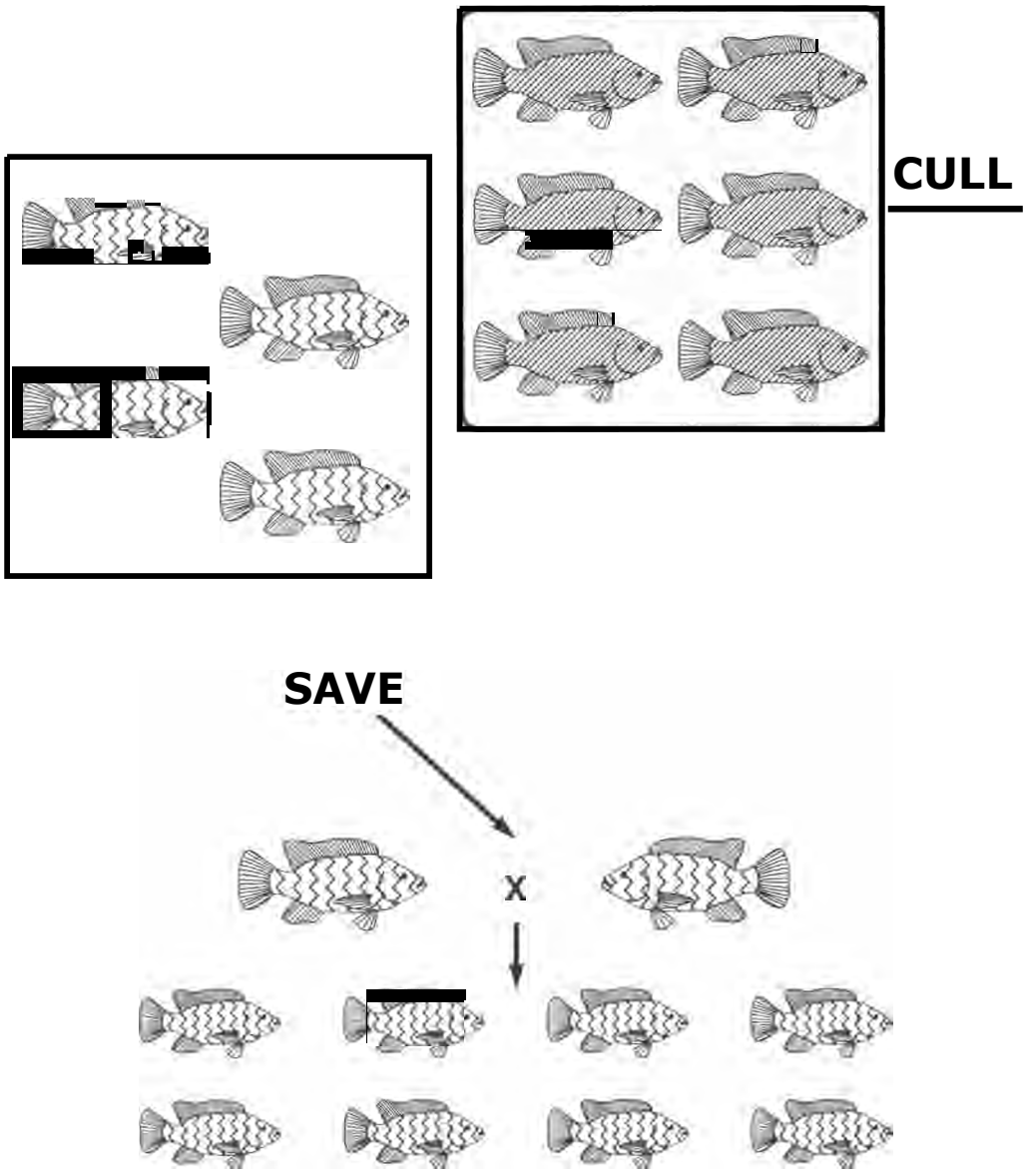


Figure 9. Selective breeding programme needed to produce a true-breeding population of pink Nile tilapia. If all normally pigmented (the dominant phenotype) fish are culled, all copies of the dominant B allele will be eliminated. The only fish that remain are pink (the recessive phenotype), and since they are homozygous recessive bb, the select population of pink brood fish will breed true and will produce only pink offspring. Pictorial representations of the phenotypes are the same as those used in Figure 2. Any recessive phenotype can be fixed this easily.

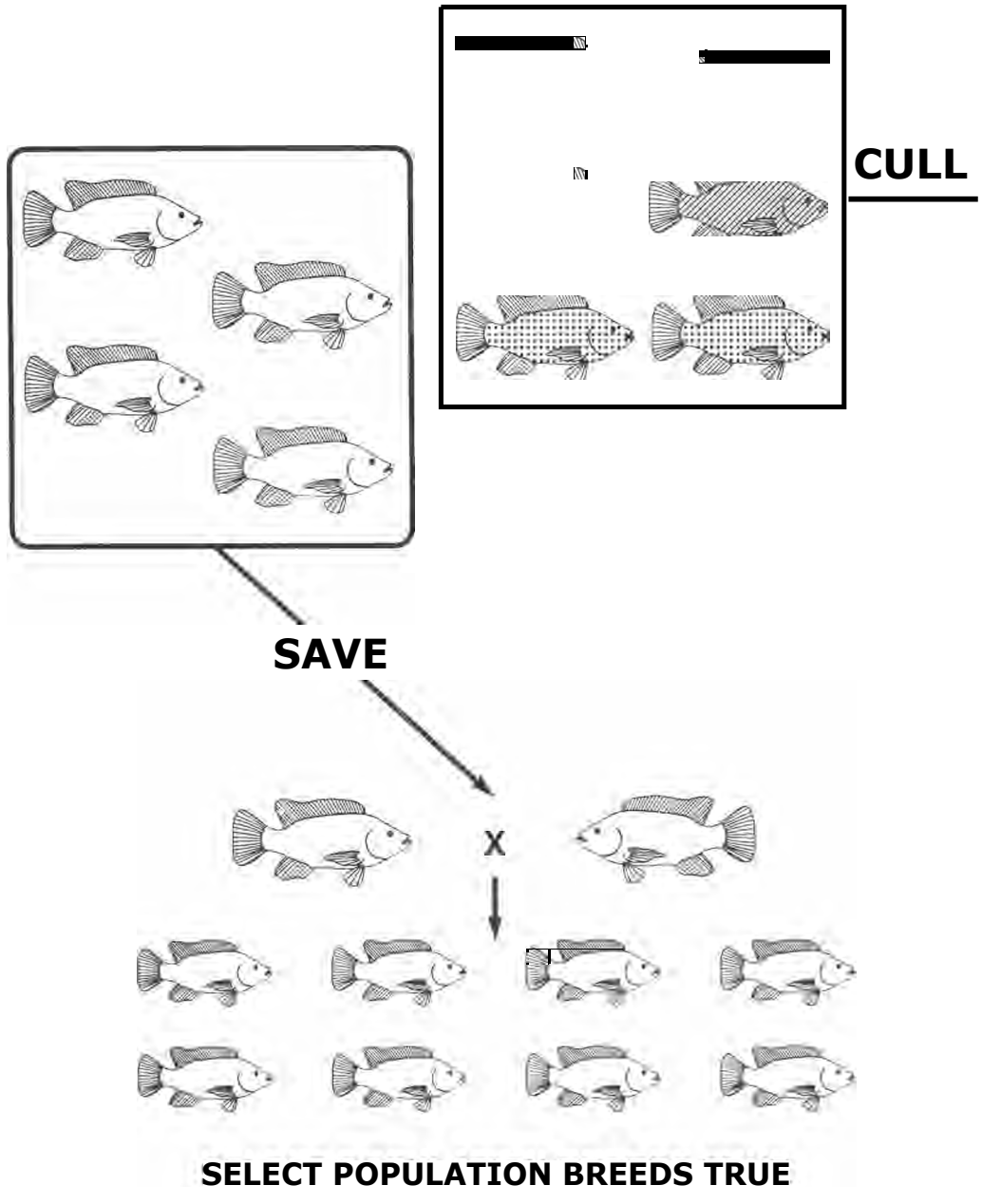


Figure 10. Selective breeding programme needed to produce a true-breeding population of gold Mozambique tilapia. If all melanistic (black [G] and bronze [Gg]) fish are culled, all copies of the dominant G allele will be eliminated. The only fish that remain are gold (the recessive phenotype), and since they are homozygous recessive gg, the select population of gold brood fish will breed true and will produce only gold offspring. Pictorial representations of the phenotypes are the same as those used in Figure 4.

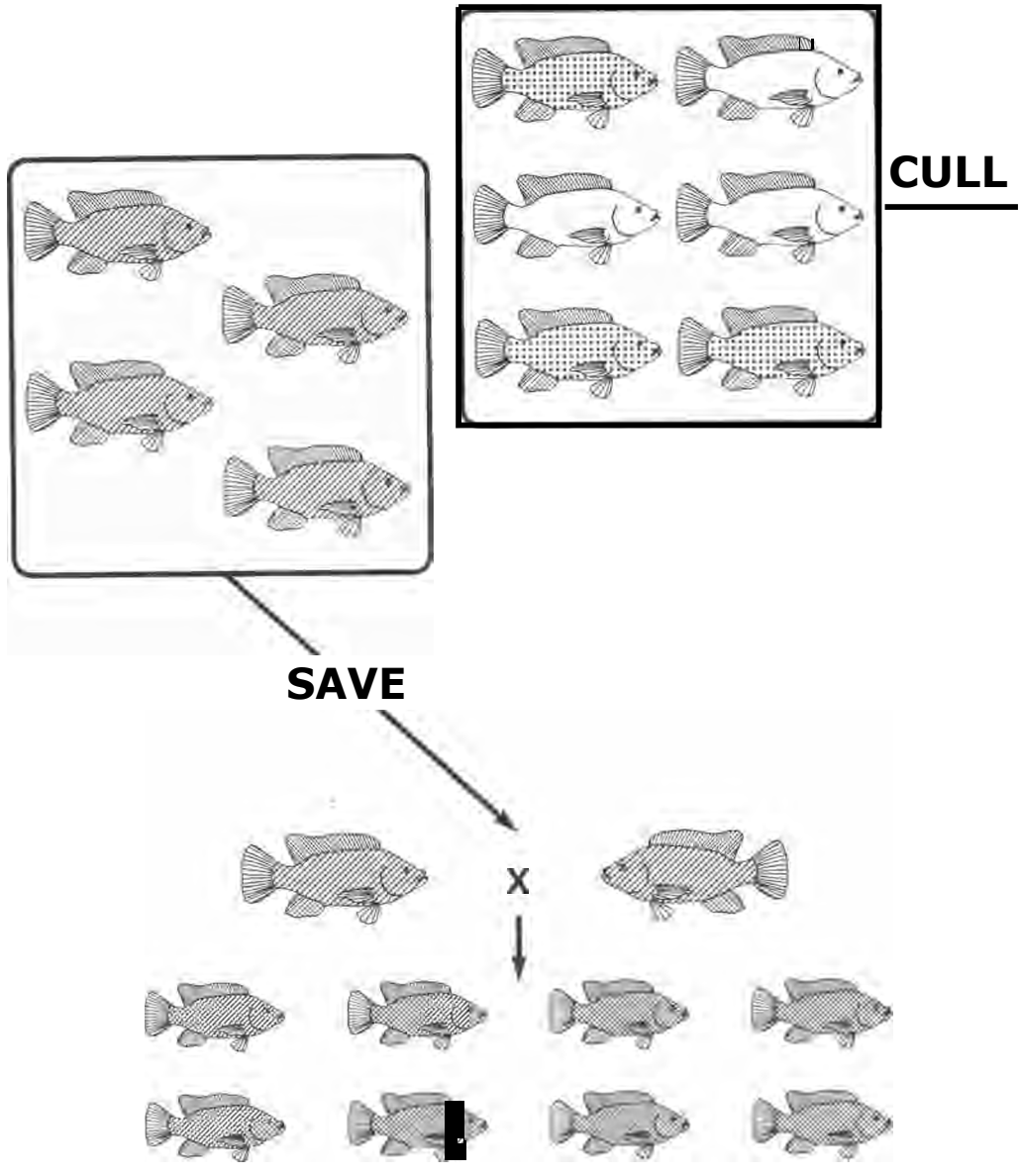


Figure 11. Selective breeding programme needed to produce a true-breeding population of black Mozambique tilapia. If all bronze (the heterozygous [Gg] phenotype) and all gold (the recessive [gg] phenotype) fish are culled, all copies of the recessive g allele will be eliminated. The only fish that remain are black (the dominant phenotype), and since they are homozygous dominant GG, the select population of black brood fish will breed true and will produce only black offspring. Pictorial representations of the phenotypes are the same as those used in Figure 4.

For example, say a tilapia farmer has black, bronze, and gold body colours in his population of Mozambique tilapia. If the farmer wants to produce either a true-breeding population of gold or a true-breeding population of black fish, he can accomplish either goal by a single act of selection. Gold is the recessive phenotype, and it is produced by the homozygous recessive genotype (gg); black is the dominant phenotype, and it is produced by the homozygous dominant genotype (GG); bronze is the heterozygous (Gg) phenotype.

A true-breeding population of gold tilapia, can be produced by culling all black and all bronze fish (Figure 10). Conversely, a true-breeding population of black tilapia can be produced by culling all gold and all bronze fish (Figure 11).

This same concept can be extended to phenotypes that are controlled by two or more genes. If the desired phenotype is controlled only by a homozygous genotype, a true-breeding population can be created by a single act of selection.

For example, if a carp farmer has a population of common carp with all four scale phenotypes and wants to produce a true-breeding population that has a reduced scale pattern, all he has to do is save the fish with the mirror phenotype and cull all other fish. Three of the scale phenotypes have a reduced number of scales, but only mirror is produced by a homozygous genotype (ss,nn), so it is the only one that is capable of breeding true. Both the leather (ss,Nn) and line (SS,Nn and Ss,Nn) phenotypes are undesired, because they are heterozygous at the N locus, which means that when two leather and/or line fish mate, 25% of their offspring will die (those that are homozygous NN, regardless of the genotype at the S locus--see Figure 6). Leather and line phenotypes are also undesired, because fish with these phenotypes have several negative pleiotropic effects, among them lowered growth rates and viabilities.

If the farmer culls all leather, line, and scaled individuals, all S and N alleles will be eliminated. The only fish that will remain in the select population will be those with the mirror phenotype, and since they are homozygous recessive (,nn) the s and n alleles will be the only ones that remain in the population of select brood fish. Consequently, a single act of selection will create a true-breeding population of mirror common carp (Figure 12).

Selection for phenotypes controlled by more than one genotype

Selection cannot fix a phenotype that is controlled by more than one genotype. This means selection cannot fix a dominant phenotype and create a true-breeding population if it is produced by a gene with complete dominance. Conversely, this also means that selection cannot eliminate a recessive phenotype (and the recessive allele) if it is produced by a gene with complete dominance. Despite the fact that this type of selective breeding programme will not work, it is routinely used in a misguided effort to eliminate undesired phenotypes that are produced or that are assumed to be produced by recessive alleles.

This type of breeding programme will not achieve its goal for either of two reasons. The first is the fact that most undesired phenotypes are abnormalities that are created by non-genetic factors (environmental disturbances or developmental mistakes). Many assume that all abnormal phenotypes are mutant phenotypes which are produced by recessive alleles. Some are, but most are not. If the undesired phenotype is produced by a non-genetic factor, selection will not work, because no selective breeding programme can fix or eliminate non-heritable phenotypes.

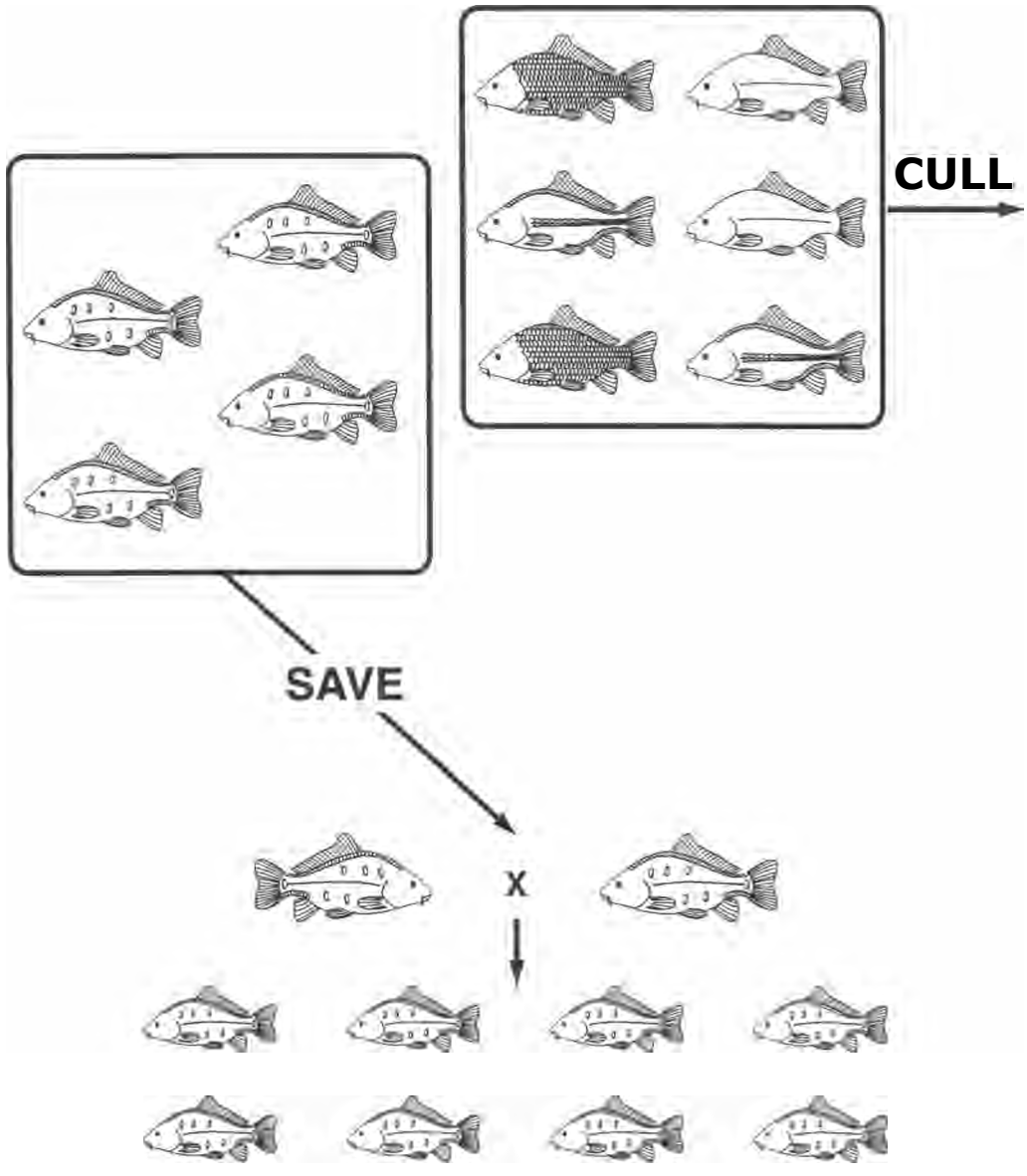


Figure 12. Selective breeding programme needed to produce a true-breeding population of mirror common carp. If all scaled, line, and leather fish are culled (phenotypes that are produced by genotypes with at least one dominant allele--see Figure 6), all copies of the S and N alleles will be eliminated. The only fish that remain are those with the mirror (the recessive) phenotype, and since they are homozygous recessive ss,nn, the select population of mirror brood fish will breed true and will produce offspring with only the mirror phenotype. Even if a set of phenotypes are produced by two or more genes, if the desired phenotype is the recessive phenotype (all loci responsible for the production of the phenotype are homozygous recessive), selection can produce a true-breeding population this easily.

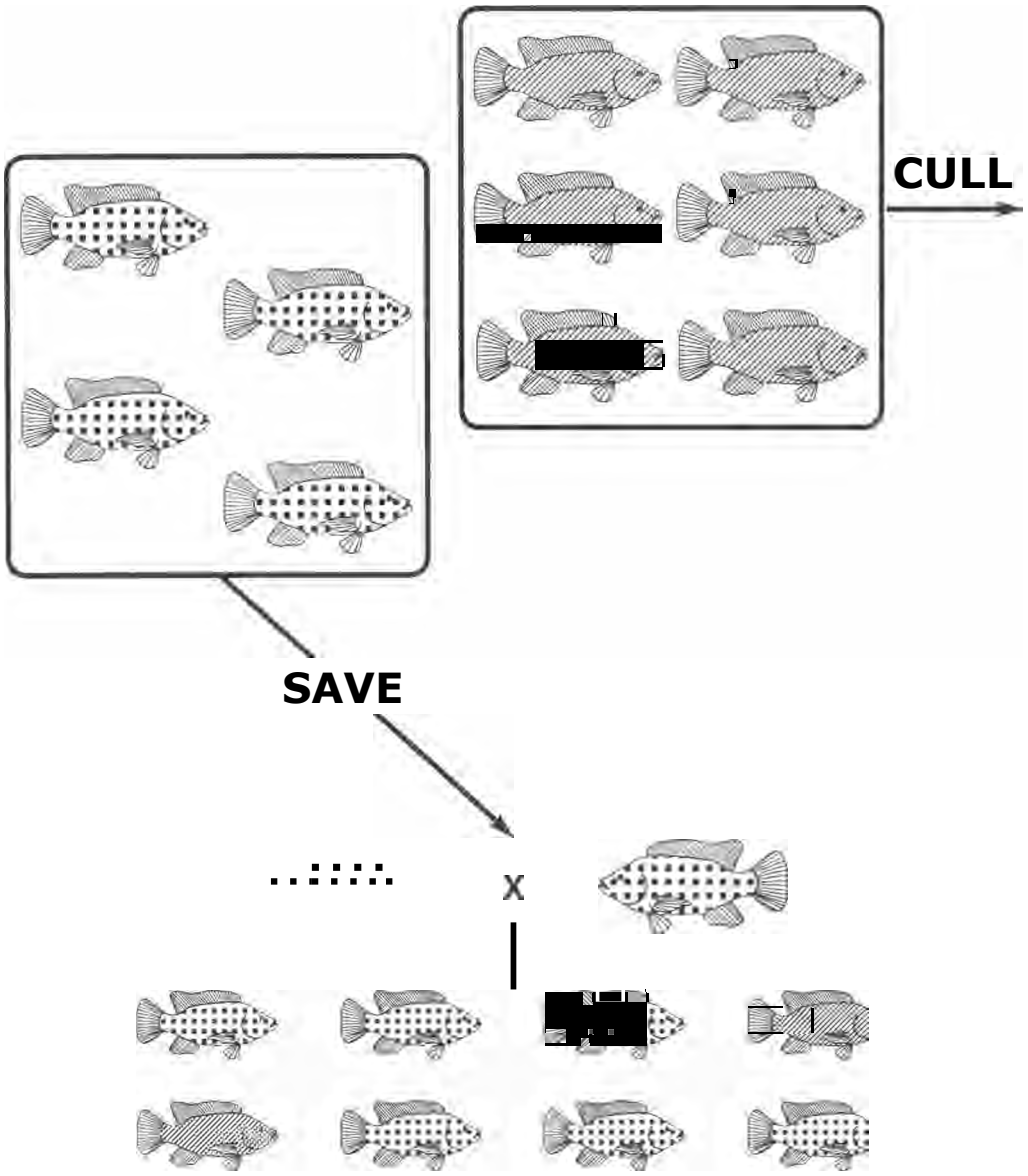


Figure 13. Selective breeding programme used in an unsuccessful attempt to produce a true-breeding population of red Nile tilapia. Red fish are represented by fish covered with squares, while normally pigmented fish are those covered with stripes (the same pictorial representations for body colour will be used in Figure 15). If all normally pigmented fish (the recessive phenotype) are culled, the select population will be composed of only red fish (the dominant phenotype). Since red body colour is produced by a dominant allele that exhibits complete dominance, red is produced by both the homozygous dominant (RR) and by the heterozygous (Rr) genotypes. Every heterozygous red brood fish (Rr) that is saved will carry a copy of the r allele to the select population; consequently, selection cannot eliminate it. When select red brood fish are spawned, the mating of two heterozygotes (Rr) will produce some normally pigmented offspring (the mating that is depicted). Recessive phenotypes cannot be eliminated by culling them; they will reappear when the select brood fish are spawned. Consequently, if the desired phenotype is the dominant phenotype and it can be produced by both the homozygous dominant and by the heterozygous genotype, selection cannot create a true-breeding population.

Even when a deformity is produced by a recessive allele, if it is an autosomal gene that exhibits complete dominance, selection will not create a deformity-free population. The reason why it will fail is quite simple: The dominant (normal) phenotype is produced by either of two genotypes, and it is impossible to differentiate normal fish that are homozygous dominant from those that are heterozygous.

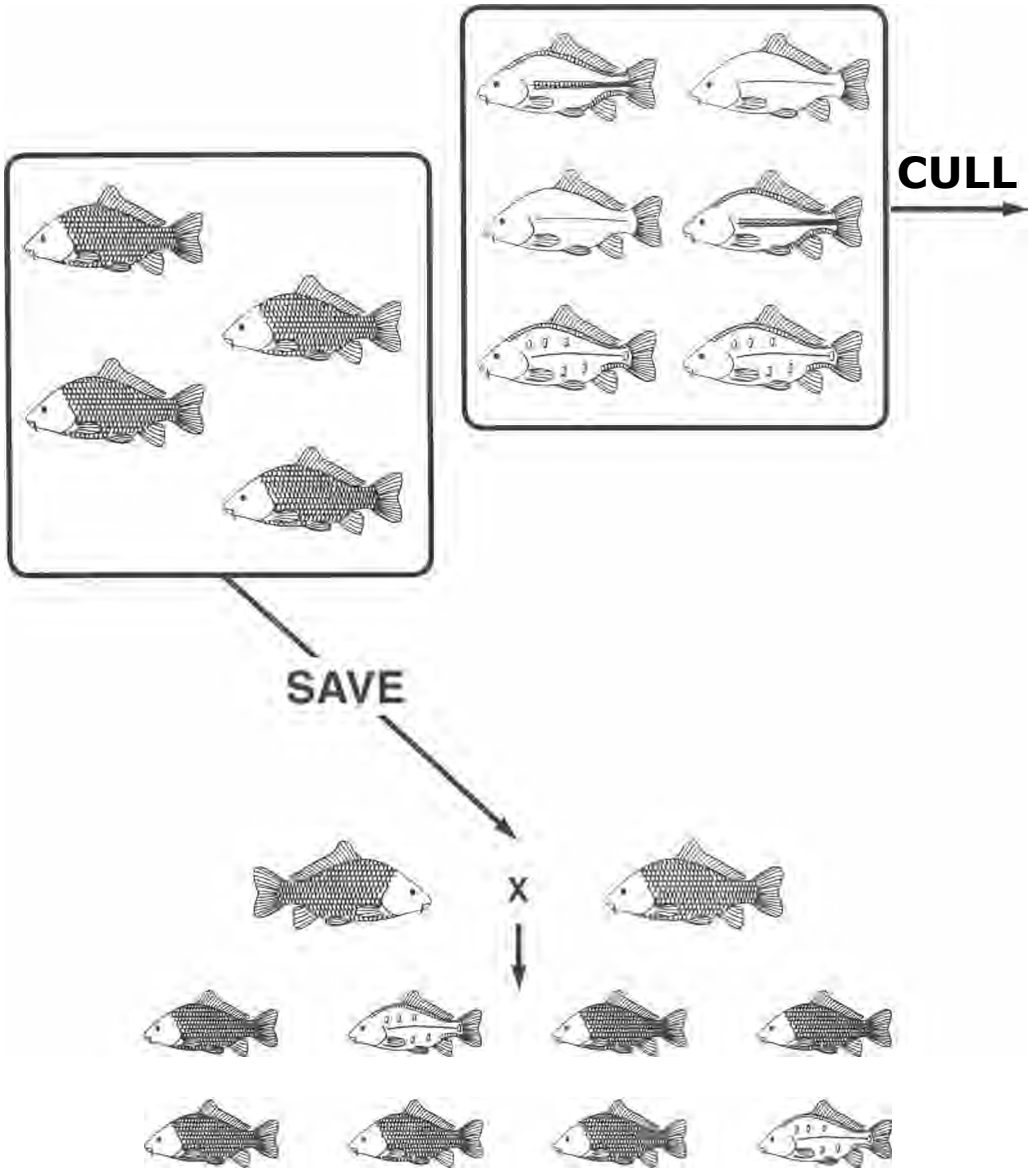
Because of that, when a farmer culls the recessive (abnormal) fish, the select population will be composed of fish with one phenotype (normal) but two genotypes, and every heterozygous select normal brood fish will carry a copy of the undesired recessive allele. Because the select population contains both alleles, it cannot breed true. When two heterozygous select normal brood fish mate, they will produce offspring with the undesired abnormal (recessive) phenotype. This type of selection will reduce the frequency of an undesired recessive phenotype, but it cannot eliminate it and produce a true-breeding deformity-free population.

For example, say a tilapia farmer has a population of Nile tilapia that contains both normally pigmented and red individuals, and decides to produce only red tilapia. If he tries to produce a true-breeding population of red Nile tilapia by culling all normally pigmented fish, he will discover that he will be unable to produce a red population that breeds true. The select red brood fish will produce both red and normally pigmented offspring. This is because red is the dominant phenotype, and it is produced by the dominant R allele (RR and Rr genotypes), while normal pigmentation is the recessive phenotype, and it is produced by the recessive r allele (rr genotype). Because the homozygous dominant and the heterozygous genotypes produce identical red phenotypes, some of the select red brood fish (the heterozygotes) will have a copy of the undesired r allele. When two heterozygous red brood fish mate, they will produce some normally pigmented offspring (Figure 13).

The same concept applies for phenotypes that are controlled by two or more genes. If the desired phenotype is produced by more than one genotype, and if at least one of the genes can be in either the homozygous or heterozygous state, selection cannot create a true-breeding population. As was the case for phenotypes produced by a single gene, some of the select brood fish will carry a copy of the undesired recessive allele(s) and, when two heterozygotes mate, they will produce offspring with the undesired phenotype(s).

For example, if a carp farmer has a population of common carp with all four scale phenotypes and decides to produce a true-breeding population of scaled common carp by selection, he will discover that he cannot create a true-breeding population. This is because the select scaled brood fish will have two genotypes-- ,nn or Ss,nn--and it is impossible to tell heterozygous scaled fish from homozygous scaled fish. The farmer can eliminate the dominant N allele by culling all fish with the line and leather phenotypes (a dominant allele can be culled by a single act of selection); those individuals with two copies of the N allele were culled by nature and died. However, the farmer cannot eliminate the undesired s allele by culling the remaining phenotype--mirror. The select population of scaled brood fish will produce both mirror and scaled offspring when two select heterozygous (Ss,nn) scaled brood fish mate (Figure 14).

Progeny testing: Since selection against (culling) a recessive phenotype cannot fix a dominant allele and produce a true-breeding population (when the mode of gene action is complete dominance), another type of breeding programme must be used to achieve this goal. The only way an undesired recessive allele can be eliminated is by progeny testing. Progeny testing is a breeding programme that deciphers a parent's genotype by determining



SELECT POPULATION CANNOT BREED TRUE

Figure 14. Selective breeding programme that is used in an unsuccessful attempt to produce a true-breeding population of scaled common carp. If all fish with the line, mirror, and leather phenotypes are culled, the select population will be composed of scaled fish. This act of selection will eliminate all copies of the undesired dominant N allele, because every heterozygote (line and leather phenotypes) will be culled (the homozygotes were culled by nature, since the NN genotype is lethal). Unfortunately, this selective breeding programme will not produce a true-breeding population because you cannot eliminate the undesired recessive **s** allele by culling the recessive phenotype (mirror). Because the scaled phenotype is produced by a dominant allele that exhibits complete dominance, both homozygous (SS,nn) and heterozygous (Ss,nn) scaled fish will be saved. Every heterozygous select scaled brood fish will carry a copy of the recessive **s** allele to the select population; consequently, selection cannot eliminate it. When select scaled brood fish are spawned, the mating of two heterozygotes will produce some offspring with the mirror phenotype (the mating that is depicted). As was the case with a phenotype produced by a single gene, if the desired phenotype is produced by more than one genotype and if one of the genotypes is a heterozygous genotype, selection cannot create a true-breeding population.

its offspring's phenotypes. Once the genotypes of the dominant parents are deciphered, selection is used to save the homozygotes and cull the heterozygotes, which will eliminate all copies of the recessive allele, fix the dominant allele, and produce a true-breeding population.

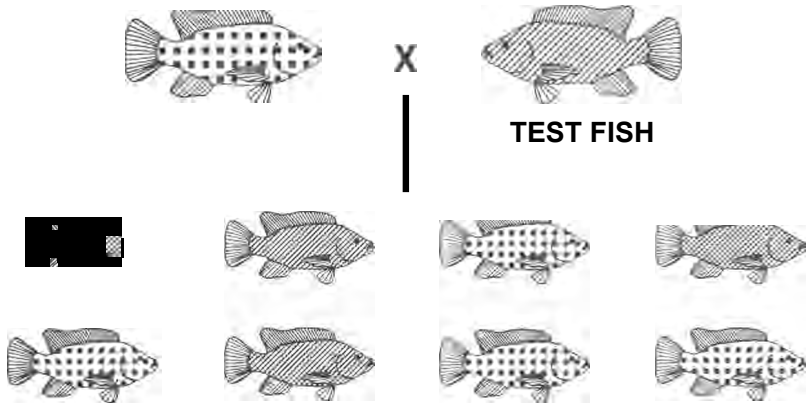
This is accomplished by pairing and mating fish with the dominant phenotype to test fish (a fish whose genotype is known). Test fish are usually fish with the recessive phenotype, because such fish are homozygous recessive (experiments are not needed to determine a recessive phenotype's genotype). Because a test fish can produce gametes with only a recessive allele, the dominant fish is the parent that determines its offspring's phenotypes (see Figure 3c and 3e). If the dominant parent is homozygous, all offspring will have the dominant phenotype (Figure 3c); if the dominant parent is a heterozygote, half the offspring will have the dominant phenotype and half will have the recessive phenotype (Figure 3e).

The production of a single offspring with the recessive phenotype is enough evidence to state with certainty that the dominant parent is a heterozygote and must be culled. If no offspring with the recessive phenotype is detected in a random sample of at least 20 offspring, the dominant parent can be declared to be homozygous and kept for breeding purposes. Once a sufficient number of males and females are progeny tested and declared to be homozygous dominant, all other fish (including all offspring produced in the progeny tests) are culled. The population will now breed true and produce only offspring with the dominant phenotype.

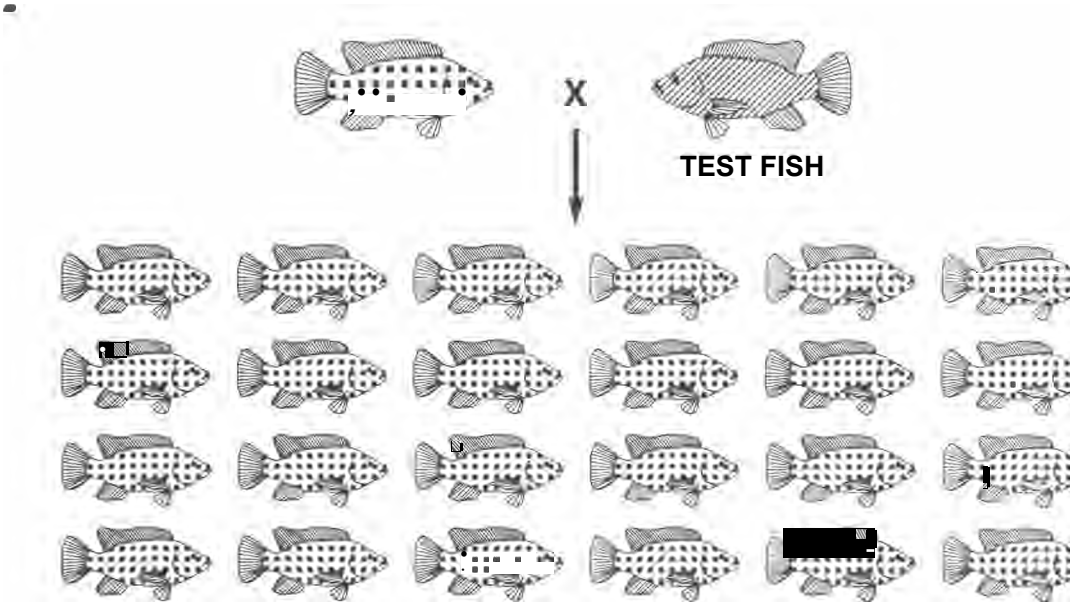
For example, a tilapia farmer that has a population of red and normally pigmented Nile tilapia can create a true-breeding red population by using progeny testing to identify and keep red fish that are homozygous (RR) and to identify and cull red fish that are heterozygous (Rr). Before initiating the progeny testing programme, the farmer will cull all normally pigmented fish except for the ones that he will use as test fish.

The farmer progeny tests the red fish by pairing a red fish with a test fish (in this case, normally pigmented tilapia are used as test fish since they are homozygous recessive rr). Red parents that are homozygotes (RR) will produce only red offspring and will be saved; red parents that are heterozygotes (Rr) will produce equal numbers of red and normally pigmented offspring and will be culled. After one generation of progeny testing, the farmer will have a select population of red brood fish that will breed true and produce only red offspring, because every select red brood fish is homozygous RR (Figure 15).

The same principle applies if the desired phenotype is controlled by two or more genotypes and the phenotype is controlled by more than one gene. For example, if a carp farmer has a population of common carp with all four scale patterns and decides to produce a true-breeding population of scaled common carp, he will have to use progeny testing to accomplish his goal. Scaled fish are produced by both the SS,nn and Ss,nn genotypes. In this case, fish with the mirror scale pattern are used as the test fish because they are homozygous recessive (ss,nn). Before initiating the progeny testing programme, the farmer will cull all fish with the line and leather phenotypes and most fish with the mirror phenotypes; he will keep a few fish with the mirror phenotype and use them as test fish.



CULL RED FISH. IT IS A HETEROZYGOTE *(Rr).*



KEEP RED FISH. IT IS A HOMOZYGOTE *(RR).*

Figure 15. Schematic diagram of the progeny testing programme that must be used to create a true-breeding population of red Nile tilapia. Progeny testing is used to identify and cull the heterozygous (Rr) red fish and to identify and save the homozygous (RR) red fish. A red fish's genotype is deciphered by mating it to a test fish (a normally pigmented fish [rr]), and by then determining the phenotypes of its offspring. In the top mating, the red fish is identified as a heterozygote (Rr) and is culled, because half of its offspring are normally pigmented. In the bottom mating, the red fish is considered to be a homozygote (RR) and is saved, because no normally pigmented fish was found in a random sample of a least 20 of its offspring. Progeny testing will create a population of select red brood fish that are all certified to be homozygous and such a population will breed true and produce only red offspring. Pictorial representations of the phenotypes are the same as those used in Figure 13.

Progeny testing is done to identify and save scaled fish that are homozygous at the S locus (SS,nn) and to identify and cull scaled fish that are heterozygous at the S locus (Ss,nn). If the scaled parent is homozygous at the S locus (SS,nn), all offspring will have the scaled phenotype; if the scaled parent is a heterozygote (Ss,nn), half the offspring will have the scaled phenotype and half will have the mirror phenotype. After one generation of progeny testing, the farmer will have a select population of scaled brood fish that are all SS,nn, and it will breed true and produce only scaled progeny (Figure 16).

When progeny testing, if the fish can be stripped, a single test fish can be used to progeny test a number of fish with the dominant phenotype. Additionally, it is not necessary to raise thousands of individuals from each family. A random sample of 100-200 fertilized eggs should be sufficient, if survival to the early fingerling stage is good. Consequently, progeny testing does not have to be expensive; it can be done in a small hatchery in aquaria, in small plastic swimming pools, or in hapas suspended in a single pond no larger than 0.04 ha. While the families are being raised, the dominant brood fish must be kept in isolated tanks or hapas so they can be saved or culled once the progeny are examined. Several fish can be kept in a tank or hapa if they are marked by fin clips. A single generation of progeny testing will create a true-breeding population, and it will not be needed again, unless fish carrying the undesired recessive allele are acquired from another farm or the allele arises by mutation.

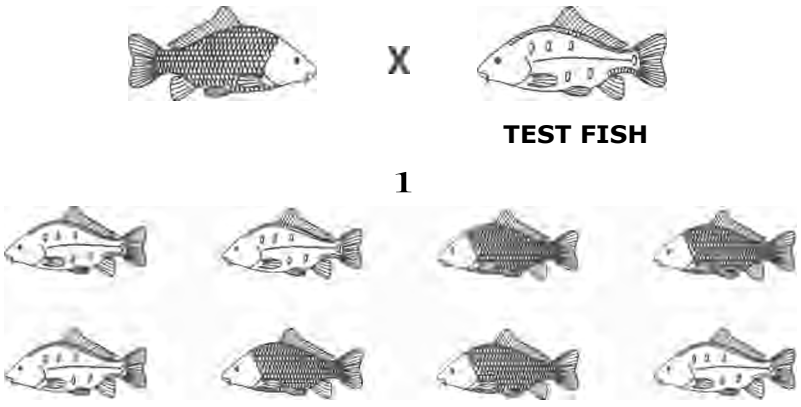
Selection for phenotypes controlled by heterozygous genotypes

If the heterozygous phenotype is desired, no breeding programme can be used produce a true-breeding population. This is because fish with the desired phenotype are unable to breed true. Heterozygotes produce two types of gametes and produce them in equal numbers. Consequently, when they mate, they produce offspring with three phenotypes (selection for the heterozygous phenotype can only be done for phenotypes controlled by autosomal genes with incomplete dominance or with additive gene action). A farmer who culls the two homozygous phenotypes and creates a select population containing only the heterozygous phenotype, will quickly discover that the selective breeding programme is a failure, because only half the offspring produced by the select brood fish will have the desired phenotype.

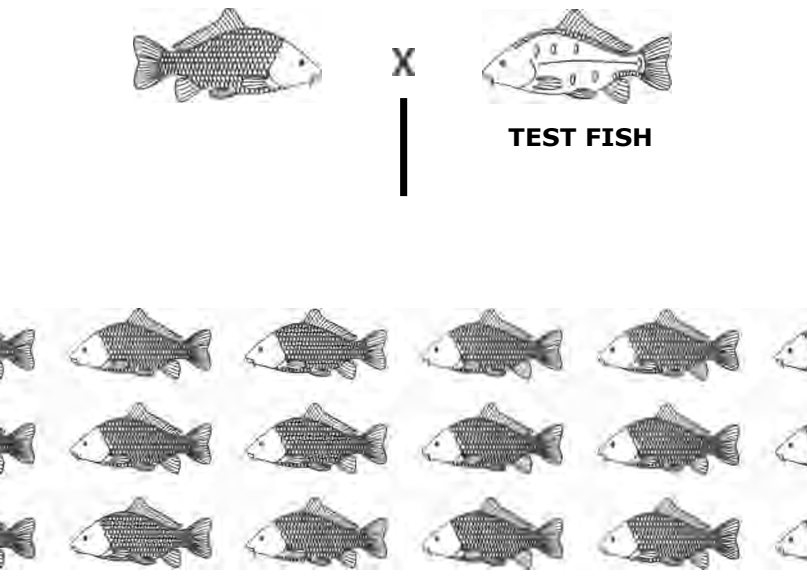
For example, if a tilapia farmer has black, bronze, and gold phenotypes in his population of Mozambique tilapia and decides to produce a true-breeding population of bronze fish, he will find that it is impossible. If he conducts a selective breeding programme, he will cull the gold (the recessive phenotype) and the black (the dominant phenotype) fish and will save the bronze ones (the heterozygotes). When he breeds the select population of bronze brood fish, they will produce offspring with all three phenotypes (Figure 17).

If the farmer wants to produce nothing but bronze fish, he must mate gold fish with black fish. This type of mating (the mating of the two homozygotes; it is illustrated in Figure 5c) will produce 100% heterozygous offspring (Figure 18).

The only requirement for this breeding programme is that the farmer must be able to accurately sex his fish. If the sex of a single fish is mis-identified, gold or black offspring will be produced. This type of mating scheme requires the use of at least two ponds (or tanks) for offspring production: one will be stocked with gold females and black males; the other will be stocked with black females and gold males.

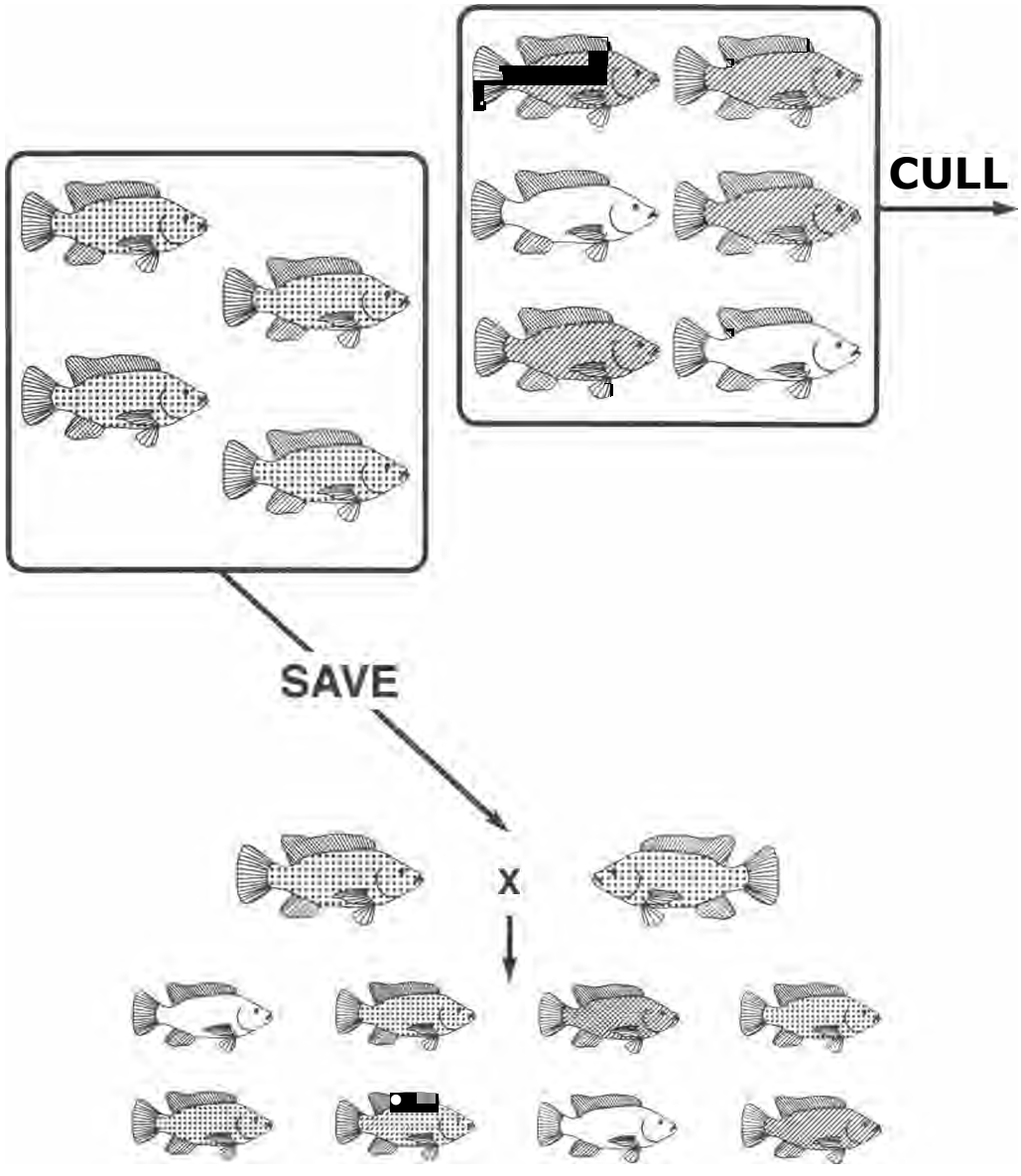


CULL SCALED FISH. IT IS A HETEROZYGOTE *(Ss, n n).*



KEEP SCALED FISH. IT IS A HOMOZYGOTE *(SS, n n).*

Figure 16. Schematic diagram of the progeny testing programme that must be used to create **a** true-breeding population of scaled common carp. Progeny testing is used to identify and cull the heterozygous (Ss,nn) scaled fish and to identify and save the homozygous (SS,nn) scaled fish. A scaled fish's genotype is deciphered by mating it to a test fish (a fish with the mirror phenotype [ss,nn]), and by then determining the phenotypes of its offspring. In the top mating, the scaled fish is identified as a heterozygote (Ss,nn) and is culled, because half of its progeny have the mirror phenotype. In the bottom mating, the scaled fish is considered to be a homozygote (SS,nn) and is saved, because no fish with the mirror phenotype was found in a random sample of at least 20 of its offspring. Progeny testing will create a select population of scaled brood fish that are all certified to be homozygous SS nn, and such a population will breed true and produce only scaled offspring.



SELECT POPULATION CANNOT BREED TRUE

Figure 17. Selective breeding programme used in an unsuccessful attempt to produce a true-breeding population of bronze Mozambique tilapia. In this case, both homozygotes--black (GG) and gold ( )--are culled, and the bronze (Gg) fish are saved. Because bronze fish are heterozygotes, the select population cannot breed true. Only half the progeny produced by the select brood fish will be bronze. Pictorial representations of body colour are the same as those used in Figure 4.

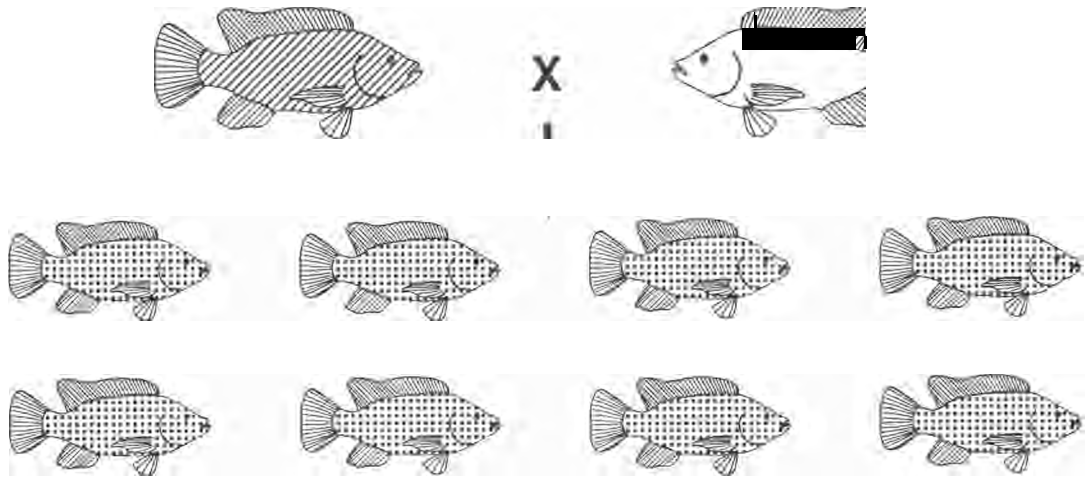


Figure 18. Breeding programme needed to produce 100% bronze Mozambique tilapia. A population of bronze (Gg) fish can be produced only by mating black (GG) fish with gold (gg) fish. If a farmer wants to grow only bronze fish, he must use this mating programme every breeding season. Pictorial representations of body colour are the same as those used in Figure 4.

Record keeping

When compared with the volume of records that must be kept when working with quantitative phenotypes, the types and amount of records that must be taken and maintained when working with qualitative phenotypes are minimal. One type of information that should be recorded is a description of abnormal or "mutant" phenotypes that are observed every year. Farmers' memories are not perfect, and they often feel that they saw more abnormal fish than really existed, simply because these fish are so unusual. A census of these phenotypes will tell a farmer what types of abnormalities have been produced and will also let him know if an abnormality is becoming a problem. These data will also provide a farmer with information about other qualitative phenotypes that exist in his population.

A farmer should have a data sheet on which he records the date, the name of the phenotype (a name can be invented if none exists), and a brief description of the phenotype. In addition, the number of fish that had this phenotype and the total number of fish that were produced should be recorded. This will let the farmer know the frequencies for each abnormality. If the frequencies begin to increase over time, the farmer will know that there is a potential problem. An example of this type of data sheet is presented in Table 7.

Table 7. Example of a data sheet that can be used to record abnormal and/or other qualitative phenotypes that are observed.

Date: March 23, 1995
Species: Nile tilapia
Number produced: 25,500

Phenotype	Description	Number	Frequency
Tail less	No tail; no caudal peduncle	3	0.000117
Semi-operculum	Right operculum short; gills partially exposed	5	0.000196
Stumpbody	Dwarf; trunk abnormally short	2	0.000078

If the farmer is going to conduct a selective breeding programme to fix a qualitative phenotype, he should record the date(s) on which selection occurred, the number of fish that were saved, the number of fish that were culled, and the pond(s) into which the select brood fish were stocked. When the select brood fish spawn, he should record whether they did or did not breed true. An example of this type of data sheet is presented in Table 8.

Table **8.** Example of a data sheet that can be used to record data from a selective breeding programme. In this case, a selective breeding programme that was used to produce a true-breeding population of gold Mozambique tilapia.

Date: June 1, 1995
Species: Mozambique tilapia
Breeding programme: Create a true-breeding gold population

Phenotype culled	**Number culled**
Black	456
Bronze	935
Phenotype saved	**Number saved**
Gold	204 females and 196 males

Did the population breed true?

Yes, on June 23, 1995, the select brood fish produced only gold offspring
Yes, on July 5, 1995, the select brood fish produced only gold offspring
Yes, on July 17, 1995, the select brood fish produced only gold offspring

If the farmer is going to conduct a progeny test, he should record the date on which each mating was made and the results of each mating. He should record whether he saved or culled a fish and should record *where* the select brood fish were stocked. When the select brood fish spawn, he should record whether they did or did not breed true. An example

of this type of data sheet is presented in Table 9. The farmer also must maintain records on where each fish and each family was held until the fish was either saved or culled during the progeny test.

Finally, if a farmer is going to produce heterozygotes for grow-out, he should record the ponds which contain each homozygote, the number of fish in each pond, and when they were stocked; the ponds/tanks where the fish are spawned; the number of brood fish that were spawned; and the results of the matings. An example of this type of data sheet is presented in Table 10.

Table 9. Example of a data sheet that can be used to record data from a progeny test. In this case, a progeny test to cull heterozygous (Rr) red fish and to save homozygous (RR) red fish in order to produce a true-breeding population of red Nile tilapia. Data on individual matings are given only for fish 1-5 in this example.

Dates: May 29-June 15, 1995
Species: Nile tilapia
Progeny test: Progeny test red fish to cull heterozygotes and to keep homozygotes. Normally pigmented fish were used as test fish.

Date	**Red brood fish**	**Progeny ratio (red:normal)**	**Cull/Save**
June 1	1	156:0	Save
June 1	2	73:70	Cull
June 1	3	did not spawn	Cull
June 2	4	75:0	Save
June 2	5	56:61	Cull

Total number of red fish saved: 75 females and 49 males
Did the select fish breed true?
Yes, on July 25, 1995, the select brood fish produced only red offspring
Yes, on July 31, 1995, the select brood fish produced only red offspring

Table **10.** Example of a data sheet that can be used to record data about a breeding programme that is used to produce heterozygotes for grow-out. In this case, a breeding programme that mates gold with black fish to produce an all-bronze population of Mozambique tilapia.

Date: July 25-August 1, 1995 Species: Mozambique tilapia
Breeding programme: Mating gold X black to produce 100% bronze

Phenotype	Date selected	Pond **No.**	**No. of males**	**No. of females**
Black	June 1, 1995	23	125	230
Gold	June 1, 1995	32	119	198

Table 10 (continued). Example data sheet.

Production of bronze fish

Date	Pond No.	Phenotype/sex	Phenotype/sex	Offspring
August 1	2	23 gold males	45 black females	8,300 bronze
August 1	3	50 gold females	30 black males	9,500 bronze
August 1	4	45 gold females	32 black males	10,300 bronze

Conclusion

The selective breeding programmes that were outlined in this chapter are not technically difficult and they require minimal record keeping. The breeding programmes needed to produce true-breeding populations are simple and, in most cases, can be conducted in a single breeding season. In some cases, they can be conducted in a single day. Once a true-breeding population is created, selection is finished. Even if a true-breeding population cannot be produced, a simple breeding programme can be designed to produce only the desired phenotype.

The selective breeding programmes that were outlined in this chapter have been used with important aquacultured species to produce populations with only the desired phenotype. For example: The undesired saddleback phenotype (deformed dorsal fin) in the Auburn University strain of blue tilapia was eliminated by a single act of selection, because it was produced by a dominant allele. State fisheries agencies in West Virginia and Pennsylvania (U.S.A.) use both selection and the mating of homozygotes to produce both golden (selection) and palomino (mating of homozygotes) rainbow trout for stocking in public waters. Many common carp farmers in Europe fixed the mirror scale pattern in their populations by culling all other scale phenotypes. Finally, ornamental fish farmers routinely conduct these types of breeding programmes to produce more valuable fish.

Prior to selection, a farmer or farmer cooperative should conduct an economic analysis to determine if a selective breeding programme should be conducted. Two pieces of information are needed: The first is the market values of the phenotypes. The second is the cost of production of the phenotypes, which will be determined by the pleiotropic effects, such as growth rate, survival, etc. If the results indicate that a farmer can increase his profits by fixing a prettier body colour, etc. then he should conduct a selective breeding programme. On the other hand, if the results indicate that increased production costs would exceed the increased market value of the crop, then the farmer should not conduct a selective breeding programme.

A farmer also needs to know when selection is unnecessary because the problem does not need to be corrected. All populations contain deformed individuals. In the wild, fish with deformities are generally eaten by predators, so the percentage of deformed fish that are observed is quite small. Fish farmers exclude predators from their ponds, so fish with deformities are more numerous, even though the incidence is still usually rare. Farmers often think that they have a problem because the odd-looking fish are very noticeable and they remember them. If the frequency of a deformity is less than one in 250 fish, the occurrence is probably not a problem that needs to be solved. On the other hand, if the deformity occurs in one out of every 100-200 fish, the problem should be investigated, and selection may be necessary if the deformity is heritable.

Finally, when a farmer conducts a selective breeding programme, he should save 100-200 select brood fish. The reason for saving this many fish is that a farmer should spawn at least 25 males and 25 females every breeding season. If this is done, he can prevent inbreeding from reaching levels that cause problems.

CHAPTER 4

Selection for quantitative phenotypes

Quantitative phenotypes are the important production traits, such as length, weight, feed conversion, and eggs/kg female. When working with these traits, a farmer does not separate fish into descriptive non-overlapping categories as he does with qualitative phenotypes (for example, red vs normally pigmented). Instead, each trait is a single phenotype (for example, length), and the differences among individuals are determined by measuring the fish. The numerical value that is assigned to a fish when it is measured is an individual's phenotypic value.

Because an individual's phenotypic value is determined by measurement (for example, length in millimeters) rather than by descriptive category (for example, colour), selection is based on numerical values rather than appearance. For example, when selecting for a qualitative phenotype such as colour, farmers select fish which have a specific colour, and cull fish which have another; the decision to select or cull fish is based solely on descriptive category. When selecting for a quantitative phenotype, farmers select fish that meet or exceed a specific numerical value, and cull those that do not; the decision to select or cull fish is based solely on numerical values.

Selective breeding programmes that work with qualitative phenotypes are designed to create true-breeding populations. They are simple programmes that are designed to eliminate an undesired allele and fix a desired allele so the population breeds true and produces only the desired phenotype. This can usually be accomplished in a single generation (often by a single day of selection), and once this is accomplished, the farmer's goal has been achieved and the breeding programme is over.

In contrast, selective breeding programmes that are used to improve quantitative phenotypes are more sophisticated than those that are used to fix qualitative phenotypes. They require a higher level of technology and record keeping. Furthermore, they are open-ended in that they continue year after year, because it is not possible to produce true-breeding populations for these phenotypes. Instead, these programmes are designed to gradually improve the population's mean each generation. It is important to realize the fact that selective breeding programmes that work with quantitative phenotypes are never finished, and it is also important to strive for small but gradual improvements over many generations. It is possible to achieve huge improvements over the first one or two generations, but this can be accomplished only by severely reducing the size of the breeding population, which can result in inbreeding depression, and this could counteract much of the gains that were made by selection.

Another reason selective breeding programmes that are used to improve quantitative traits are open-ended is because if they are abandoned, much of the gain that was realized will be lost. It is difficult to predict how much gain will be lost if a programme is abandoned; that depends on the trait, the heritability, and the population. If the phenotype is controlled solely by additive genetic variance ($h^2 = 1.0$), the mean will stay the same if the breeding programme is abandoned. However, no important production phenotype is controlled solely by additive genetic variance (Table 6). If a selective breeding programme is abandoned, much of the gain will be lost, because most of the gain due to dominance genetic variance, all of the gain due to epistatic genetic variance, and some of the gain due

to genetic-environmental interactions will also be lost. Some of the gain due to additive genetic variance will remain, but the exact amount is difficult to predict.

If selective breeding greatly improved the population before the programme was abandoned, the mean might stabilize at a level recognizably greater than the original mean. However, if the gain was small, which is probably the case, the final mean might be only marginally greater than the original mean, and the difference might be obscured by yearly environmental effects.

Factors that must be considered before conducting selective breeding programmes

Before initiating a selective breeding programme, a farmer must ask the following question: Is a selective breeding programme appropriate or necessary? The answer to this question depends on individual circumstances. The answer can even be different for neighbouring farmers.

The decision to conduct or not to conduct a selective breeding programme must be made at the individual level; it should never be made on a region-wide basis. There is a tendency by extension agents to try and get all farmers in their region to adopt new technologies. On an intellectual level, this makes sense because the extension agent knows that if every farmer adopts the new technologies, production will increase; farmers will get richer; and there will be more food.

The adoption of a selective breeding programme, like any aspect of technology, should be made only on a case-by-case basis. For the most part, the adoption of a selective breeding programme should be restricted to farmers who are capable of keeping and maintaining records, who are good managers, who adopt and maintain new technologies, and who are willing to incorporate some long-term planning into their management programmes. Finally, these farmers must be willing to spend the extra time that it takes to conduct a selective breeding programme and must also be willing to spend the money that it takes to conduct a programme.

Some farmers will never use nor should they be encouraged to use selection. These farmers are those that have small farms or that produce fish for only one or several families or perhaps for a small village. Farmers who do not have the expertise to keep good records or who do not have a sufficient number of ponds to devote to a breeding programme or who are unable or unwilling to spend money on a breeding programme should not attempt one or even be encouraged to attempt one.

A selective breeding programme is designed to improve productivity over generations (a generation is the replacement of brood fish by their offspring). It is designed to increase growth rates and yields gradually over many years. If a farmer cannot incorporate long-term (1-10 years) planning into his fish farming programme, he will abandon his selective breeding programme within months and will then discourage other farmers from initiating a selective breeding programme by telling them that selective breeding programmes do not work.

Farmers who cannot keep good records because they cannot read or write or who do not know how to measure fish are not good candidates to become breeders and conduct a selective breeding programme. In general, these types of farmers will not be able to conduct a successful breeding programme. On the other hand, if they are reliable farmers who work hard and who accept and adopt new technologies, they can initiate a selective breeding programme if an extension agent is willing to work closely with them and assume the responsibility for keeping records and for conducting much of the labour involved in the breeding programme.

Finally, farmers who are poor managers should never conduct a selective breeding programme. Farmers who seldom check their ponds, who feed the fish or manure the ponds only when they are reminded by the extension agent, or who make little effort to increase yields should not conduct a selective breeding programme. Farmers who cannot or who are unable to properly manage a fish pond are not going to be able to properly manage a selective breeding programme.

The major goal of most selective breeding programmes that are going to be used to improve quantitative phenotypes is to improve growth rate. This will also increase yield.

There are two basic approaches to improving yields: One is to use a breeding programme to improve the fish that are being cultured. The other is to improve the way the fish are being raised. Breeding programmes are expensive, while improvements in management are often inexpensive.

Consequently, if increases in growth rate and yield can be easily gained by alterations in management techniques or by the adoption of new management techniques, farmers should use this approach first. This approach can include the proper use of fertilizers or lime, stocking fish at the most appropriate density, stocking larger fingerlings in grow-out ponds, or feeding fish a prepared ration.

The major reason why the first approach to increasing yields and growth rates is to use better management is that it is usually cheaper and the results are immediate. Yields can often double or triple if ponds are fertilized properly or if fish are fed. The increase in yield that occurs because of fertilization or feeding can be realized during the first growing season and during the first harvest. Yields will increase as a result of a selective breeding programme, but the increase will be gradual and it will be over many years. For this reason alone, the first approach to improving productivity should be to improve management skills and to improve the way the fish are grown.

Additionally, you do not want to initiate a selective breeding programme and then change the way the fish are cultured after the programme has begun. When you select for quantitative phenotypes, you select for them as they are expressed under a specific set of culture conditions. The fish that perform best under high stocking rates in manured ponds may not be the ones that perform best under lower stocking rates when the fish are fed a prepared ration. When you select for the fastest growing fish under one set of culture conditions you are selecting for fish that contain genes that enable the fish to perform best under those conditions. Consequently, if you change the way the fish are raised, you may have already culled the genes that perform well under the new management programme.

Thus, it is important to determine if the management programme that is being used to produce fish at a given farm is that which will be used in the future. Small changes, such

as changing the stocking rate in grow-out ponds from 2,000/ha to 2,500/ha or increasing the mean size of fingerlings that are stocked from 10 g to 15 g, are probably not that important; but large changes, such as changing from manure as the sole source of nutrients to a high-quality pelleted ration, are major alterations in management. If major changes are planned or are likely, then selective breeding programmes should be postponed.

Culture techniques in a region do not have to be standardized before selective breeding programmes are initiated. Some farmers may want to culture fish using fertilizers rather than pelleted feed because they have abundant and cheap sources of manures; others may want to use pelleted rations to maximize yields. Selective breeding programmes can be designed for both types of farmers, if they are willing to devote the time and money to conduct the programme and if they can devote sufficient pond space for the programme.

When should a selective breeding programme be initiated? A programme should be initiated only when the farmer decides he is willing to devote the time and effort that will be needed to ensure its success. Farmers who do not want to devote the effort either in terms of manpower or money or who are likely to abandon the project after the initial excitement wears off should not start a selective breeding programme.

Some farmers may be interested in a selective breeding programme but say that they will start one only after they solve all other problems. This means that they will never conduct a selective breeding programme, because all other problems will never be solved. Every time one problem is solved, another roadblock to increased production appears.

A selective breeding programme should begin when a farmer is willing to spend the time and money needed to conduct one, because he is convinced that such an undertaking is a way of increasing both food production and profits, and because he also realizes that these increased yields and profits are long-term goals. Finally, a farmer must also recognize that selective breeding programmes are open-ended, in that further improvements are always possible.

Before a farmer embarks on a selective breeding programme he must conduct an assessment to determine its usefulness; he needs to quantify his goals; he needs to know how the phenotype(s) will be measured; he needs to determine the type of selective breeding programme he will use; he needs to know how the results will be evaluated; and he must plan an annual evaluation and reassessment of the programme. A farmer can do this by himself or in consultation with extension agents.

The first step is to determine whether the programme is needed. Promoters often convince farmers that they need to make changes when none was needed. A salesman may have been impressed with the body shape of a fish that he saw in another province and feels that it would be a great idea if farmers would select for that body shape. If consumers truly desire that body shape and market surveys bear this out, then a farmer should consider a selective breeding programme to alter body shape. But if local consumers do not care and if there is no demand for the altered body shape, then the programme should not be initiated. Frivolous breeding programmes are a waste of money and manpower and may be counterproductive. The farmer must always consider what the consumer wants and what the consumer is willing to pay for when he initiates a selective breeding programme.

Another part of the assessment is to determine what traits should undergo selection. A farmer should prepare a wish list of all traits that he would like to improve. Once created, the list should then be pared to a handful of traits that make sense, in terms of the culture of the fish and its marketing. Some traits, like body weight, will be included in almost every selective breeding programme. Other traits that can make the initial cut are those that a farmer would like to improve, simply because they would make fish farming less risky or easier, such as increased disease resistance or increased catchability.

Some traits are totally unnecessary and should be eliminated immediately. A fish processing plant may want farmers to improve dressing percentage or to decrease visceral fat content because it will improve profits for the plant owners. But unless the plant owners are willing to pay more for fish with a better dressing percentage or with less fat, these traits should not be incorporated into a selective breeding programme.

Farmers should also eliminate some traits that are more easily improved by management. For example, it make little sense to use selective breeding to increase fecundity, because it is much easier and far less expensive to increase egg production by altering hatchery management. It also makes little sense because most fish are already highly fecund. Improving egg production from 4,000 eggs/kg female to 4,500 eggs/kg female is really not that important, and it is not necessary. If a farmer wants to produce more eggs, all he has to do is spawn more females or spawn larger females. Improving egg production via selective breeding is expensive, and an increase in egg production will not occur for at least one generation. On the other hand, improving egg production by altering hatchery management is inexpensive, and the increase is immediate.

Farmers should try to improve only the major phenotypes that improve profits--either because the fish grow faster, grow more efficiently, or survive better or because consumers are willing to pay more for them.

Hatchery managers who work at fingerling production centers might consider selecting for traits which could improve an industry or open new area to fish farming. For example: increasing salinity tolerance might enable fish farmers to grow fish in thousands of hectares of brackish water ponds; selection for earlier spawning date might enable farmers either to produce marketable sized fish in one growing season rather than two or to produce larger fish which command a premium price.

A second aspect of the assessment should be to decide whether the farmer is going to produce genetically improved fingerlings solely for his own use or whether he will become a fingerling farmer and produce genetically improved fish for a local fish farming industry. This decision determines how much money must be spent on the programme and the scope of the programme. If a farmer is going to produce genetically improved fish only for his own use, he needs to use only a portion of his farm for the project. On the other hand, a farmer who wants to produce genetically improved fingerlings for the local fish farming industry may need to use most, if not all, of his farm for this project.

One of the major purposes of reducing the wish list down to a few phenotypes is that the efficiency by which a trait can be improved is inversely related to the number of phenotypes that are incorporated into the selective breeding programme. Consequently, if one or two phenotypes are far more important than the others, the list should include only the one or two most important ones. The inclusion of traits that are not crucial will slow down the rate of improvement for the important ones. For this reason, most selective breeding programmes should try to improve only one or two phenotypes. Some

programmes may include a third trait; few should incorporate more than that, and the only ones that should are those conducted by geneticists at research stations.

Once a farmer has pared his wish list to the one or two phenotypes that he would like to improve, he needs to determine how they will be defined and measured. Goals that cannot be precisely defined and phenotypes which are difficult to measure should be dropped. For example, every farmer wants to improve disease resistance, but what is disease resistance? Some may define it as "fish that do not get sick," while others may define it as "fish that do not die." There is a great difference in these definitions. If you define the trait as "does not get sick," what does that mean? Does this mean that the fish were infected but exhibited no clinical signs of the disease, or does it mean that they never were infected? If the fish are grown in a pond, how will you be able to tell which fish were infected and which were not? Even "does not die" is not that precise, because so many variables enter into health management. Fish can die from non-infectious sources during a disease outbreak or over the course of a growing season. Because this trait is difficult to measure, it is a trait that should probably be avoided by most farmers. Furthermore, if resistance to a particular disease is heritable, it will be improved over time by what is called "domestication selection." Domestication is the process by which the farm and the farmer's management selects for or against genes as a natural consequence of farming. Consequently, disease resistance is a trait that should be removed from most farmer's lists. Some advances are being made in selection for disease resistance; however, these breeding programmes are complicated and should be conducted by scientists at research stations.

Other traits that must be pared are those that a farmer wants to improve but that are difficult to measure because of the way the fish are raised. Farmers that feed fish with a pelleted ration want to improve feed conversion because, if this trait can be improved, the fish will convert feed more efficiently, which means that yields and profits will soar. But how does one determine feed conversions for individual fish? This can be accomplished only by raising fish in individual tanks or hapas, which would be prohibitively expensive. A farmer could use family selection to improve this trait, if he were able to raise dozens of families in hapas. Such a programme would be expensive, and improving feed conversion is not as important as improving growth rate. If they are needed, the development of selective breeding programmes to improve feed conversion should be left to geneticists who work at research stations.

Even traits that every farmer wants to improve and that will be incorporated into a selective breeding programme need to be accurately defined and measured. Every farmer wants to improve growth, but how should it be defined and how will it be measured? This is important, because it will determine the rate of progress that can be made via selection. Growth rate is usually defined as weight or as length at a given age, so the first question that must be answered is: Should growth be defined as weight or as length?

It is easy to accurately measure hundreds of fish to the nearest millimeter, and the fish are minimally stressed during the process. However, length includes head length and tail length. Fish with an overly long tail could be selected over heavier fish, and consumers buy their fish by the kilogram, not by the centimeter. Weight more accurately reflects how fish are bought and sold, but it is difficult to accurately weigh hundreds of fish to the nearest 0.1 g. Unless the farmer has access to an electronic scale, the process can be very tedious, and it often stresses the fish. Furthermore, the weight recorded for each fish includes water in the fish's mouth, faeces and food in its digestive tract, and head and viscera weight, so it too is subject to error.

Although it would be best to measure growth as weight, a large correlation exists between length and weight (the two are highly related--an increase in one means there is an increase in the other), so assessing growth by measuring length is a good approximation of assessing growth by measuring body weight. If a farmer wants to remove some of the error that can occur when growth is assessed by measuring length, he could take standard lengths instead of total length, which would negate the effect of tail length on selection.

If more than one person is going to measure fish, a standard method for measuring them must be determined and worked out in advance so that everyone will provide uniform measurements. Otherwise, the phenotypic values assigned to the fish (lengths) will be subject to human error. If only one person will measure the fish, the only requirement is that he measure all fish using the same technique.

If weight is improved by selection for length, weight is said to have been improved by "indirect selection." This occurs because the two phenotypes are positively correlated (related genetically), so improving one will automatically improve the other. Because of this, selection to improve growth rate can often improve other traits, such as survival, disease resistance, and feed conversion. Breeders often exploit genetic correlations and use indirect selection to improve phenotypes that are difficult or expensive to measure by selecting for more easily measured phenotypes. For example, harvest weight in rainbow trout has been improved via indirect selection by selecting for fingerling weight; selective breeding programmes are being conducted to improve disease resistance via indirect selection by selecting for stress response or for cell membrane strength.

Another question that must be answered before growth rate can be improved is: At what age will growth be assessed? Fish growth is not constant. If it were, the age at which the measurement was taken would be relatively unimportant. It makes sense to measure fish when they are normally moved or harvested. For example, fish can be measured when they are transferred from fingerling ponds to grow-out ponds and when they are harvested for market. This is usually defined as measurement at a specific age. After a number of generations of selection, it might be defined as the time needed to reach market size. If fish are measured and selected at two ages instead of one, growth rate will be improved more rapidly.

The ability to precisely define the goal and to accurately measure the phenotype is crucial. If a farmer cannot perform these tasks, he should not conduct a selective breeding programme. If he conducts a selective breeding programme using imprecisely defined goals and measures the phenotype inaccurately, his breeding programme can decrease growth rate and may also prevent future improvements by culling the truly valuable alleles.

For example, selection for growth rate in some populations of Indian carps produced slower-growing fish because growth rate was imprecisely defined and measured inaccurately. These carps were cultured using a production system called "multiple batch" production. When this form of management is used, a pond is seined many times over a several-year period to continually remove market-sized fish. Fingerlings are often stocked in the pond to replace fish that are removed to ensure that fish can be continually harvested. After several years of continual production, the pond is drained because large fish that have escaped the repeated seinings adversely affect production.

When these carp ponds were drained, farmers and hatchery personnel saved the largest fish, because they defined growth rate as body size at draining, and measured it only when

a multiple batch production pond was drained. Additionally, they saved these fish because they would produce more eggs than smaller brood fish.

Unfortunately, their definition of growth rate and the way the trait was measured (size when the ponds were drained) produced a selective breeding programme that reduced growth rate, because the select fish were actually the oldest fish and were are also slow-growing fish. They were the largest fish when the ponds were drained simply because they were experts at escaping a seine. Not only did this selective breeding programme produce shower-growing fish, it also selected for fish that were escape artists.

Once a farmer has quantified his goals and has determined how the phenotypes will be measured, he needs to determine what type of selective breeding programme he will use to achieve his goal. There are two basic types of selective breeding programmes: individual selection (also called "mass selection") and family selection. In individual selection, family relationships are ignored, and comparisons are made among individuals. Individual fish are ranked in order, and the best become the select brood fish. In family selection, family relationships are of paramount important, and either family means are compared and ranked and whole families are either saved or culled, or individual rankings are made within each family and selection occurs independently within each family. The most efficient breeding programme is determined by the phenotype and how it will be measured, the biology of the fish, and by the trait's heritability. Individual and family selection will be discussed in greater detail later in this chapter.

A farmer needs to outline the plan he will use to achieve his goal. This includes the number of fish that will be spawned, the number of fish in each family that will be raised, the number of ponds that will be stocked, the stocking density, and the management programme that will be used to culture the fish.

Selective breeding programmes are expensive, so it is important to be able to accurately assess the effects of selection. The best way to determine this is to compare the phenotype's mean over time. To do this properly, the mean of the select population must be compared to that from an unselected control population. The reason the select population must be compared to a control population is that the mean is determined by both the population's genome (which you are trying to improve via selection) and by the environment. Techniques that are needed to create a control population and the way it is used to assess the results of selection will be discussed in a later section of this chapter.

Finally, a farmer must review his selective breeding programme at least once a year. He must evaluate how it is progressing and determine if there are ways to improve the programme. Conversely, he may decide to end the programme if the results indicate that the programme is not working or if the results are not worth the effort. Farmers often want to end one selective breeding programme and start another when they get frustrated, but this type of decision should be discouraged. If a farmer changes programmes every year or two, all he will do is spend money and accomplish nothing. On the other hand, if the programme is not working, it would be foolish to persist and spend money needlessly.

Individual selection

Once a farmer has decided to improve a quantitative phenotype by selection, he must choose the type of selective breeding programme that will be most efficient. There are two major types of selective breeding programmes: individual selection and family selection. Individual selection is simpler, requires less record keeping, and is less expensive.

In individual selection, all individuals are measured, and the decision to select or to cull a fish is based solely on that fish's phenotypic value. Each fish is compared to a value called the "cut-off value," and fish whose phenotypic value is equal to or larger than the cut-off value are saved, while fish whose phenotypic value is smaller than the cut-off value are culled. The cut-off value is a pre-determined phenotypic value that is often expressed as the "top 10%" or "top 5%" or whatever value is desired. Fish that are saved become the first generation (F_1) of select brood fish. The cut-off value and how it is determined is discussed in a later section of this chapter.

When the first generation of select brood fish are spawned, they produce the first generation of select fish, which is called the "F_1 generation"; their offspring, in turn, are called the "F_2 generation," etc. When a farmer spawns the select brood fish he should allow them to mate among themselves at random or should pair them in a random manner, unless he wants to select for post-market growth rate or for maturity-related phenotypes. This process is then repeated in succeeding generations (Figure 19).

Environmental effects that must be controlled

Environmental variables have a significant influence on the production of quantitative phenotypes. Even when a phenotype has a large heritability, the environmental component of phenotypic variance can be larger than the heritable component. If the environmental influence on phenotypic variance were the same for all fish, it would be of minimal concern during selection, as long as there is sufficient heritable variance to enable selection to work. Unfortunately, many sources of environmental variance have a differential effect on individuals or families and, when selection is used, a farmer must control these environmental variables or they will give some individuals or families an advantage. If this occurs, the select brood fish may be better because of an environmental advantage, not because they are genetically superior. If this happens, selection will not work.

For example, older fish are usually the largest fish in a population because they have had more growing days. It has been shown that an age difference as small as 24 hours can give the older fish a size advantage that they never relinquish, which means that selection will choose the older fish, not the genetically superior fish; consequently, if age-related size differences are not controlled, a selective breeding programme that is trying to improve growth rate would actually be trying to improve it by exploiting environmental variance (age) rather than additive genetic variance, and the programme would be a failure. Thus, if it is possible, all fish should be spawned on the same day. If this is not possible, then the population should be split into cohorts of equal-aged fish, and selection can occur independently in each cohort. After selection, the select brood fish from each cohort can be mixed.

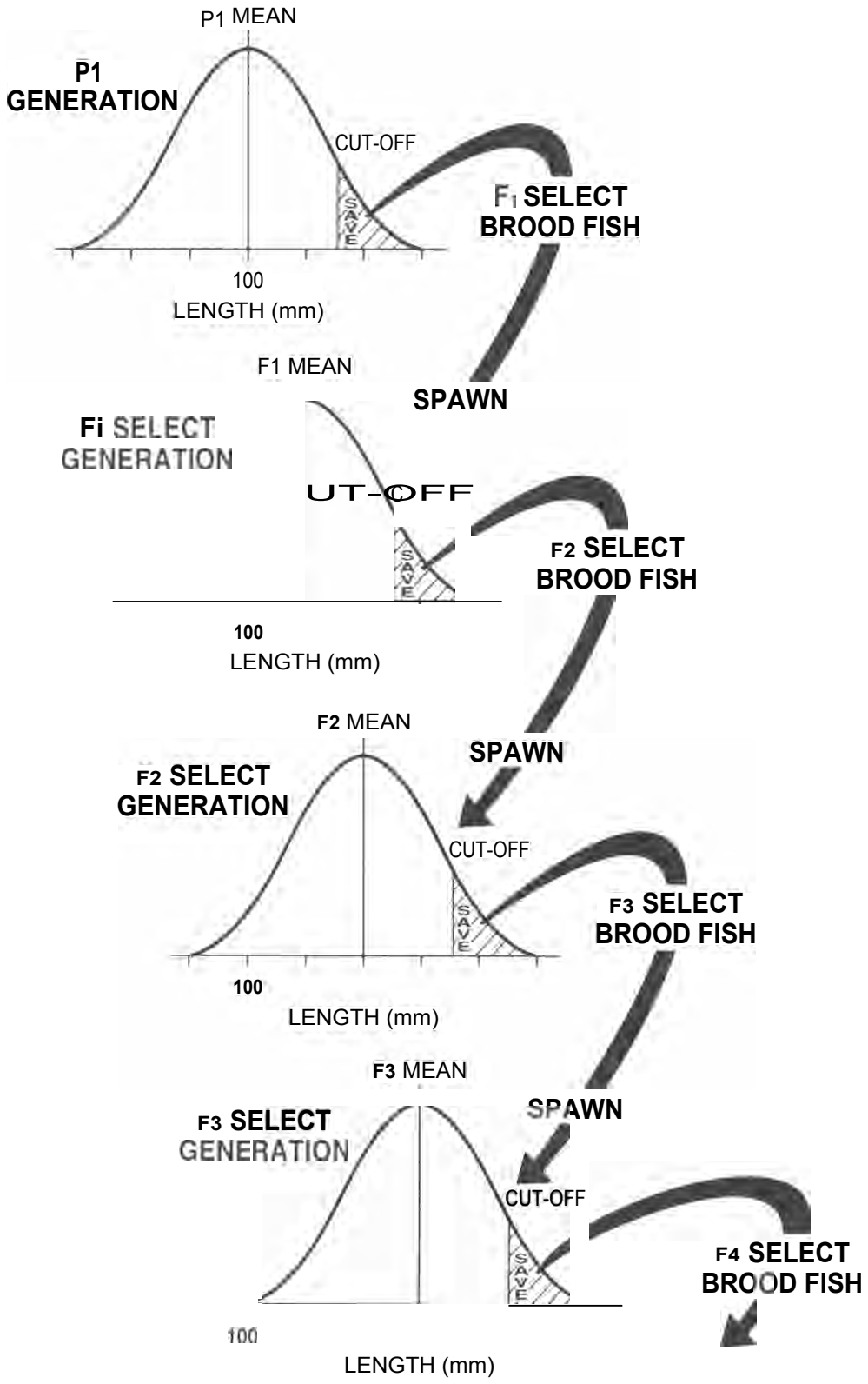


Figure 1 9. Schematic diagram of individual selection to improve growth rate by selecting for increased length. The figure shows four generations of selection and shows how length can be improved over time.

Other factors that need to be controlled are female age and female size and management differences among the fingerling or the grow-out ponds. For example, if each family is stocked in a single pond, individual selection will be unable to differentiate the fish that are largest because they are genetically superior from those that are largest because they were grown at the lowest density or had the most food. If a farmer does not control these variables, the largest fish may all come from one family, and they may be largest because of environmental variance. If this is the case, no progress can be made by selection.

Even seemingly insignificant environmental variables such as feed particle size can be a major sources of phenotypic variance. Studies with common carp have shown that if feed particles are improperly sized, some individuals will grow significantly faster than the rest of the population; the size advantage that these fish have is not exploitable in a breeding programme, because it is an environmental advantage, not a heritable one.

When conducting a selective breeding programme, a farmer must control all environmental factors that can give individuals or families an advantage. If these variables are not controlled, selection will either be less effective than it is for others who are conducting similar programmes or it will not work. Since selective breeding programmes require considerable effort and time, the inability to control these variables will be costly.

Cut-off

In order to create a population of select brood fish, a farmer needs to decide where to place the cut-off value. This is usually expressed as a percentage, such as the top 10%. It can be expressed as a minimum size, such as 500.0 g, but this can be risky if no fish reaches the cut-off value during a bad year.

A cut-off value is usually determined just before selection will occur, and it is usually based on saving a pre-determined percentage of the population. The easiest way to determine the cut-off value and the least stressful for the fish is to measure a random sample of 1 00-200 fish. Once these measurements are determined, they are ranked, and the value that corresponds to the desired percentile is the cut-off value. For example, if the top 10% will be saved, the cut-off value is the 90th percentile. If 200 fish are measured, you simply count down 20 measurements from the largest phenotypic value after they have been ranked and that value is the cut-off value (Figure 20).

Sexual dimorphism: One final refinement of the selection process is necessary. A farmer must determine if selection will be conducted in the population as a whole or separately in both sexes. This is an important decision, because many species exhibit sexual dimorphism in that one sex grows to a larger size or grows faster. If the species does not exhibit sexual dimorphism or if selection will occur before sexual dimorphism begins, then a single cut-off value can be created for the entire population. If the species exhibits sexual dimorphism, separate cut-off values must be created for each sex, or the select population may be composed of only the larger sex (Figure 21).

Many species exhibit sexual dimorphism for body size. All important cultured species of tilapia exhibit pronounced sexual dimorphism. After tilapia are a few months old, males grow much faster than females, and can be twice as large after 1 year. This is why tilapia farmers want to grow all-male populations rather than all-female populations in their effort to control reproduction. Common carp and Chinese carps also exhibit sexual dimorphism for body size, in that the females grow to a larger size; however, the size difference in

carps does not appear until after maturity, whithimeans that selection for pre-maturity growth rate in carps requires only a single cut-off value.

Length (mm)	No. Fish	Length (mm)	No. Fish	Length (mm)	No. Fish
160	I	173	NNN	186	III
161	II	174	I II	187	N
162	N	175	N NI	188	IIII
163	NI	176	NN	189	HI
164	III	177	N I	190	III
165	N	178	ℕ IIII	191	HI
166	ℕ III	179	ℕ N	192	H
167	NI	180	NII	193	HI
168	NIII	181	NNI	194	II
169	NIII	182	NIII	195	I
170	ℕ ℕ I	183	Nor	196	II
171	NNIII	184	ℕ I	197	I
172	ℕ ℕ ℕ IIII	185	ℕ	198	I

50th Fish

Figure 20. A quick and simple way to determine a cut-off value. The goal of this selective breeding programme is to increase 10-month length by selecting the top 20% of the population. To determine the length that corresponds to the 80th percentile, a sample of 250 ten-month-old fish was obtained from a pond that was stocked with 5,000 fish that were produced on the same day. Each fish in the sample was measured to the nearest millimeter, and the phenotypic values were entered onto this data sheet. The cut-off value was determined by counting down from the largest fish (198 mm) to find the fish that corresponds to the 80th percentile. Because the goal is to select the top 20%, the length of the 50th fish will give the cut-off value (50 fish is 20% of 250 fish). The 50th fish has a value of 183 mm, so the cut-off is 183 mm. Fish > 183 mm will be saved and will become the select brood fish, while fish < 183 mm will be culled.

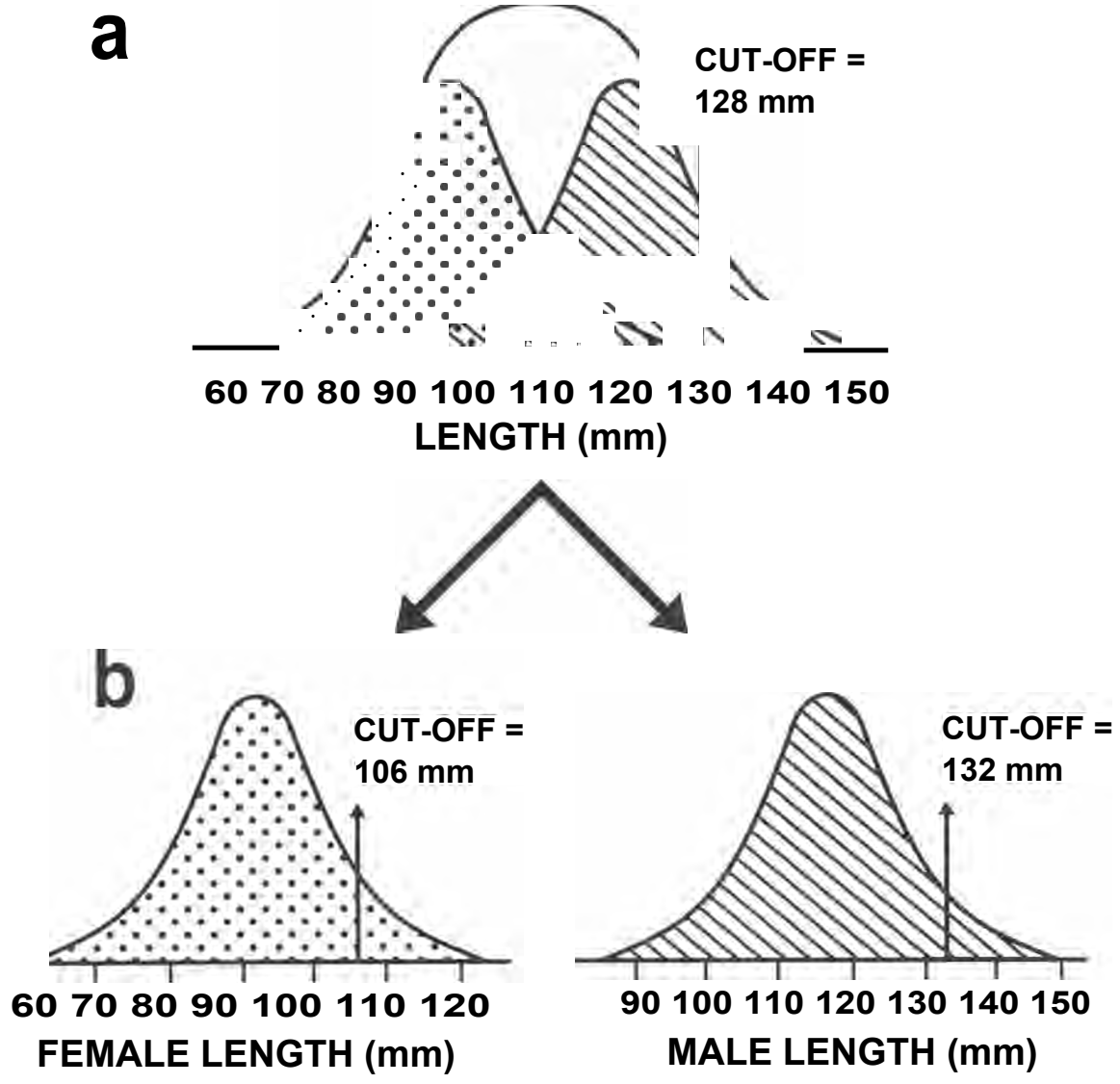


Figure 21. The effect of sexual dimorphism on selection for size. Graph a shows length distribution in a population of fish where males grow to a larger size than females: the length distribution of males in the population is shown by the striped graph, and that exhibited by the females is shown by the dotted graph. In graph a, a single cut-off value (128 mm) was used in a selective breeding programme to improve length. Because of sexual dimorphism, all select brood fish were males. This means the farmer either will be unable to produce any offspring or will have to obtain and spawn unselected females. Graph b shows how selection should occur in species that exhibit sexual dimorphism. Separate cut-off values must be determined for each sex, and selection must occur independently for males and for females. Graph b shows that the farmer selected the best males by establishing a male cut-off value of 132 mm and selected the best females by establishing a female cut-off value of 106 mm.

If selection will be conducted independently in the two sexes because of sexual dimorphism, the procedure that was outlined to determine a cut-off value (Figure 20) must be conducted separately for males and for females. If selection will be conducted for each of several cohorts the process needs to be conducted within each cohort.

Selection for more than one phenotype

In general, the easiest and usually the most efficient programme is one that selects for a single phenotype. As was mentioned previously, the efficiency with which each phenotype can be improved is inversely related to the number of phenotypes that are incorporated into a selective breeding programme.

If a farmer wants to improve more than one phenotype, he can use either tandem selection, independent culling, or a selection index. Tandem selection is inefficient, and it is not recommended. A selection index is too sophisticated for most farmers, but aquaculturists who work at research stations and hatchery managers who work at fingerling production centers might wish to use it. Farmers who wish to select for two, or at most three, phenotypes should use independent culling.

Tandem selection: In tandem selection, you first spend several generations selecting for one phenotype; you then stop selecting for that trait, and start a new breeding programme and select for the second phenotype. Basically, this is a two-step selective breeding programme designed to first improve one phenotype, and after a while you quit and suddenly change directions and begin a second selective breeding programme to improve another phenotype. If improving the first phenotype is important and if the selective breeding programme is working, it would be foolish to abandon it. For this reason and also because it takes so long to try and improve two phenotypes using this back-to-back procedure, tandem selection should not be used if a farmer wants to improve two or more traits. It is very inefficient.

Independent culling: Independent culling is probably the easiest selective breeding programme that a farmer can use to improve two or three phenotypes. Independent culling is a breeding programme where a farmer selects simultaneously for two or more phenotypes by establishing cut-off values for each phenotype independent of the other(s), and each fish must reach or exceed all cut-off values in order to be saved. A fish which fails one cut-off value is culled. This type of breeding programme is illustrated in Figure 22.

For example, say a farmer wants to improve both growth rate, by selecting for length, and body conformation, by selecting for body depth at the first dorsal fin spine. The procedure that is used to establish the cut-off values is the same as that outlined earlier. The farmer will either establish pre-determined phenotypic values or will select the top 10% or top 20%, etc. If he establishes pre-determined percentiles, he determines the cut-off values that correspond to these percentiles by measuring a random sample of 100-200 fish and by discovering what those values are, as was illustrated in Figure 20. In this example, the farmer has established cut-off values of 243 mm for length and 130 mm for body depth at the first dorsal fin spine. Once both cut-off values are established, the farmer measures each fish, and only those that meet or exceed both cut-off values will be saved. In this breeding programme, the decision to save or to cull these six fish will be:

Fish	Length (mm)	Depth (mm)	Save/Cull
1	254	129	cull
2	243	130	save
3	241	138	cull
4	240	120	cull
5	280	129	cull
6	250	131	save

Although independent culling is more efficient than tandem selection and it is easy to conduct, this type of breeding programme has two liabilities. The first is that when you select simultaneously and independently for two phenotypes, you could end up with very few select fish. For example, if you select for two phenotypes and the cut-off value is the top 10% for both traits, only 1% of the population will be saved (0.1 x 0.1 = 0.01). If you add a third phenotype and the cut-off value for it is also at that level, only one fish out of every thousand will be saved. The severity of this type of selection can be seen in Figure 22.

The severe restriction in the number of fish that are able to meet or exceed all cut-off values can lead to two problems: If this occurs, you may not be able to produce enough select fingerlings for grow-out the following season. Even worse, high levels of inbreeding could be produced after 1-2 generations, which could negate much of the gains made by selection.

The problem created by independent cut-off values can be solved by deciding in advance how severe selection will be; that is, what percentage of fish will be selected. Once this is determined, you back-calculate the cut-off percentages that are needed to produce this value. For example, if you want to retain 15% of the population and will select for two equally important phenotypes, simply take the square root of 0.15, and that tells you to select the top 39% for both phenotypes (0.39 x 0.39 = 0.15). If you want to put more emphasis on one phenotype, simply establish a higher cut-off value (in terms of percentiles) for that trait and then adjust the cut-off value for the second downwards. For example, if you want to save 10% of the population, you can have the cut-off values at the 25th and 40th percentiles for two phenotypes (0.4 x 0.25 = 0.1).

A second draw-back that occurs as a result of independent culling is the fact that you must cull fish that are outstanding in one phenotype. For example, fish number 5 in the example given above was culled despite the fact that it far exceeded the length cut-off value. This problem can be circumvented by using modified independent culling. In modified independent culling, fish that meet or exceed both cut-off values are saved, and fish that exceed one cut-off value but that are just under the cut-off value for the second phenotype are also saved (Figure 23).

Because of the ease with which they can be conducted and because the record keeping is not that cumbersome, independent culling or modified independent culling are the selective breeding programmes that most farmers should use if they want to simultaneously improve two or perhaps three phenotypes.

Selection index: A selection index is the most efficient selective breeding programme that can be used to improve two or more phenotypes. Unfortunately, it is also more sophisticated and more expensive than independent culling. This type of selective breeding

programme should only be used by aquaculturists who work at research stations or by hatchery managers who work at fingerling production centers. Farmers and most aquaculturists should use independent culling if they want to improve two phenotypes. A selection index is really only needed if three or more phenotypes will be improved simultaneously.

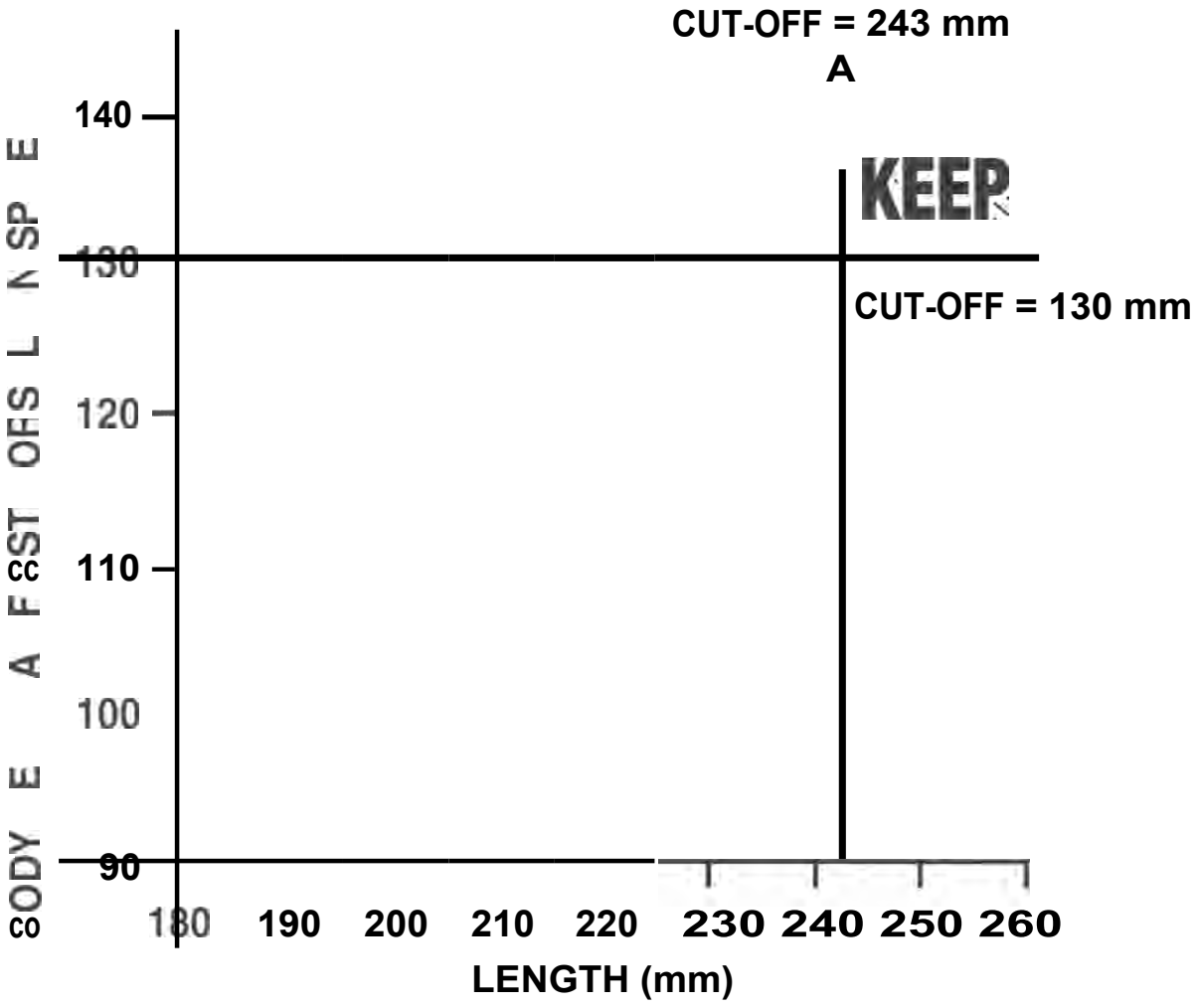


Figure 22. Schematic diagram ot independent culling. In this selective breeding programme, a farmer is selecting for increased growth rate (by selecting for length) and is also trying to improve body conformation (by selecting for body depth at the first dorsal fin spine). He has established independent cut-off values of 243 mm for length and 130 mm for body depth at the first dorsal fin spine. Fish which meet or exceed both cut-off values are saved and become the select brood fish; all other fish are culled. The graph illustrates the relative percentages of fish that will be saved (shaded portion) and culled (unshaded portion) with this type of selective breeding programme.

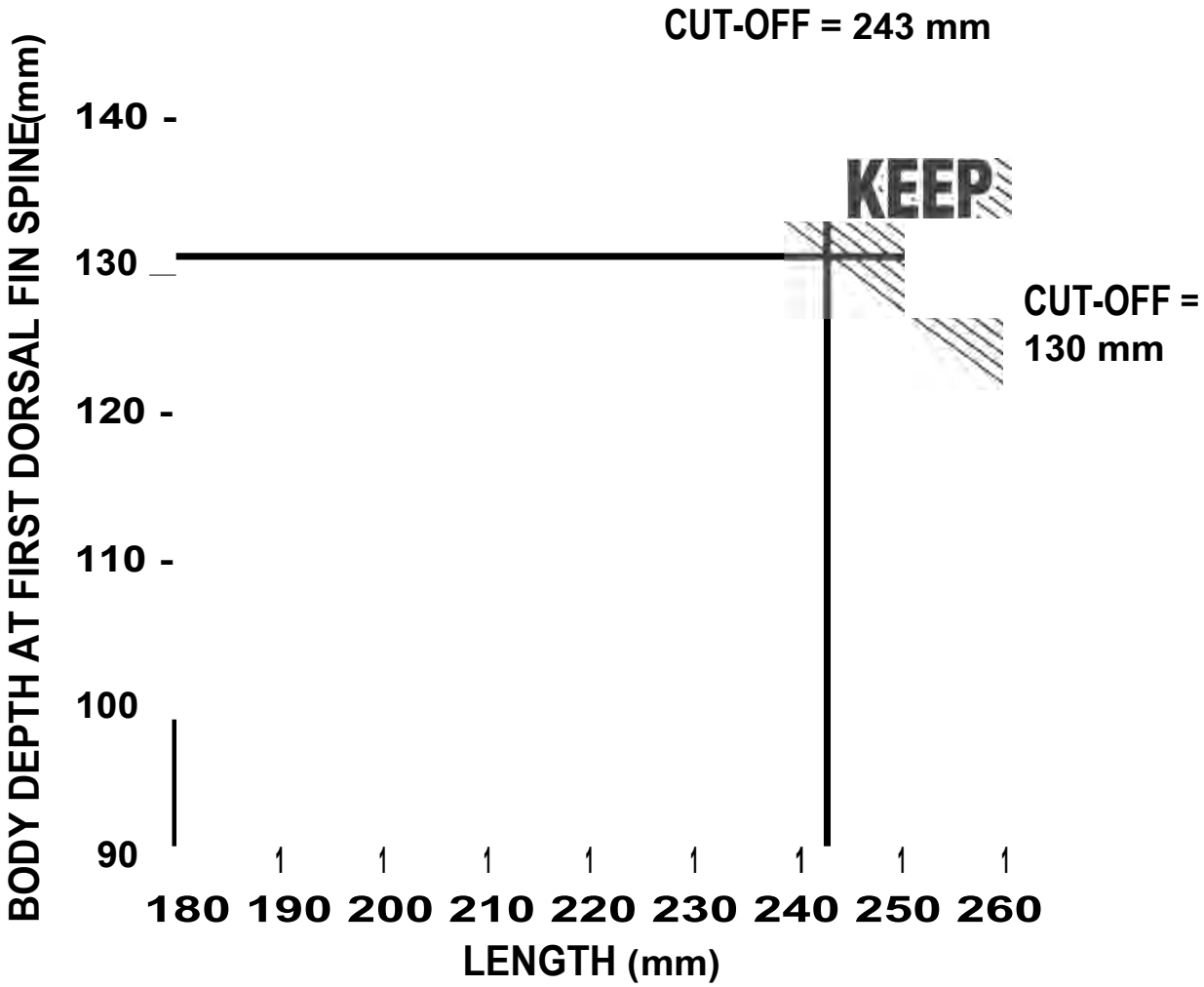


Figure 23. Schematic diagram of modified independent culling. In this selective breeding programme, a farmer is selecting for increased growth rate (by selecting for length) and is also trying to improve body conformation (by selecting for body depth at the first dorsal fin spine). As was the case for the breeding programme illustrated in Figure 22, the farmer has established independent cut-off values of 243 mm for length and 130 mm for body depth at the first dorsal fin spine. In this case, not only will the farmer select fish that meet or exceed both cut-off values, he will also select fish that exceed one cut-off value and that are just under the cut-off value for the other phenotype (the shaded portion of the graph). All other fish are culled. Modified independent culling allows you to select a greater number of fish, and individuals which have a truly outstanding phenotypic value for one trait do not have to be culled.

A selection index is a selective breeding programme where two or more phenotypes are simultaneously evaluated and an overall numerical value is assigned to each fish. The fish are then ranked by these numerical values. The rankings are established so that a fish that is at the 50th percentile for every phenotype receives an I value of 100.0. Consequently, fish that have I values > 100 are considered to be above average, while those with I values <100 are considered to be below average. The ultimate goal of every large-scale sophisticated selective breeding programme is to develop a selection index.

A selection index requires heritabilities, genetic correlations among the phenotypes, and the economic importance of the phenotypes; unfortunately, this information is not known for most cultured populations of food fish. The need for this information can be circumvented by modifying the selection index and by creating what are called "importance factors" for each phenotype.

The techniques that are used to create a selection index using importance factors are outlined in Table 11. The index in Table 11 is designed to improve three phenotypes: length at 12 months, body depth at the first dorsal fin spine, and dressing percentage (as approximated by the ratio: trunk length [length from the back of the head to the end of the caudal peduncleVtotal length). Once an I value is computed for each fish, the fish are ranked by I values and the top 10% or top 15% or top 20% are selected, while the remainder are culled. A selective breeding programme that uses the selection index derived in Table 11 is outlined in Figure 24.

This type of selective breeding programme requires far more labour than independent culling. In independent culling, a farmer assigns a cut-off value for each phenotype (usually based on a sample of 100-200 fish) which will enable him to quickly save or cull each fish. In a selection index, all phenotypes must be measured for each fish, and the fish must be given an individual tag or mark and placed in a tank or hapa until all fish are measured. After all fish are measured, the fish are once again identified and either saved or culled, based on their I values. Not only is this process labour intensive, but the extra handling stresses the fish. For all these reasons, if a farmer wants to improve two or perhaps three phenotypes, he should use either independent culling or modified independent culling.

Family selection

Family selection differs from individual selection in that the decision to save or to cull fish is conducted at the family level, and individual phenotypic values are important only as they relate to their family's mean. Family selection is most often used when individual selection is inefficient because the heritability of the phenotype is small (generally < 0.15). When heritability is small, the heritable component of phenotypic variance is small, which means that most of the measurable differences among individuals are due to non-heritable sources of variance. By selecting at the family level, a significant portion of environmental variance can be negated, which makes it easier to identify genetic differences and to select the fish that are best because of heritable variance.

Family selection is also used when environmental sources of variance are uncontrollable, which can make improvement by individual selection difficult or impossible. For example, if fish cannot be spawned synchronously and if they usually spawn over a several-week to several-month period, family selection is the type of selection that is often used. This approach to selection can control age-related size differences.

Table 11. Techniques that can be used to create a selection index, using importance factors.

Step 1 Determine the phenotypes that will be entered into the selection index. In this example, a selection index will be created to improve three phenotypes:

1) length at 12 months (mm);
2) body depth at the first dorsal fin spine (mm);
3) dressing percentage (as approximated by the ratio: trunk length [length from the back of the head to the end of the caudal pedunclel/total length).

Step 2 Determine the importance factors for the phenotypes. Importance factors are determined by using the following formula:

Importance factor (I) = relative importance of the phenotype/population mean

Step 2a Determine the relative importance of the phenotypes. This is determined by assigning an arbitrary value to each phenotype. These values range from 1 to 99% (and total 100%) and represent the portion of selection pressure that will be assigned to a phenotype (if you assign a value of 0% to a phenotype, it means that you will not try to improve it, so it is dropped from the programme; conversely, if you assign a value of 100% to a phenotype, it means that you want to improve only that phenotype, so all other phenotypes will be automatically dropped from the breeding programme).

The following relative importance values are assigned:

Phenotype	Relative importance
Length	60%
Body depth	30%
Dressing percentage	10%

Step 2b Determine the mean for each phenotype.

The farmer measures a random sample of 200 fish and determines the following means:

Phenotype	Mean
Length	195 mm
Body depth	100 mm
Dressing percentage	55%

Step 2c Calculate the importance factor for each phenotype using the formula presented at the beginning of Step 2. The importance factor for each phenotype is:

$(I_L) = 60\%/195\ \text{mm} = 0.3076923$

$I_{\text{body depth}}\ (IB) = 30\%/100\ \text{mm} = 0.3$

$(I_D) = 10\%/55\% = 0.1818182$

Step 3. Create the selection index that will be used to determine the breeding (I) value for each fish. The value for each fish is determined by entering its phenotypic values and the importance factors into the following formula:

$= (I_L)(\text{length}) + (I_B)(\text{body depth}) + (I_D)(\text{dressing percentage})$

Step 4. Determine the breeding value for a fish that has the following phenotypic values: length = 201 mm; depth = 119 mm; dressing percentage = 54%:

$I = (0.3076923)(201\ \text{mm}) + (0.3)(119\ \text{mm}) + (0.18181821(54\%)$

$I = 107.364$

Family selection is the only type of breeding programme that can be used when an animal must be killed in order to determine its phenotype. For example, if you want to improve dressing percentage or to reduce visceral fat content, you must kill the fish to obtain an accurate measurement. Once you kill a fish, you cannot spawn it (unless you are able to cryopreserve gametes). Consequently, you must use family selection to improve such phenotypes.

Between-family selection

There are two major types of family selection: between-family selection and within-family selection. In between-family selection, the mean values for each family are determined, and the mean values are then ranked. Whole families are then either saved or culled (Figure 25). When using this type of selection, a pre-determined minimal cut-off value is usually not determined. Instead, the farmer decides to save the best 10 or 15 or 20 families.

The whole family does not have to be saved. If family size is large, a random and equal sample from each select family can be saved. The sample chosen from each family must be random, or the breeding programme will not be between-family selection. The farmer cannot purposely choose the best fish from each of the select families. Even if entire families will be kept, family size of the select families should be equalized, or one family will make a greater contribution to the select breeding population.

As was the case with individual selection, sexual dimorphism can complicate selection to improve growth rate. If a species exhibits sexual dimorphism, the males and females within each family must be weighed or measured separately. Selection can then occur in one of two ways: Once the average values are known for each sex, the two average values can then be averaged (half the contribution by each family to the next generation will come from the males, and half will come from the females), and this overall average value is used to save or to cull the families. Alternatively, selection can be done separately for each sex. If this is done, it is likely that the males in some families will be culled while its females are saved, and vice versa.

In order to conduct family selection, a farmer must be able to assign fish to individual families. This can be accomplished in two ways: First, each family can be cultured in separate tanks, hapas, or ponds until they reach a size where they can receive family marks, brands, or tags. Once marked, the fish can be grown communally (mixed and grown together); at harvest, the fish must be separated by family in order to conduct selection. The second method is to culture the fish in separate tanks, hapas, or ponds from the moment eggs are fertilized until selection occurs. Even after selection has occurred, if fish cannot be marked, they often must be maintained in separate units. If fish can be marked, the select brood fish can be stocked communally until it is time to spawn them.

Between-family selection is more expensive than individual selection, because it requires more facilities and more labour. It also requires more record keeping. If the fish can be marked and grown communally, the programme costs will be far less than if each family has to be cultured separately.

Step 1. Determine the phenotypic values for every fish in the population. In this example, we will only determine them for 10 fish:

Fish	Length (mm)	Body depth (mm)	Dressing percentage
T-1	198	103	54
T-2	210	110	55
T-3	180	108	57
T-4	195	100	55
T-5	197	101	56
T-6	190	98	54
T-7	188	97	53
T-8	195	102	57
T-9	185	95	52
T-10	199	102	55

Step 2. Determine the I value for each fish using the importance factors derived in Table 11:

I_{T-1} = (0.3076923)(198) + (0.3)(103) + (0.1818182)(54) = 101.641
= (0.3076923)(210) + (0.3)(110) + (0.1818182)(55) = 105.777
= (0.3076923)(180) + (0.3)(108) + (0.1818182)(57) = 98.148
I_{T-4} = (0.3076923)(195) + (0.3)(100) + (0.1818182)(55) = 100.000
= (0.3076923)(197) + (0.3)(101) + (0.1818182)(56) = 101.097
= (0.3076923)(190) + (0.3)(98) + (0.1818182)(54) = 97.680
I_{T-7} = (0.3076923)(188) + (0.3)(97) + (0.1818182)(53) = 96.583
= (0.3076923)(195) + (0.3)(102) + (0.1818182)(57) = 100.964
I_{T-9} = (0.3076923)(185) + (0.3)(95) + (0.1818182)(52) = 94.878
= (0.3076923)(199) + (0.3)(102) + (0.1818182)(55) = 101.831

Step 3. Rank the fish by I values. Select or cull the fish, based on these values. In this example, the top 20% of the population will be saved:

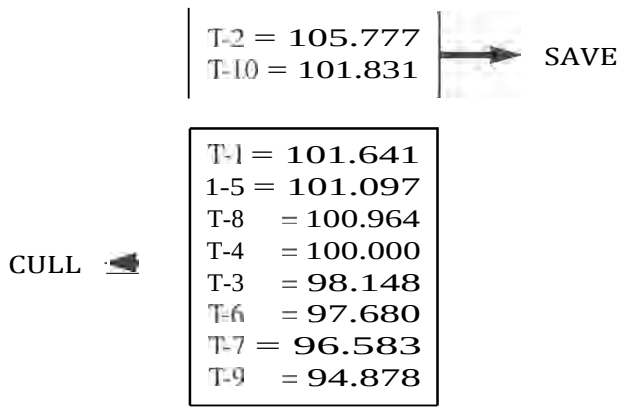


Figure 24. Schematic protocol needed to conduct a selection index. A preliminary step is to determine the importance factors, which are determined from phenotypic means and the relative importance of each phenotype. The methods used to calculate the importance factors for the three phenotypes are described in Table 11. The first step in determining a fish's I value is to determine the phenotypic values for every fish in the population. In this example, only 10 fish are presented. Step 2 is to calculate the I value for every fish. Step 3 is to rank the fish by their I values and to select or to cull fish, based on the I values. In this example, the top 20% of the population was saved, so fish T-2 and T-10 were saved because they were the top two fish; the rest were culled. Note that fish T-4, which had phenotypic values that were the same as the population means, had an I value of 100.0; by definition, such a fish must have an I value of 100.0.

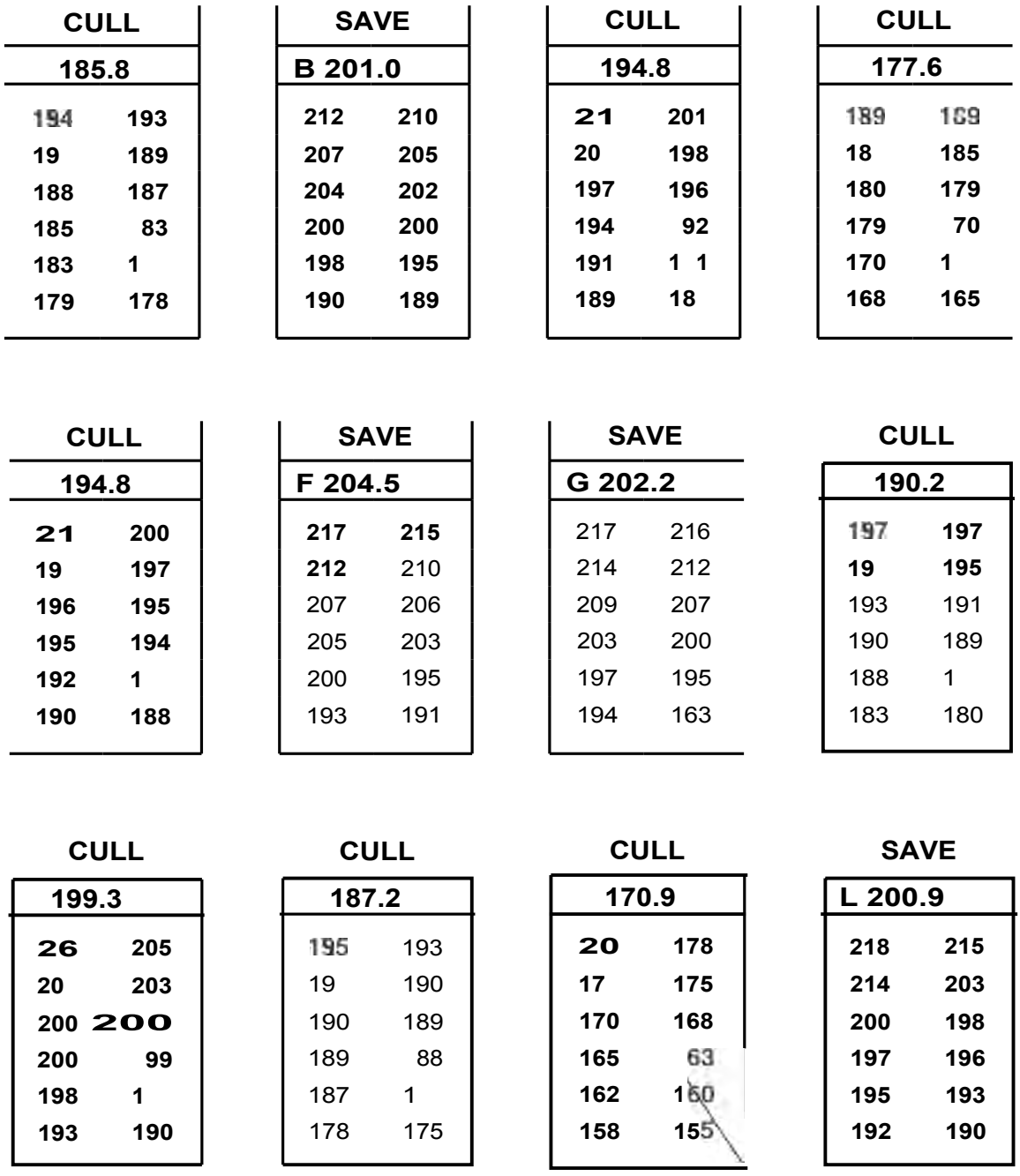


Figure 25. Schematic diagram of between-family selection. Family means are compared, and selection occurs at the family level. Either whole families (or random and equal samples) are saved or whole families are culled. In this example, the goal was to improve growth rate by selecting for length. This was accomplished by selecting the top 33% of the families (only 12 families are included in this example). To do this, family means were ranked, and the families with the four largest mean lengths were saved (families B, F, G, and L). Every fish in the other eight families were culled. In this example, 12 fish from each family were measured to the nearest millimeter (the values are listed below the letter that identifies the family. In reality, 30-100 fish should be measured. The value next to the letter that identifies the family is the family mean. This example assumes that sexual dimorphism does not exist. If sexual dimorphism exists, the means for both sexes within each family must be determined. Selection can then proceed, based either on the average values of the two sexes, or it can occur independently for males and for females.

Interestingly, between-family selection can reduce some of the labour needed to improve growth rate and can also enable a farmer to easily improve growth rate by selecting for weight. Because between-family selection is based on family means, it is not necessary to determine individual values if a farmer selects for weight. The fish from each family can be batch weighed, and the family mean can be obtained by dividing that value by the number of fish were weighed.

If each family is raised in a separate grow-out pond or tank, you must replicate each unit at least three times and then determine the overall average of the three units before selecting or culling families. If each family is raised in only one pond or tank, it is not possible to determine if the family's mean phenotypic value represents that family's breeding value or if it represents the quality of the pond or tank. Every one who has ever raised fish knows all too well that ponds and tanks have individual personalities. Some ponds are "good" ponds while others are "bad" ponds. Some ponds always have good water quality, have good algal blooms, and produce large yields; others are cursed with dissolved oxygen problems, poor algal blooms, and low yields. If each family is grown in a single pond, differences among family means may be due to algal populations in the ponds or to other environmental factors, rather than to the families' heritable variance. If most of the differences among family means are due to pond-to-pond differences, selection will be ineffective.

Farmers must strive to grow each family under uniform conditions. One environmental factor that a farmer can and must control when conducting between-family selection is stocking density. Each family must be cultured using the same stocking density, or differences among family means will be partly due to density differences rather than to heritable differences.

Because selection is based on family means and whole families are either saved or culled, selection can cull some of the fish with the best phenotypes. For example, in Figure 25, family K was culled because it had the smallest family mean. Because the entire family was culled, the largest fish in the population was culled along with its sibs. Conversely, this type of selection also incorporates runts into the population of select brood fish. For example, in Figure 25, family G was saved because it had the second largest mean. Because the entire family was saved, the smallest fish in the population became a select brood fish.

Even though it may seem foolish to exclude some fish that would have been saved and to include some that would have been culled if individual selection were used, this type of selection can be very effective. By basing selection on family means, you neutralize some of the environmental sources of phenotypic variance. It may be argued that the large fish in family K was large simply because of some environmental advantage that enabled it to receive more than its fair share of food. It is tempting to bend the rules of between-family selection and to save some of the culls and to cull some of the select brood fish, but this should not be done. No single approach to selection is perfect and frustration-free, but if you base a selective breeding programme partially on personal prejudice and whimsy rather than genetics, you will decrease its effectiveness.

Within-family selection

Within-family selection is a second type of family selection. In within-family selection, each family is considered to be a temporary sub-population, and selection occurs independently within each family (Figure 26). When fish are measured to determine which will be saved and which will be culled, the fish in each family are ranked, and the best fish are saved from each family. When conducting this type of selection, a farmer usually saves the best 10 or 15 or 20 fish from each of 15 or 20 or 30 families. If sexual dimorphism exists, selection must be conducted independently for each sex, and a farmer saves the best 10 or 15 or 20 males and the best 10 or 15 or 20 females from each family.

In Figure 26, the top four fish were saved from each family. In theory, you save or cull the fish in each family based on the family mean, but you do not need to determine the family mean in order to conduct within-family selection. If you measure and rank every fish in each family (or every fish in a random sample of 30-100 fish from each family), you simply save the pre-determined number.

Because selection occurs independently in each family, fish that are saved from one family might be smaller than many of the fish that were culled from another family. For example, in Figure 26, three of the fish that were saved from family K are smaller than many of the fish that were culled from other families. Conversely, Figure 26 demonstrates that outstanding fish from a family can be culled if they fall below that family's cut-off value (number saved).

As was the case with between-family selection, the culling of large fish and the inclusion of smaller fish into the population of select brood fish can be frustrating, but a farmer should resist the temptation to save or to cull some fish because of personal prejudice. When using within-family selection, it is inevitable that select fish from some families will be smaller than many of the culls from others. In fact, it is expected. This is because within-family selection is usually used when there is a major uncontrollable source of environmental variance that is felt at the family level but not at the individual level, such as spawning date or age of female. By subdividing the population into a large number of families and by then selecting within each family, these environmental factors are neutralized (they are the same for all fish within a family), and they do not influence phenotypic expression and selection.

Research with tilapia has shown that, for the most part, individual selection to improve growth rate has been ineffective for a number of reasons, one of which is the inability to synchronously spawn tilapia. Research has suggested that because tilapia spawn over a several-month period, within-family selection is the selective breeding programme that is needed to improve growth rate because it can neutralize the influence of spawning date on size.

As was the case with between-family selection, a farmer must be able either to mark the families or grow them in individual grow-out units. However, unlike between-family selection, the families do not have to raised in replicate grow-out units because the fish will be compared only within a family (only with fish grown in the same grow-out unit). Because no between-family comparison will be made, environmental differences among ponds will not influence the selection process. Consequently, each family can be raised in a single pond or tank, which means the grow-out aspects of within-family selection are far cheaper than those associated with between-family selection.

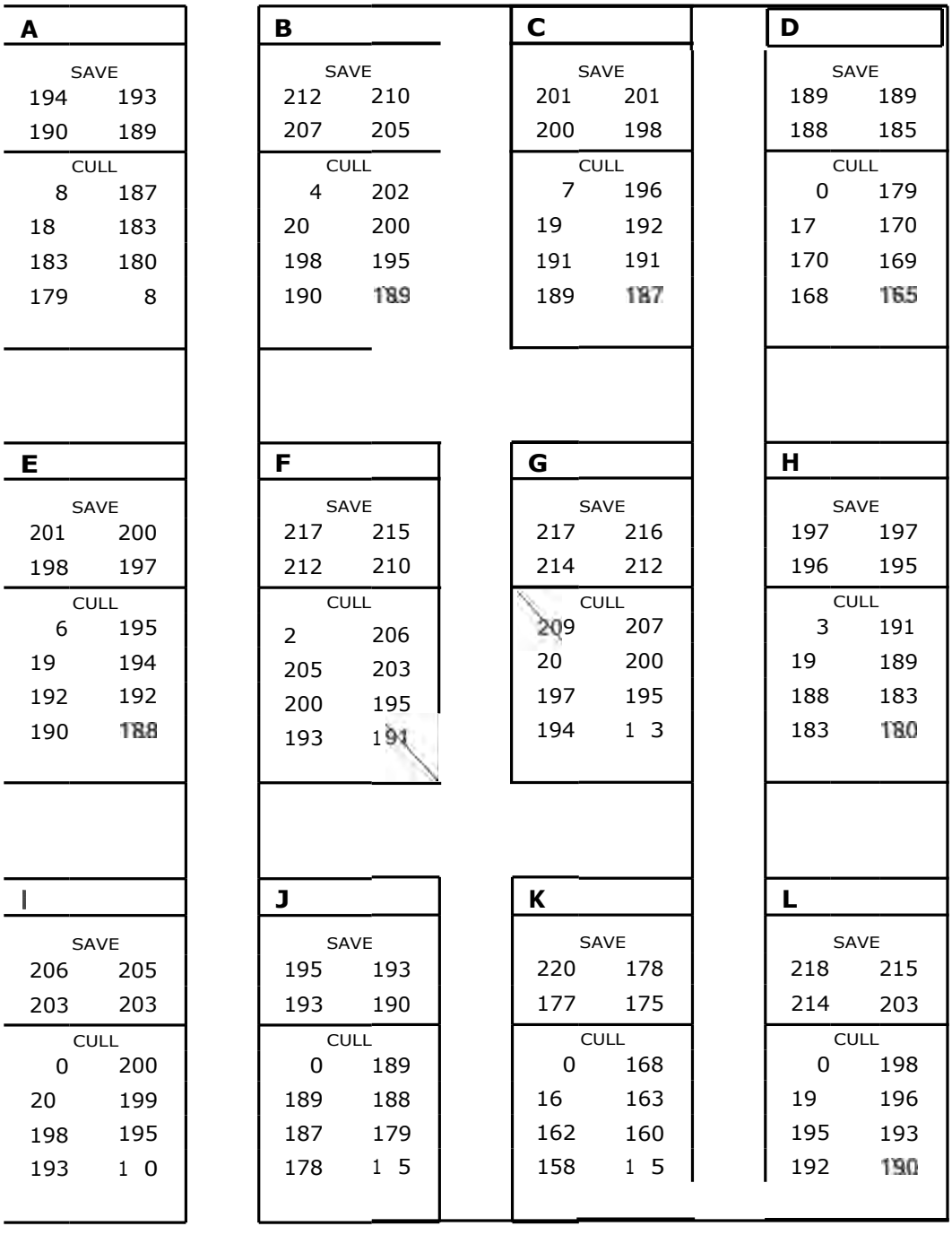


Figure 26. Schematic diagram of within-family selection. This type of selection assumes that each family is a temporary sub-population, and selection occurs independently within each family. In this example, the goal was to improve growth rate by selecting for length. This was accomplished by selecting the top four fish from each family. The rest of the fish were culled. In this example, 12 fish from each family were measured. In reality, 3 0-1 0 0 fish should be measured, and the best fish should be chosen from that sample. Individual lengths (in millimeters) are given below the letter that identifies the family. This example assumes that there is no sexual dimorphism. If sexual dimorphism exists, selection would occur independently in males and females and, in this example, the top two males and the top two females from each family would be saved.

It is possible to conduct within-family selection in a single pond. If fish can be marked, fish can be stocked communally after receiving family marks. At harvest, fish from each family must be separated and selection can proceed as described. Alternately, if a large number of hapas can be placed in a pond, each family can be raised in a single hapa. The only requirement for this is that growth rate in hapas must be similar to that which occurs in ponds.

Combining between and within family selection

One technique that can be used to resolve some of the frustration that occurs when you use either between-family or within-family selection is to combine them into an integrated two-step breeding programme (Figure 27). In this breeding programme, between-family selection is first used to select the best families. Within-family selection is then used to choose the best fish from each of the select families. If this combination is used, the fish must be grown as described for between-family selection, because selection is first done between families. When between-family and within-family selection are combined, all small fish should be culled, so the population of select brood fish will contain no runts. Some large fish will be culled during the between-family portion of the breeding programme but, as was described earlier, their large size may be non-heritable.

Spawning select brood fish

Once family selection has been used to create the population of select brood fish, offspring can be produced using either of two mating protocols. The first and simplest is to randomly spawn the select fish. The second, and one that is often used, is to mate the males from family 1 to the females from family 2, mate the males from family 2 to the females from family 3, mate the males from family 3 to the females from family 4 . . and mate the males from the last family to the females from family 1. This type of mating scheme (called "rotational mating") is done to prevent or minimize inbreeding. In the second generation, the matings are staggered (males from family 1 x family 2 are mated to females from family 3 x family 4, etc.), and so on in succeeding generations.

As can be imagined, this requires that the select brood fish be marked, requires the use of many spawning ponds or tanks, and also requires considerable record keeping. Although this type of mating is desirable for a large-scale commercial breeding programme, it is not necessary for medium-scale aquaculture. Random mating of the select brood fish will suffice.

Assessing results of selection with a control population

Selective breeding programmes are expensive, so it is important to be able to accurately assess the results of selection. The best way to determine this is to compare the phenotype's mean over time to an unselected control population. There are other techniques that can be used to assess the results of selection, but they either require the breeding and maintenance of another select population (selected in the opposite direction) or require the use of sophisticated statistics.

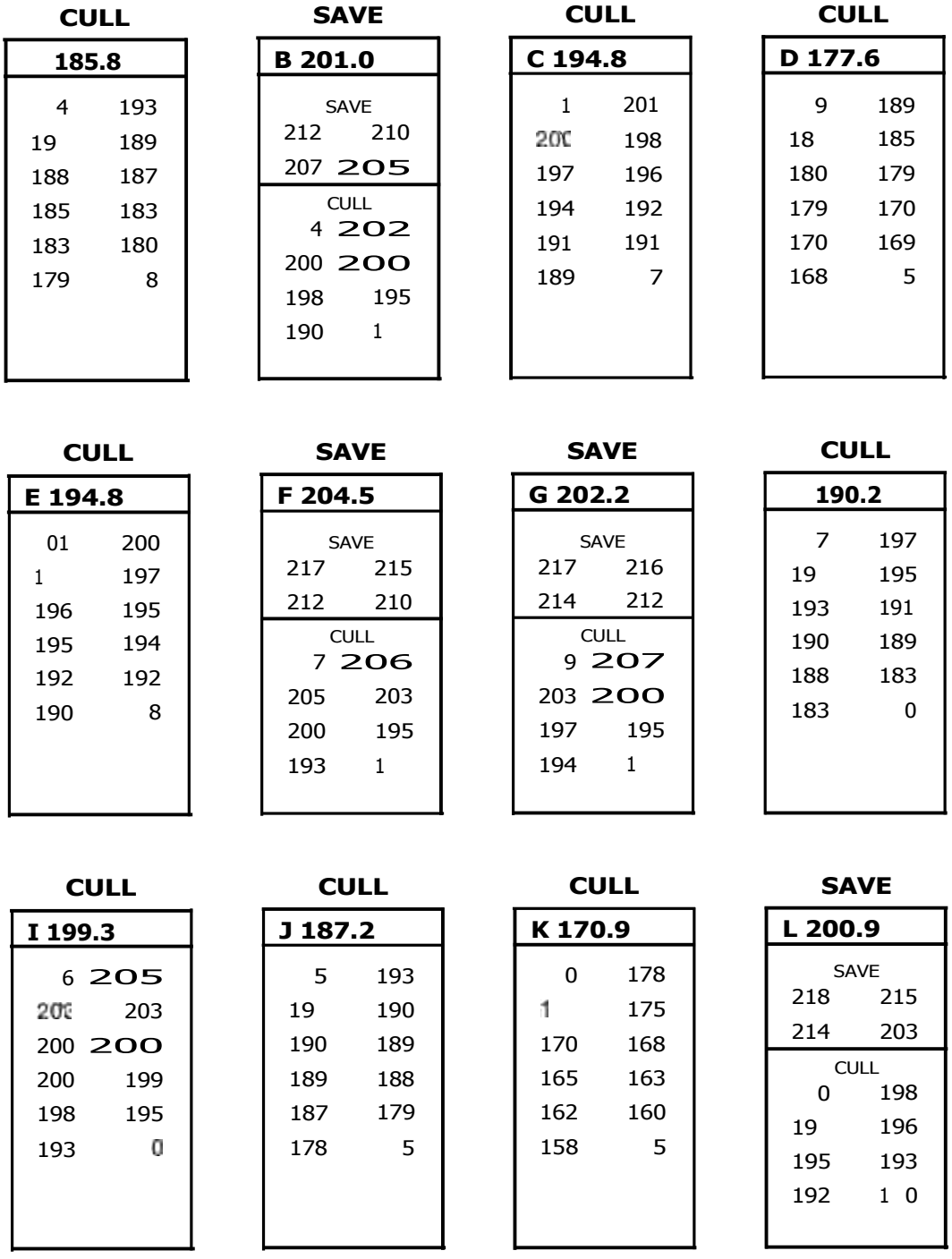


Figure 27. Schematic diagram of a selective breeding programme that combines between-family and within-family selection. This breeding programme is a two-step process. In this example, the goal was to improve growth rate by selecting for length. The value next to the letter that identifies each family is the mean (in millimeters); individual lengths are given below the letter. The first step is to conduct between-family selection; the second is to conduct within-family selection on the select families. In this example, in the initial step, the top four families (B, F, G, and L) were saved by between-family selection. Then the top four fish in families B, F, G, and L were saved by within-family selection. All other fish were culled. As was the case with Figures 25 and 26, this example assumes that there is no sexual dimorphism. If sexual dimorphism exists, it is handled as was described in Figures 25 and 26. This two-step selection programme creates a population of select brood fish that are the best fish from the best families.

The reason why the select population must be compared to a control population is that a population's phenotypic mean is determined by both its genome (which you are trying to improve via selection) and by the environment. If the weather during a growing season is unusually cool or cloudy; if a feed mill unknowingly uses poor-quality fish meal in their feed; or if a farmer increases stocking rate from, say, 4,000/ha to 8,000/ha, the mean weight of the select population can either go down or stay the same because of the adverse environmental factors. If all you have is the mean weight of the select population, you would compare it to the mean weight of the previous generation and would conclude that selection was not working. This decision might be incorrect. Conversely, no genetic improvement may occur as a result of selection, but the mean weight may increase because the weather is exceptionally good, because the feed mill produces a better quality ration, or because a farmer acquires better management skills. If all you have is the mean weight of the select population, you would compare it to the mean weight of the previous generation and would erroneously conclude that selection was improving growth rate.

Unless there is a control population, there is no way to determine if your conclusion is correct. Mean weight should increase with time as a farmer acquires better handling skills and through domestication, but unless there is a control population there is no way to determine what percentage of the increase was due to selective breeding and what percentage was due to improved management skills, etc.

At a major fish hatchery, the F_1 control brood fish can be a random sample that was obtained from the P_1 generation (the original population) before selection occurred (Figure 28). Obtaining a sample of fish from around the P_1 generation's mean is another way of obtaining F_1 control brood fish. F_1 control brood fish are maintained at the hatchery and cultured using the same management programme that is used to culture the F_1 select brood fish. The brood fish in the two populations must be treated, managed, and spawned identically. Their offspring must be cultured identically, or with as few differences as possible; differences in culture techniques can influence the phenotype, which will make it difficult to accurately assess the results of selection. The only exception is that in subsequent generations (F_2, etc.) brood fish in the control population are chosen in a random manner each generation from the control population, while the select brood fish are chosen from the select population.

Another way to produce a control population is to maintain the P_1 brood fish and respawn them for several generations and use their offspring as the control population. The only liability of this approach would be if the age and size of the females had a significant effect on growth of the offspring. This is often the case with fish, but when it occurs, the effects are usually gone 20-180 days after hatching. If selection occurs before such effects are gone, then this approach should not be used to produce the control population.

The creation and maintenance of a control population is the same for both individual and family selection. Different processes are not needed.

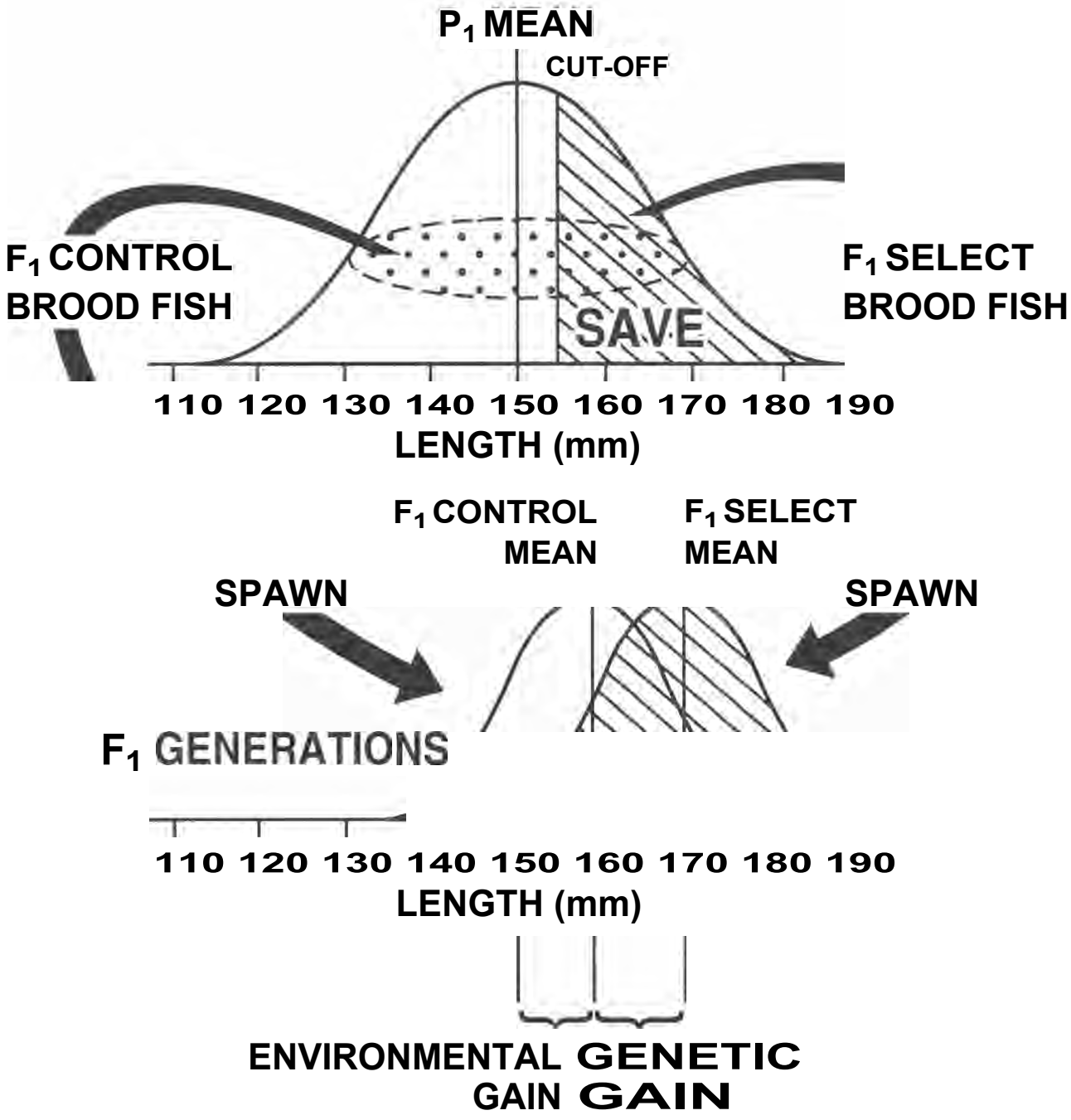


Figure 28. A control population is needed in order to assess gains that have been made via selection. In this example, the P_1 generation had a mean length of 150 mm. Prior to selection a random sample of the population was obtained to create the F_1 control brood fish (the dotted portion of the curve). After the F_1 control brood fish were obtained, the top 30% of the population was selected (cut-off = 155 mm). Both the F_1 select and F_1 control brood fish were managed identically and were spawned when mature; this produced the F_1 generations. Both the F_1 select and F_1 control generations were grown using identical management programmes. When the F_1 generations were harvested, the F_1 select fish averaged 169 mm, and the F_1 control fish averaged 159 mm. Had there been no control, the results would have suggested that selection increased mean length from 150 to 169 mm, a gain of 19 mm. However, the F_1 control generation reveals that a significant portion of that 19-mm improvement was environmental. The mean of the F_1 control fish was 159 mm, which means that the environmental gain was 9 mm (159 mm - 150 mm); consequently, the genetic gain was 10 mm (169 mm - 159 mm).

The creation and maintenance of a control population is the best way to evaluate the results of selection, but it is expensive in terms of time, space, and money. Most farmers do not want to or are unable to maintain a control population, so what should they do? They can compare the mean yield or mean size of their select fish to those grown on a neighbour's farm or to those grown at a government hatchery. If this plan is used, a farmer should carefully evaluate the management plans used at various farms and at government hatcheries and try to choose one that approximates what he uses. He should also choose a farmer or hatchery manager who will cooperate and who is likely to be in business for the next 10 years.

Table 12. How to use a control population to assess the results of selection.

Given: mean length of the P_1 generation = 150 mm
mean length of the F_1 select generation = 165 mm
mean length of the F_1 control generation = 159 mm

Total improvement is calculated as follows:

Total improvement = (mean length of F_1 select generation - mean length of P_1 generation)
= 165 mm - 150 mm = 15 mm

Environmental gain is calculated as follows:

Environmental gain = (mean length of F_1 control generation - mean length of P_1 generation)
= 159 mm - 150 mm = 9 mm

Genetic gain is calculated as follows:

Genetic gain = (mean length of F_1 select generation - mean length of F_1 control generation)
= 165 mm - 159 mm = 6 mm

or

Genetic gain = (total improvement - environmental improvement)
= 15 mm - 9 mm = 6 mm

Table 12 shows how a control population can be used to assess the results of selection. In the example used in Table 12, the mean of the P_1 generation was 150 mm, and the mean of the F_1 generation select fish was 165 mm. If no control population had been grown, you would know that the mean increased by 15 mm, but there would be no way to determine what percent of the 15-mm increase was due to the selective breeding programme and what percent was due to better management skills, etc. Since a control population was produced, you can determine that 9 of the 15 mm was environmental gain. This means that had there been no selective breeding programme, the mean length would have increased from 150 mm to 159 mm. The difference between the F_1 select and the F_1 control generations (or the difference between total improvement and environmental improvement) is 6 mm, and that is the genetic gain.

The control population also enables you to determine the percent improvement gained as a result of selection. One generation of selective breeding improved mean length by 3.8% (6 mm/159 mm). Note that percent improvement is assessed using the value of the contemporary control group (in this case, the F_1 control generation) as the standard.

There are two ways of expressing genetic improvement when it is expressed as a percentage. The first is to express it as percent per generation, as was done above. The second is to express it as percent per year. If the generation interval is one year, the values are identical, but if the generation interval is longer or shorter, the values are smaller or larger, respectively. For example, if the species does not mature and spawn until it is 4 years old, then the percent improvement per generation is divided by four to determine percent improvement per year.

When a farmer compares his select fish to the control population, he must compare the overall mean values that are determined from fish that are grown in at least three ponds. It does not matter if a farmer maintains his own control or if he uses a neighbour's fish. If each population is grown in a single pond, he will be unable to separate pond effects from genetic effects. One population may have a larger mean because the pond had a better algal bloom.

One way to circumvent the need to grow both populations in replicated ponds is to mark the control group and to stock it communally with the select population in a single pond. If the two groups are stocked communally, only 30-50 control fish need to be stocked in a pond.

A truly accurate assessment of the results of a selective breeding programme cannot be done simply by comparing the means of the select and control populations. The means must be compared statistically. Unfortunately, statistical analyses of the data from a selective breeding programme requires a sophisticated knowledge of experimental design and a basic understanding of statistics. Consequently, virtually all farmers will require expert assistance with data analysis. However, if such assistance is not available, a farmer should not be discouraged from conducting a selective breeding programme simply because the results will not be subjected to statistical analysis. The raw means will provide a good indication of what occurred.

Conclusion

The selective breeding programmes that are needed to improve quantitative phenotypes are more difficult, more sophisticated, and take longer than those needed to fix qualitative phenotypes. In fact, these breeding programmes are open-ended; if selection stops, the population usually loses much of the gain that has been made. Additionally, they require more sophisticated record keeping and also require some mathematical/statistical analyses of the data that are gathered. Examples of simple and inexpensive selective breeding programmes that can be conducted to improve growth rate and other quantitative phenotypes, as well as examples of the types of records that must be maintained, are presented in Chapter 5.

Selective breeding programmes are tried-and-true methods of improving growth rate and yield. But selective breeding programmes are not free, nor are they low-technology methods of increasing yields. If yield can be increased by proper use of lime, fertilizers, and/or feeds or if yield can be increased by stocking fish at a more appropriate density or by better water quality management, this should be the first approach used, because improvements will be immediate and will be relatively inexpensive.

Relatively few farmers should be encouraged to conduct selective breeding programmes. Selective breeding programmes require ponds, labour, money, and record keeping. They

also require long-term planning and patience. Farmers who are unable to or who are unwilling to devote part of their farm to a breeding programme; those who cannot or who are unable to provide the labour needed to conduct the breeding programme; or those who cannot take, record, and maintain data should not conduct selective breeding programmes. Farmers who are incapable of long-term planning (1-10 years) should also be discouraged from initiating a selective breeding programme.

Farmers do not have to become geneticists in order to conduct selective breeding programmes to improve growth rate in fish. They do not need to know the heritability for length or weight; they do not even need to know what a heritability is. But they do have to be good managers.

Before initiating a selective breeding programme a farmer should conduct a survey to determine if a breeding programme is needed and should then determine what phenotypes need improving. The most logical decision for most farmers will be to improve growth rate. As a general rule, selective breeding programmes that are conducted on medium-sized fish farms should try to improve only growth rate. The major reason for this is the fact that the improvement that can be made for a phenotype is inversely related to the number of traits that are incorporated into the breeding programme. Secondly, improvements in growth rate will improve other important production phenotypes via indirect selection.

Once a farmer has decided what phenotype he wants to improve, he then needs to determine how the phenotype will be measured, when it will be measured, and the type of selective breeding programme that will be used to create his population of select brood fish--individual selection, within-family selection, or between-family selection. The differences among these types of breeding programmes are outlined in Table 13. If possible, individual selection should be used, because it is easier, less expensive, and requires less record keeping.

If a farmer wants to improve two phenotypes he should use independent culling or modified independent culling. Tandem selection should never be used. Improving two phenotypes by using a selection index is the most efficient type of selective breeding programme, but it is not recommended for farmers who run medium-sized fish farms.

A farmer who conducts a selective breeding programme must have a way of assessing the results of his labour. If he has the space and resources, he can maintain a control population. Otherwise, he can compare the mean of his select population over time to that from a neighbour's farm or that at a government hatchery.

When a farmer determines the gains that he has made as a result of his selective breeding programme, he should conduct a reassessment of the programme. He needs to examine all facets of the programme and to determine if there are easier and more efficient ways of conducting the programme. He also needs to determine if his investment is providing the desired dividends. Although a farmer should abandon a selective breeding programme that is not working, he should not be too hasty in judging the results of selection. If conducted properly, a selective breeding programme will produce small but steady gains.

Table 13. Comparison of the basic strategy and some of the advantages and disadvantages of individual selection, within-family selection, and between-family selection.

Type of selection	Strategy	Advantages	Disadvantages
Individual	Choose best individuals; family relationships not important.	Best when h^2 ,0.25; inexpensive; can be done in few ponds; relatively easy to use for 2 or 3 phenotypes; all select fish are the largest; easy to retain large breeding population; least amount of data needed; least amount of record keeping.	Ineffective when h^2 <0.15 as V_E makes it difficult to choose best fish; asynchronous spawning can cause problems.
Within-family	Choose best individuals within each family.	Best when h^2 <0.15 and V_E affects family more than individuals; can be used with asynchronous spawning; moderately easy to maintain large breeding population; less expensive than between-family.	Moderately expensive; requires many ponds; hard to incorporate 2 or 3 phenotypes; small fish can become select brood fish. Requires lots of data and lots of record keeping.
Between-family	Choose best families based on family means; individual values not considered.	Best when h^2 <0.15 and V_E affects individuals more than families; can be used when fish must be killed.	Very expensive; requires many ponds; hard to incorporate 2 or 3 phenotypes; small fish can become select brood fish; can lead to high levels of inbreeding. Requires lots of data and lots of record keeping.

CHAPTER 5

Simple selective breeding programmes to improve growth rate and other quantitative phenotypes

Even though selective breeding programmes can be designed to improve all sorts of production phenotypes, the single most important phenotype is growth rate. Improving growth rate will decrease the time it takes to grow a fish to market, which means a farmer can produce more crops in a given time period, which means he will make more money. It also means yields will increase. This will increase production efficiency, increase food production, and also increase a farmer's income. As an added bonus, increasing growth rate can improve other production phenotypes via indirect selection. Some studies have shown that faster-growing fish also have more efficient feed conversions and seem to be more disease resistant.

Selection can be used to improve other quantitative phenotypes, if improving them will improve production efficiencies or profits. In most cases, as important as these phenotypes are, they are not as important as growth rate. Occasionally, a breeding programme other than selection is needed to solve the most important goal. For example: in tilapia farming, controlling reproduction in grow-out ponds is the most important goal, and this is accomplished by interspecific hybridization and/or sex reversal; in grass carp farming in the U.S., producing sterile fish is the most important goal, and this is achieved by chromosomal manipulation.

The object of this chapter is to outline simple, relatively inexpensive selective breeding programmes that can be. conducted by farmers on farms with about 2 ha of ponds and to provide examples of the types of data that must be collected, as well as data tables that can be used to record these data. This chapter will not discuss selective breeding programmes that use tandem selection; a selection index; or those that combine selection with crossbreeding, inbreeding, or some facet of biotechnology such as chromosomal manipulation.

When describing these simple selective breeding programmes, information will be provided on the number of ponds that will be needed in order to grow the fish that will be evaluated. This number will not include the number of ponds that will be needed to hold or to spawn brood stock. Additionally, this chapter will not discuss ancillary facilities that are needed, such as holding tanks, hatchery buildings, counting tables, etc.

The main goal for the selective breeding programmes that are outlined in this chapter will be to improve growth rate by selecting for length. As was described in Chapter 4, growth can be improved by selecting for either length or weight. Because it is far easier to accurately measure hundreds of fish than it is to accurately weigh them, and also because most farmers do not have access to accurate balances, most farmers should select for length.

Examples of selective breeding programmes that are designed to improve two phenotypes will also be outlined. In these examples, selection to improve growth rate is still the primary goal, but a second phenotype is added.

The selective breeding programmes outlined in this chapter are designed to be conducted by a farmer who is creating genetically improved stock for his farm. If a farmer wants to embark on a breeding programme so that he can sell genetically improved fingerlings to support a local or regional industry, the size and costs of the projects that are outlined must be increased: more ponds must be built; more cohorts must be created; and more select brood fish must be produced. In fact, if this is a farmer's goal, it is likely that he will convert his entire farm to this enterprise, and he will no longer produce food fish.

One of the things a farmer must do if he is to run a successful selective breeding programme is to determine how many select brood fish must be saved. If too few are saved, a farmer will be unable to produce enough select fish for future grow-out. If this happens, he will have to spawn unselected fish, which will negate much of his efforts.

An additional problem is that if a farmer saves too few fish, inbreeding can build to levels which will result in inbreeding depression. If this occurs, much of the improvements created by selective breeding would be used simply to counteract inbreeding depression.

A farmer should spawn at least 25 males and 25 females every generation to minimize inbreeding depression. This number is not carved in stone, but it can be used as a general rule. This means that a farmer should save a minimum of 100-200 brood fish. The reason why a farmer needs to save this many select brood fish is some will die before they can be spawned, and spawning success is seldom 100%. These guidelines also apply for a control population.

A second factor that determines how many brood fish a farmer needs is the size of his operation; that is, how many fingerlings are needed for the grow-out ponds. If a farmer saves too few brood fish, he will not be able to stock his grow-out ponds. Saving enough select brood fish can be a problem on large fish farms, but it is seldom a problem on medium-sized (2 ha) fish farms, especially if a farmer saves at least 100-200 select brood fish.

The selective breeding programmes described in this chapter are bare-boned skeletal outlines that are presented to demonstrate that relatively simple and relatively inexpensive programmes can be conducted by farmers and that, if the programmes are conducted properly, they can be integrated into everyday farming practices. The programmes outlined in this chapter are not absolute. They can be and should be modified in order to customize the programme for a particular species, for a farmer's income, and for his farm.

The breeding programmes that are outlined in this chapter are for species that do not exhibit sexual dimorphism. This means a single cut-off value can be used during selection.

If the species that a farmer grows exhibits sexual dimorphism a slight modification of the programmes that are outlined will be necessary. Sexual dimorphism can increase the effort needed to conduct selection, because once it occurs, the fish must be sexed and selection must occur independently in each sex. The age at which sexual dimorphism occurs will determine if a single cut-off value can be used or if separate cut-off values will be needed for males and females. In some species, sexual dimorphism occurs when the fish are small and separate cut-off values are needed at both the fingerling and food fish phases of selection. If sexual dimorphism does not occur until after the fingerling stage, a single cut-off value can be used at the fingerling stage, while separate ones will be needed when food

fish are harvested. If sexual dimorphism occurs after the age at which food fish are harvested, a single cut-off value can be used during both phases of selection.

The selective breeding programmes outlined in this chapter do not describe the creation and use of a control population to assess the results of selection. This was described in Chapter 4.

Individual selection

If possible, individual selection should be used to improve growth rate. Individual selection is easier and less expensive than family selection, because it can be done in only one or two ponds and fewer fish need to measured.

Selection for growth rate

Growth rate is the most important production phenotype. The following programmes outline how individual selection can be used to improve only this trait. When conducting individual selection, if a farmer can synchronize spawning, selection will be relatively simple. If the species spawns asynchronously, care must be taken to ensure that age-related size differences do not confound and obscure genetically-produced size differences. If the selective breeding programme is not modified to accommodate asynchronous spawning behaviour it will be impossible to identify fish which are genetically superior from those which are environmentally superior (older).

Synchronous spawning: If a farmer can synchronize spawning and can produce at least 25 families on a single day (or at most, over a 48-hour period), he can conduct a simple, inexpensive selective breeding programme in only one or two ponds. In addition, an extra pond will be needed for the select brood fish, once they have been saved.

To initiate the selective breeding programme, the fish should be spawned using normal management techniques. If possible, egg masses should be collected and incubated. If the eggs are usually incubated by the females in the ponds, they should be closely monitored, and fry should be collected as soon as they hatch or begin to swim away from each female.

If possible, family size should be equalized before fish are stocked. This will prevent one family from skewing the results of selection; additionally, it will help minimize inbreeding. Because of this, families should be isolated until they are equalized. In addition, if families are isolated until they are stocked, the complete mortality of one or more families will be noticeable and can be recorded.

If the fish are traditionally raised in a two-phase process (phase one is stocking fry and raising them to fingerlings; phase two is stocking fingerlings and raising them to food fish), selection can be done when fingerlings are harvested and when fish are harvested for market; if this is the case, selection will require two ponds. If production is only a single-phase process (no fingerling phase; fry are stocked and raised to food fish), selection will occur when fish are harvested for market, and selection will require only one pond.

If fish are raised in a two-phase process, fry should be stocked in a single pond and fingerlings should be produced using normal production techniques. Just prior to harvest,

a random sample of 100-200 fingerlings should be measured to the nearest millimeter in order to determine the phenotypic value that corresponds to the desired cut-off percentage, as was outlined in Figure 20. At fingerling harvest, the top 35-50% should be saved and stocked in the food fish production pond. The culled fingerlings can be grown for food or sold. If they are grown for food, no fish from this population should be saved and spawned.

The select fingerlings should be raised using normal production management. Prior to harvest, a random sample of 100-200 fish should be measured to the nearest millimeter to determine the phenotypic value that corresponds to the desired cut-off percentage. At harvest, the top 10-20% of the fish should be saved, and these fish will become the select brood fish. Culled fish can be eaten or sold.

If fish are raised in a single-phase process, a random sample of 100-200 fish should be obtained to create the F_1 control brood fish when fish are harvested. The population of F_1 control brood fish should be created prior to selection. If fish are raised in a two-phase process and if selection will occur at both the fingerling and food fish harvests, the F_1 control brood fish need to be saved at the end of the fingerling phase. If the F_1 control brood fish are saved just prior to the second act of selection during a two-phase selection process, the control will not be a true control population, since some selection will have occurred prior to its creation.

If fish are raised in a single-phase process, fry should be stocked in a single pond, and fish fish should be produced using normal production techniques. Selection at harvest is done as described above.

These simple selective breeding programmes are outlined in Figures 29 and 30. Figure 29 outlines the procedures that will be used when selection will occur twice--at fingerling harvest and at food fish harvest. Figure 30 outlines the procedures that will be used when selection occurs only once at food fish harvest.

The cut-off percentages were mentioned as ranges, not as specific values (35-50% for fingerlings and 10-20% for food fish). This is because the exact cut-off values are not that critical. The intensities of selection that are used are individual decisions. A farmer can increase the rate of gain by using higher cut-off percentages (saving a smaller percentage). But rate of gain must be balanced against inbreeding-related problems and with the ability to produce enough fish in the next generation. Most selective breeding programmes conducted on medium-sized farms will encounter few problems and will also be able to achieve desired results if cut-off values in these ranges are used.

The pond(s) used in this project should be 0.04-0.4 ha. Pond size is determined by the stocking rate that will be used to grow the fish and by the intensity of selection. Once a farmer decides what his cut-off percentages will be and how many select brood fish will be saved, he can determine how big the ponds must be. This will tell him the percent of the farm that will be devoted to the breeding programme. The procedure used to determine pond size is outlined in Table 14. The values derived in Table 14 are valid only for the assumptions that were given in Table 14.

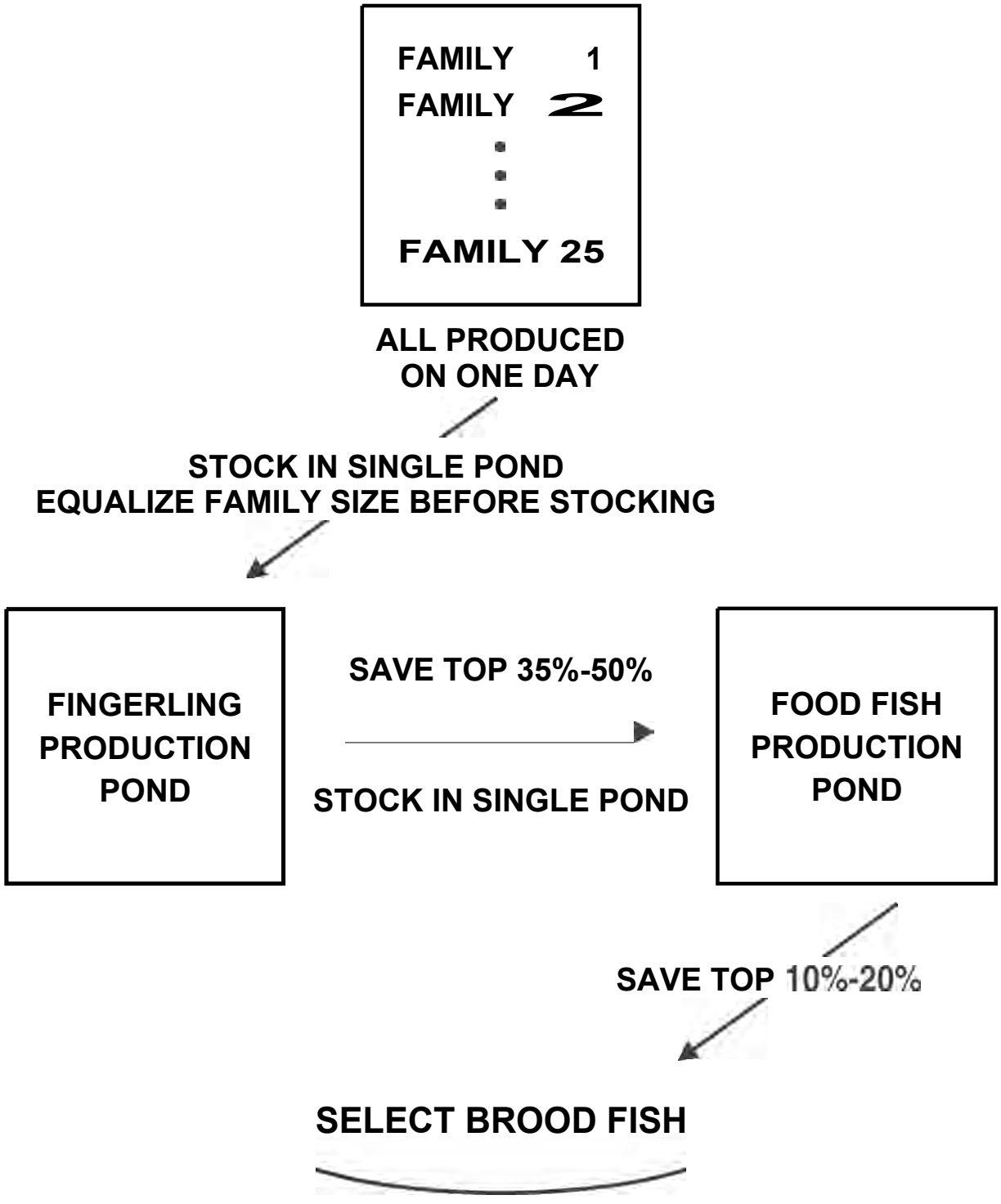


Figure 29. Schematic diagram of a simple and inexpensive selective breeding programme to improve growth rate by selection at two ages--at fingerling harvest and at food fish harvest. This breeding programme can be conducted in two ponds. Fish that are culled at the fingerling stage can be sold or grown for food. Fish that are culled at harvest can be eaten; sold as food; or some can be retained and used as brood fish to produce the production fish (fish raised and sold as food), if the select fish cannot produce enough offspring for both the selective breeding programme and for the production ponds.

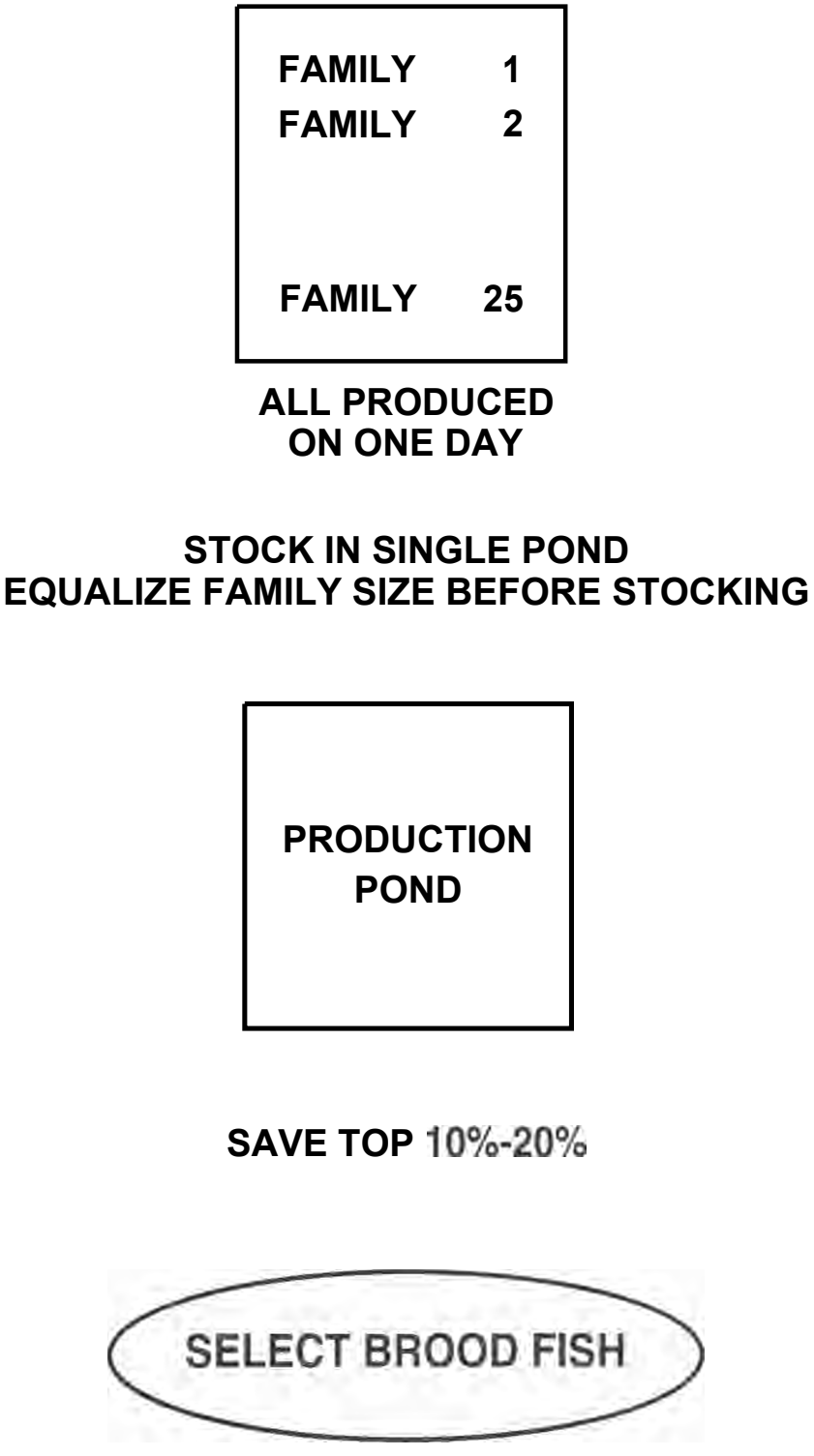


Figure 30. Schematic diagram of the least expensive selective breeding programme that can be designed to improve growth rate. In this breeding programme, fry are stocked in a pond, and the fish are not harvested until they are ready for market. Selection occurs when the pond is drained and the fish are harvested. This breeding programme can be done in one pond. The fate of the culled fish was described in Figure 29.

If ponds of approximately the correct size already exist, a farmer does not have to destroy them and custom-build new ponds in order to conduct a selective breeding programme. A farmer who uses existing ponds should adjust stocking rates and/or cut-off values to achieve the desired results. The formulae presented in Table 14 can be used to generate this information.

The information generated in Table 14 can also be used to determine how many fish are needed from each family. For example, if a farmer needs to stock 8,892 fry and if he has produced 25 families, he needs 355.7 fry/family (8,892/25). Because you cannot have 0.7 fry, he needs 356 fry/family. Because the number is rounded up, the farmer will stock 8,900 fry. If he maintains the stocking rate at 200,000 fry/ha, the size of his fingerling pond would change only by 0.001 ha to accommodate the 8 additional fry, so a larger pond would not be needed (pond size had already been rounded to the nearest thousandth). The rounding up of family size also means that the initial culling will produce an additional 2 select fingerlings. This will have little effect on stocking rate in the food fish pond, nor will it require a larger food fish pond. If the farmer does not want to alter stocking rate one iota from his planned rate, he can randomly cull 2 select fingerlings once that population has been created.

Brood fish that are saved should be stocked in a select brood stock pond. No other fish should be stocked with the select brood fish. When mature, these fish will be spawned to produce the F_1 select generation. No selection for secondary sexual traits and no selection for other criteria should be done with the brood fish prior to the mating season. The only goal of this selective breeding programme was to improve growth rate by selecting for length, and the select brood fish were selected for that phenotype and should be selected only for that phenotype; they should not be selected for any other reason. The select brood fish should be allowed to mate among themselves in a random manner or, if they will be paired in pens or manually stripped, they should be randomly paired.

If a farmer has enough select brood fish, he can use these fish to produce both the F_1 select generation and the production fish (fish that the farmer will stock and grow for market in his production ponds). If the select brood fish cannot produce a sufficient number of offspring for both purposes, their fry should first be used to produce the F_1 select generation; any surplus fish can be grown for food. If the select brood fish cannot produce enough fingerlings for both purposes, the farmer should use other brood fish (culls from the harvest selection) to produce fry for the production ponds.

Table 14. Procedure that can be used to determine the size of the ponds that are needed in a selective breeding programme.

Goal: To have 200 select brood fish

Given: Cut-off at food fish harvest: select top 10%
Cut-off at fingerling harvest: select top 50%
Fry-fingerling mortality: 50%
Fingerling-food fish mortality: 10%
Stocking density in fingerling pond: 200,000/ha
Stocking density in food fish pond: 7,000/ha

Step 1. How many food fish must be harvested to produce 200 select fingerlings, if you save the top 10%?

Number of food fish harvested = number saved/percent saved = 200/0.1 = 2,000.

Step 2. How many select fingerlings should be stocked in the food fish pond, if mortality is 10%? If mortality is 10%, survival is 90%:

Number of fingerlings stocked = number harvested/survival rate = 2,000/0.9 = 2,223.

Step 3. How many fingerlings must be harvested from the fingerling pond to produce 2,223 select fingerlings, if you save the top 50%?

Number of fingerlings harvested = number saved/percent saved = 2,223/0.5 = 4,446.

Step 4. How many fry must be stocked in the fingerling pond to produce 4,446 fingerlings, if mortality is 50%? If mortality is 50%, survival is 50%:

Number of fry stocked = number harvested/percent survival = 4,446/0.5 = 8,892.

Step 5. How big should the fingerling pond be, if it is stocked at 200,000/ha and if you will stock 8,892 fry?

Size of fingerling pond = number of fry that will be stocked/stocking rate = 8,892/200,000 = 0.0446 which is rounded to 0.045 ha.

Step 6. How big should the food fish pond be, if it is stocked at 7,000/ha and if you will stock 2,223 fingerlings?

Size of food fish pond = number of fingerlings that will be stocked/stocking rate = 2,223/7,000 = 0.3175 ha which is rounded to 0.318 ha.

The second, third, etc. generation of selection can proceed as described above. If the select brood fish cannot produce enough fish for both the selective breeding programme and for the production ponds, genetic improvements that are being achieved in the select population can be transferred to the production fish beginning with the second generation of selection, if the farmer uses the culls from the breeding programme as brood fish to produce fry for his production ponds. Even though these brood fish were culled, they came from the selective breeding programme, and their parents were select brood fish. This will enable a farmer to transfer the genetic gain to the farmed fish, but it will be with a one-generation delay. Additionally, when a farmer replaces one generation's select brood fish with their successors, he can transfer the previous generation's select brood fish to the production brood fish population. This will also enable the farmer to transfer genetic gain to the production population. Some of the ways genetic gain can be transferred to the production ponds are illustrated in Figure 31.

If selection will occur only when food fish are harvested, a farmer will not be able to transfer the genetic improvement to the production population as quickly, unless the select fish can produce enough offspring for both the breeding programme and for the production ponds. If the select brood fish can produce only enough offspring for the breeding programme, a farmer must use unselected brood fish to produce fry for the production ponds after the first generation of selection. After the second generation of selection, he can either use F_1 select brood fish or fish that were culled when he created **F2** generation brood fish. This means a farmer will realize no genetic improvement in his production fish for one generation, but thereafter, he will be able to transfer it with a one-generation delay.

Asynchronous spawning: If a farmer cannot spawn his fish synchronously, he should divide the population into age cohorts and select for growth rate independently within each cohort. To initiate this breeding programme, a farmer should spawn the fish using normal management techniques. As before, it is better if egg masses can be collected and incubated. If the eggs are usually incubated by the mother in the ponds, females should be closely monitored, and fry should be collected from each female as soon as they hatch or begin to swim away.

Egg masses or newly hatched fry should be grouped into daily (24-hour) age cohorts. If it is not possible to collect enough families within a 24-hour period, the time interval for each cohort can be stretched to 48 hours. Each cohort should be composed of at least 5 families, and there should be at least five cohorts. These numbers are not carved in stone. A farmer does not have to discard a cohort simply because it is made up of only four families. There are two basic premises behind this work plan: the first is that a cohort should be composed of several families; the second is that at least 50 parents (25 males and 25 females) should produce offspring for the breeding programme.

As before, if this species is usually produced by a two-phase production process, selection for increased length will occur when fingerlings are harvested and when food fish are harvested. If production is usually a single phase with no fingerling phase, selection will occur only when fish are harvested for food. Individual selection will be used to select the best fish from each cohort.

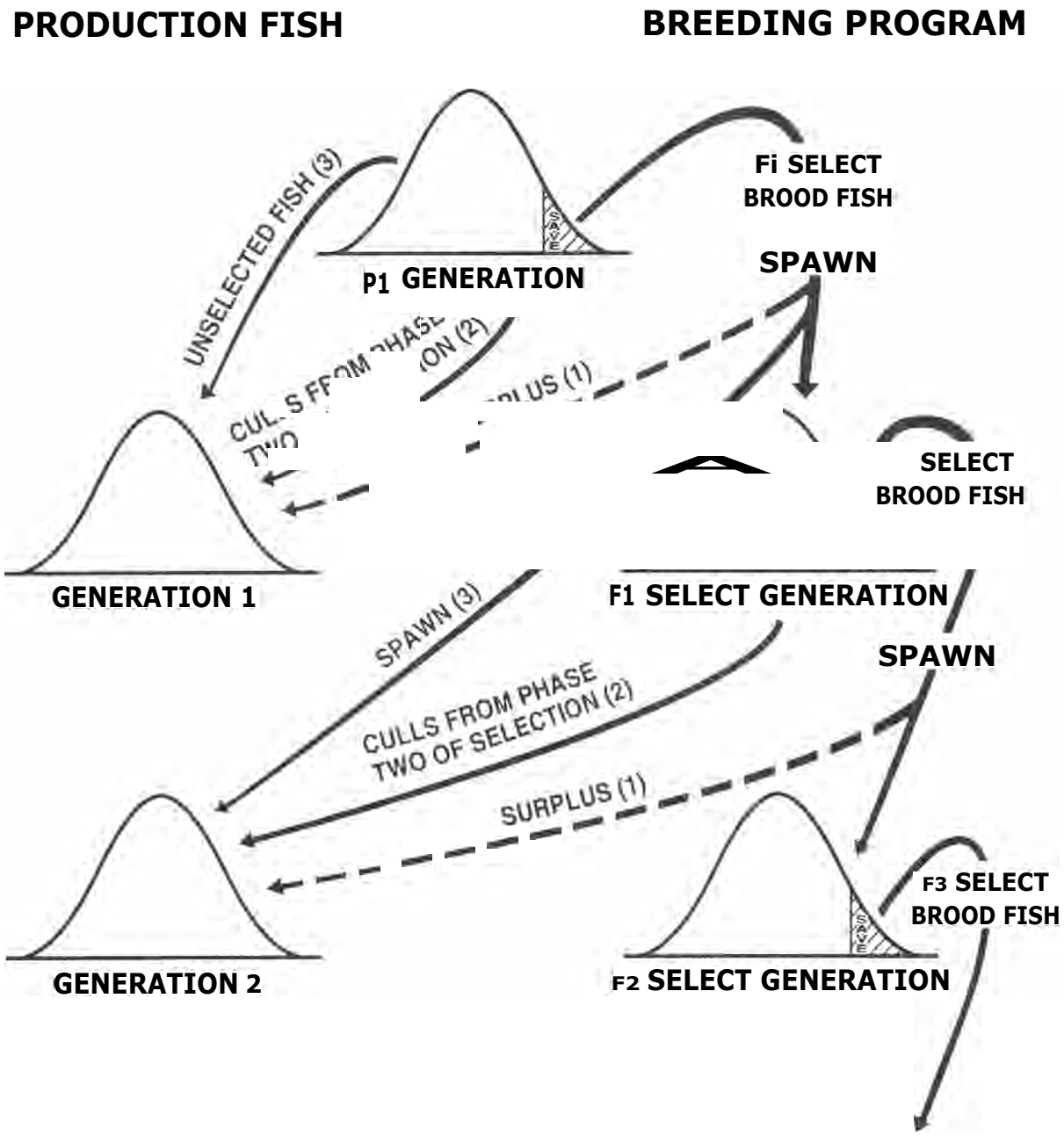


Figure 31. Schematic diagram illustrating the ways genetic gain can be transferred from the selective breeding programme to the production fish that a farmer grows for market. If the select brood fish can produce enough for both populations, the transfer will be immediate, and the means of the two populations will be the same (path 1). If selection is a two-phase process, the culls from the second phase can be used as brood fish to produce the production fish (path 2). If this approach is used, some of the genetic gain will be transferred immediately, but the production mean will always lag behind the select mean. If selection is done only at harvest, unselected fish will have to be used to produce the first generation of production fish, and either the culls from the breeding programme or the previous generation's select brood fish can be used thereafter (path 3). This approach will transfer the gains with a one-generation delay if the previous generation's select brood fish are used; if culls from the breeding programme are used to produce the production fish, the production mean will be slightly better than the mean of the previous generation of select fish. All assumptions about mean values were generated using the premise that there is no environmental influence on the phenotype and the trait has a large heritability.

This breeding programme will require five to ten 0.04-ha ponds. The number of ponds depends on the size of the project (how many cohorts will be produced) and whether production is a two-phase or a one-phase process. The exact size of the ponds can be determined as was described previously and as was outlined in Table 14. The exact size is not that important, but all ponds should be similarly sized. The reason you want small ponds is because a large number can be squeezed into a small space. Additionally, it is cheaper to build a 0.04-ha pond than a 0.1-ha pond.

If selection is a two-phase process, select fingerlings could be restocked in the ponds where they were produced, if the ponds can be drained and refilled in a single day. This would reduce the number of ponds needed for the programme by one-half. The only prerequisites are: all fish must be harvested; the farmer must have holding facilities where he can safely hold the select fingerlings until they are restocked.

Farmers who cannot afford to build the ponds could conduct this breeding programme in large hapas (20-40 m^2) that are placed in one or more ponds. Even though hapas are less expensive than ponds, it is better to use ponds, because if the fish are grown in ponds they should be selected on the basis of growth in ponds, not on the basis of growth in hapas.

Each cohort should be stocked in a single pond; stocking rates for each cohort should be identical, but it is not critical, since selection will occur independently in each cohort. Even though it is not necessary to have identical stocking rates in all ponds, it is advisable to have similar stocking rates, or selection could select for slightly different genes in the different cohorts.

The best way to create the population of fish that will be stocked in each pond is to choose an equal number of fish from each family within a cohort. The fish chosen from each family must be randomly selected; they cannot be chosen because they are the largest, etc. Therefore, families must be isolated until family size is equalized. If the families within a cohort are mixed before the proper number is chosen to create the desired stocking rate, the largest family will be over-represented and the smallest will be under-represented.

When the fingerlings are harvested, the top 35-50% from each cohort (pond) should be stocked in a single grow-out pond. To determine the fingerling cut-off value for each cohort, a sample of 100-200 fingerlings from each cohort should be measured to the nearest millimeter, and the phenotypic value that corresponds to the desired cut-off percentage should be determined, as was outlined in Figure 20. The cut-off value must be determined independently for each cohort, because they are managed as temporary, separate sub-populations during the selection process, and selection will occur independently in each cohort.

As before, the intensity of selection is not that critical, but it must be the same for each cohort. Fish from different fingerling ponds (cohorts) should not be mixed when they are harvested and measured. After selection, the select fingerlings from each cohort should be stocked in a separate food fish ponds. Fish from different cohorts should not be mixed.

As was the case when stocking the fingerling ponds, the stocking rates for the food fish ponds should be the same or at least similar. The select fingerlings in each cohort should be grown using normal production techniques. Just prior to harvest, a random sample of 100-200 fish from each cohort should be measured to determine the cut-off value for each

cohort. The top 10-20% from each pond (cohort) should be saved to form the population of select brood fish. Again, the intensity of selection is not that critical, but it must be the same for all cohorts.

Once the select brood fish have been chosen from each cohort, they can be mixed and stocked into one or two select brood stock ponds. These ponds should contain no other brood fish. As before, a major goal of the selection process is to have at least 100-200 select brood fish. The two-phase selective breeding programme is outlined in Figure 32.

The brood fish should be managed and used to produce fry for the breeding programme and for the production ponds, as was described in the previous sub-section.

If this selective breeding programme were going to be conducted by a scientist at a research station, a major aspect of his experimental plan would be to make all aspects of management identical for all cohorts. But a farmer does not have to worry about this. It would be nice if all cohorts were managed identically during each phase of selection, but because each cohort is stocked in a single pond and because selection will occur independently within each cohort, minor management differences among the cohorts will not affect selection. For example, if one food fish pond is stocked with 5,000 fingerlings/ha and the others are stocked with 4,000 fingerlings/ha, the different stocking rates could affect the average growth rate of the cohorts, but since selection will occur independently in each pond (cohort), it probably will not affect the selection process.

However, large differences in management among the ponds could affect the outcome. For example, if one food fish pond is stocked with 15,000 fingerlings/ha and if cattle manure is used as the sole source of nutrients while the others are stocked with 4,000 fingerlings/ha and if fish are fed rice bran, selection may select for different genes in the differently managed cohorts.

Selection for growth rate and another phenotype

The breeding programmes that have been outlined can be expanded to include another phenotype. If a farmer wants to improve phenotypes other than growth rate, he can easily add traits such as body conformation and/or harvestability. Farmers should use independent culling or modified independent culling to simultaneously improve two phenotypes. Aquaculturists at fingerling production centers should also use independent culling; however, they could use a selection index if they are technically sophisticated and have the expertise and labour needed to conduct this programme.

When independent culling is used, a farmer needs to determine the overall intensity of selection in order to calculate the cut-off percentage for each trait. This process was described in Chapter 4. A farmer should try to save 10-20% of the population at the food fish phase of selection. The phenotypic values that correspond to the desired cut-off percentages should be determined as was described previously and as was outlined in Figure 20.

Body conformation is an important phenotype, and improving this trait can increase yields. A deeper-bodied fish or a thicker-bodied fish will carry more muscle on its frame, which means each fish weighs more per centimeter body length than a normal, streamlined fish.

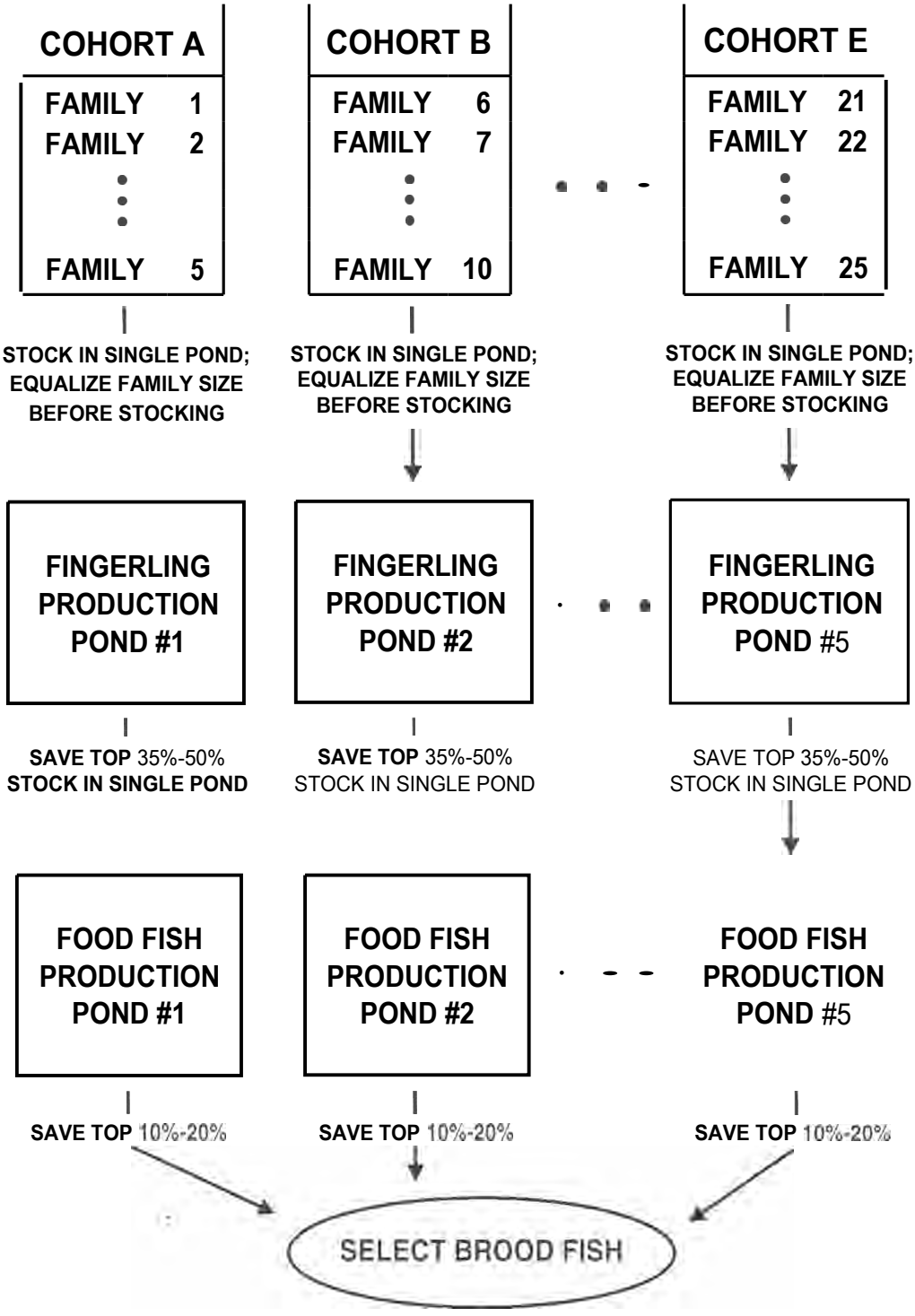


Figure 32. Schematic diagram of a selective breeding programme that uses individual selection to improve growth rate when a farmer cannot synchronize spawning. This selective breeding programme divides the population into age cohorts, and selection occurs independently within each cohort. In the programme outlined in this figure, there are five cohorts (A-E), and there are five families within each cohort. If there is no fingerling phase, step one can be eliminated, and the selective breeding programme can be conducted in five ponds. If the number of families can be increased in each cohort, fewer cohorts will be needed, which will decrease the number of ponds that are required. The fate of the culled fish was described in Figure 29.

Selecting for weight might improve body conformation, but this type of selection does not guarantee that body conformation will be improved. Selecting for weight simply improves average weight, and heavier fish might be fish that are longer, that have larger heads, etc. Improving body conformation has been a continuing goal of many cattle, swine, sheep, and poultry breeding programmes, because animals with better body conformations produce more meat.

One way to improve body conformation is to select for both length and body depth at the anterior margin of the dorsal fin (at the first dorsal fin spine). Since the primary goal of the breeding programmes that are outlined in this chapter is to select for length as a way of increasing growth rate, all a farmer has to do is add selection for body depth, and he will add body conformation as the second phenotype.

Alternatively, body conformation can be improved by selecting for a body length:body depth ratio. This has been done with common carp and it succeeded. However, even though body conformation was improved, average weight did not increase. This occurred because fish were selected only for the body length:body depth ratio. Consequently, small, but deep bodied fish could have become select brood fish. To improve both growth rate and body conformation, both traits should undergo selection.

If selection will occur at the end of both the fingerling and food fish phases of production, the initial act of selection (fingerling phase) can be for length only, as was described earlier. The rate of progress will be slower for body conformation (body depth) than for growth rate (length) if selection for body depth is conducted only on food fish, but if independent culling is conducted twice, a farmer may end up with only a few select brood fish.

When fish are raised in ponds and harvested by seining, harvestability is a phenotype that a farmer might wish to improve. Anyone who has seined a pond knows all too well that fish are experts at escaping a seine. Most farmers never consider the costs of harvesting when they determine annual production budgets, but it can be significant in terms of labour and equipment. Hard-to-capture fish can become stressed and killed as a result of repeated seinings. Finally, fish that are not captured cannot be sold or eaten.

If a farmer wants to produce fish that are easier to capture, he can add this phenotype to his selective breeding programme and select for both growth rate (length) and harvestability by using independent culling. If a farmer decides to select for harvestability, he needs to define it as "fish that are captured during the first seine haul." If this is done, independent culling will be a two-step process: The initial step will be to save only those fish that are harvested during the first seining; all other fish will be culled. The second step will be to select for length in the fish that were saved (seined).

It may be that so few fish are harvested during the first seining that a farmer cannot select for length efficiently or meaningfully. If this is the case, the goal should be modified so that fish that are captured during the first two seinings are saved.

The ability to escape a seine is not only a detrimental phenotype in that it increases production costs, it is detrimental because it can produce slower-growing fish, if a farmer conducts selection for growth rate improperly. If a farmer cultures fish using multiple batch production, selection for growth rate can be done only during the first harvest after the pond is filled.

Thereafter, size and age are confounded, especially if fingerlings are stocked to replace fish that are harvested or if fish can reproduce in the pond.

If a farmer chooses to select for growth rate and for a second phenotype, growth rate will be improved more slowly than it would be if it were the only phenotype under selection. A farmer could select for growth rate, harvestability, and body depth (or any other phenotype he wants to improve) by using independent culling, but the rates of improvement for all three traits would be small.

Family selection

In general, family selection is used when heritability is small and/or when there are uncontrollable sources of environmental variance which obscure genetic differences and which make individual selection ineffective.

Within-family selection is usually used when there is a large environmental source of variance that has a major influence on phenotypic variance at the family level. Chief among these factors are spawning date and age and size of the mother.

Between-family selection is usually used when most of the phenotypic variance is due to environmental sources of variance, and they are felt at the individual rather than at the family level. When this occurs, an individual's phenotypic value does not accurately reflect its breeding value; consequently, individual selection will be ineffective and between-family selection must be used. By comparing family means, a farmer can neutralize much of the environmental component of phenotypic variance, and the family means can be used to assess the average breeding value of every fish in each family.

Between-family selection is also used when animals must be killed before their phenotype can be measured. For example, between-family selection is usually used to improve carcass traits, because animals have to be slaughtered in order to be measured.

Within-family selection

The simplest type of family selection that can be used is within-family selection. This is because each family can be considered a separate sub-population, and selection will occur independently within each family, in a manner similar to that described for individual selection when the population was divided into age cohorts. In this case, each family can be considered a cohort. Unless families can be given permanent family marks, families will have to be cultured in individual ponds or hapas.

The size of the ponds that are needed in this type of breeding programme will depend on the fecundity of the species. With some species, pond size could be as small as 100 m^2. For example, despite their reputation for being incredibly prolific, tilapia produce relatively small families. In general, family size ranges from 50-1,500, depending on the female's size. If the desired stocking rate is 5,000/ha, a family of 50 would have to be stocked in a 100-m^2 pond to achieve that stocking rate. If family size is 50-100 fish, it might be more efficient to raise the families in 10- to 20-m^2 hapas that are suspended in a 0.1- to 0.2-ha pond.

Twenty-five to 50 families should be produced and entered into the selective breeding programme. This means that 25-50 ponds must be constructed for the project.

If the ponds can be drained and filled in a day and if selection is a two-phase process, the number of ponds that are needed can be reduced by one-half if the farmer has holding facilities. When the ponds are refilled, the fingerlings from each family can be restocked into the pond where they were produced.

Twenty-five families is the minimum number that should be entered into this selective breeding programme, because you want 25 males and 25 females to produce offspring for reasons that were described earlier. If a farmer wants to use the minimum number of families, he should produce 27-35 families, because mortalities in some families may reduce family size below that needed to stock a pond with the desired number of fry.

Fish should be spawned and families should be produced as was described for individual selection. Families must be isolated, because selection will be at the family level.

Because each family will be treated as a temporary sub-population and because selection for length will occur independently within each family, minor differences in management among the ponds (families) will not affect the selective breeding programme. This means that a family does not have to be discarded because a farmer cannot stock it at the desired rate. As was the case for individual selection when the population was divided into age cohorts, minor differences in management among the ponds are of little consequence, but a farmer should try to manage all ponds similarly.

At harvest, a sample of 30-100 fish from each family (or every fish if family size is small) should be measured to the nearest millimeter to determine where the cut-off should be placed. In this case, the cut-off value is expressed as the largest 5 or 10 or 20, etc. fish. A farmer should save the top 5-10 males and the top 5-10 females from each family. If no sexual dimorphism exists at harvest, a farmer can simply save the top 10-20 fish from each family. This selective breeding programme is outlined in Figure 33.

This type of selective breeding programme obviously requires more effort than individual selection. If 25 families are raised and if a farmer measures 30-100 fish from each family, he will measure 750-2,500 fish to determine cut-off values, as opposed to the 100-1,000 fish that were needed in the programmes that were outlined for individual selection.

Furthermore, this type of selective breeding programme could stress the fish. A farmer has to measure every fish in each family twice--once to establish the cut-off value and once to determine which fish should be saved.

Once the select brood fish from each family are saved, they can be mated using either of two techniques: The first and easiest is to stock the fish in a single pond and spawn them in a random manner. The second is to use rotational mating, which was described in Chapter 4. If rotational mating is used, either each family must be given a unique mark and stocked communally until the next breeding season when they will be isolated once again for spawning, or each family must be stocked in a separate pond. Rotational mating is very expensive in terms of facilities and labour, and it greatly increases the costs of the breeding programme. For these reasons, the first approach is recommended for most farmers.

The genetic gain should be transferred to the production fish as was described earlier. If possible the select brood fish should be spawned to produce both the F_1 select generation and fry for the production ponds.

If a farmer wants to improve two phenotypes by within-family selection, he can add a second phenotype such as body depth or catchability as was described earlier for individual selection. A farmer must be judicious in his use of within-family selection to improve two or three phenotypes. If family size is small, only one or two fish from each family may be able to meet or exceed all cut-off values. If this occurs, a farmer must either greatly relax his cut-off values or evaluate 100-200 families, which might not be possible on a 2-ha farm.

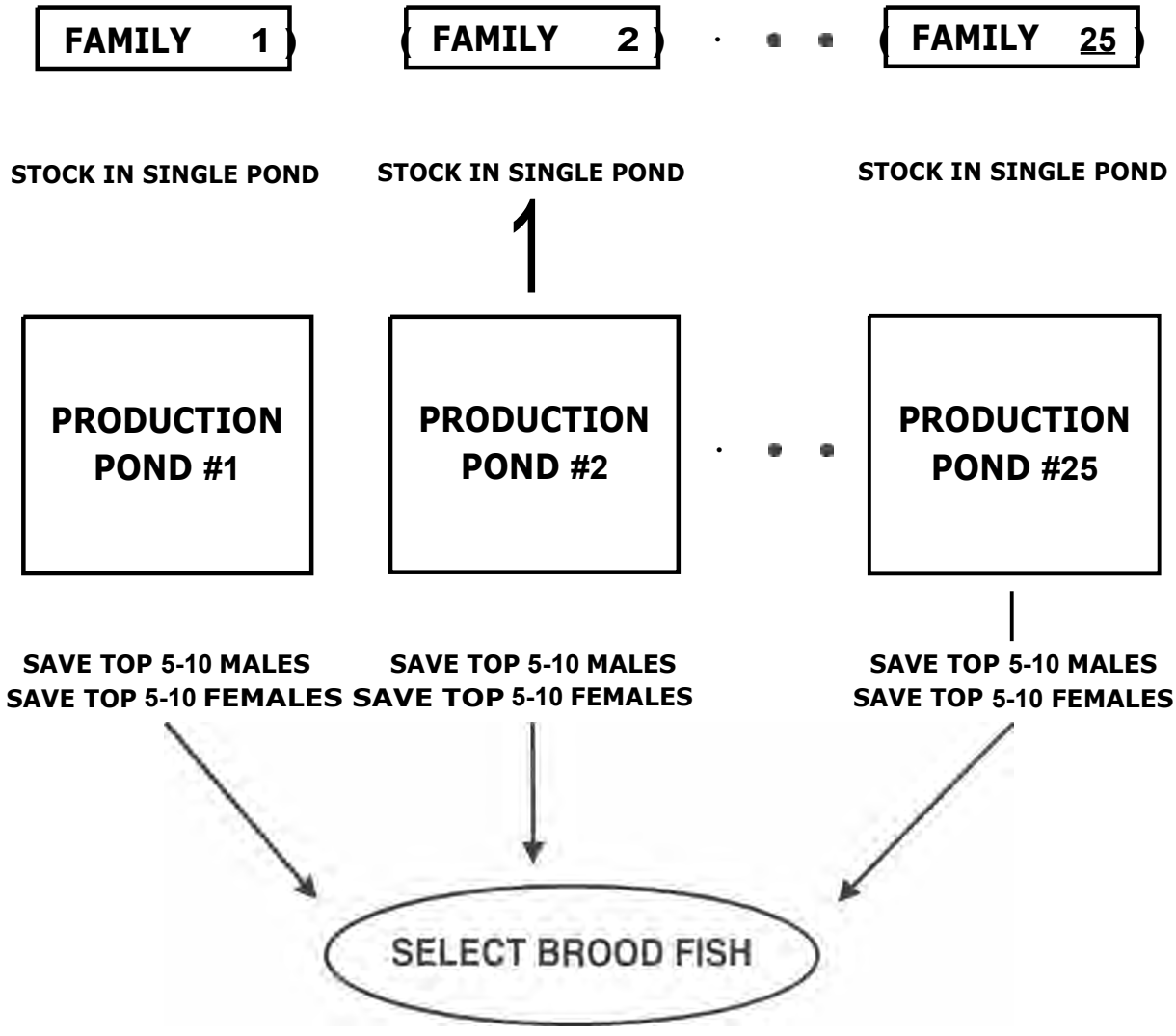


Figure 33. Schematic diagram of within-family selection to improve growth rate. A minimum of 25 families should be evaluated, and each family can be stocked in a single pond. The fate of the culled fish was described in Figure 29.

Between-family selection

Between-family selection is more expensive than individual selection and within-family selection, because it requires more ponds. Because whole families will be saved or culled, a farmer should enter 25-50 families. It is better if a farmer can evaluate 50 families, but the costs will probably be prohibitive for most farmers.

Because family means will be compared, a farmer must raise each family in at least three ponds, and the assignment of the families to the ponds must be random; consequently, a farmer will need 75-150 ponds for this programme. When fish are measured to determine which families will be saved and which will be culled, the means from the three ponds are averaged, and it is the overall mean from the three ponds which is used as each family's mean. Families must be raised in replicated ponds because this is the only way to isolate pond-related size differences from gene-related size differences. If each family were stocked in only one pond, the largest family might be the largest simply because the pond had the best algal bloom.

Because this type of selection requires the use of so many replicated ponds, it might be cost-prohibitive for farmers who only want to produce genetically improved fish for their own use. For example, if a farmer evaluates 50 families, he will need 75 ponds. If each pond is 0.01 ha, he will use 37.5% of his 2-ha farm for the breeding project.

This unfortunate side-effect of family selection can be circumvented only if a farmer is able to give each family a unique mark. If he can, the fish can be stocked communally in one or two 0.1- to 0.25-ha ponds. Even if this is possible, each family must be raised in an individual tank or pond until it can be marked. At harvest, the fish must be separated into families once again, so the farmer must have adequate holding facilities.

Because whole families will be saved or culled, even if production is a two-phase process, selection needs to be conducted only when food fish are harvested. If the farmer wants to select the families twice, he can cull the worst 5-10 families during the fingerling phase of selection. This will make the grow-out phase less expensive.

If there is a large genetic correlation between fingerling size and food fish size, selection can occur at the fingerling phase instead of the food fish phase. This will reduce the costs of the breeding programme because it will reduce the number of ponds that are needed for the food fish phase, since only the select families will be grown to market size. This approach has been used with rainbow trout, and it improved harvest size by indirect selection.

At the end of the food fish phase of production, the top 5-10 families should be saved; these are the select brood fish. A farmer can save either the entire family or a random and equal number from each select family. As before, a farmer should save at least 100-200 select brood fish. This selective breeding programme is outlined in Figure 34.

The one aspect of between-family selection for increased growth rate that can be inexpensive is obtaining data to determine which families should be saved. Because selection is based on family means, the fish from each pond can be batch weighed. If the number of fish that are weighed is known, the mean weight can be easily determined. This will enable the farmer to improve growth rate by selecting for weight rather than for length.

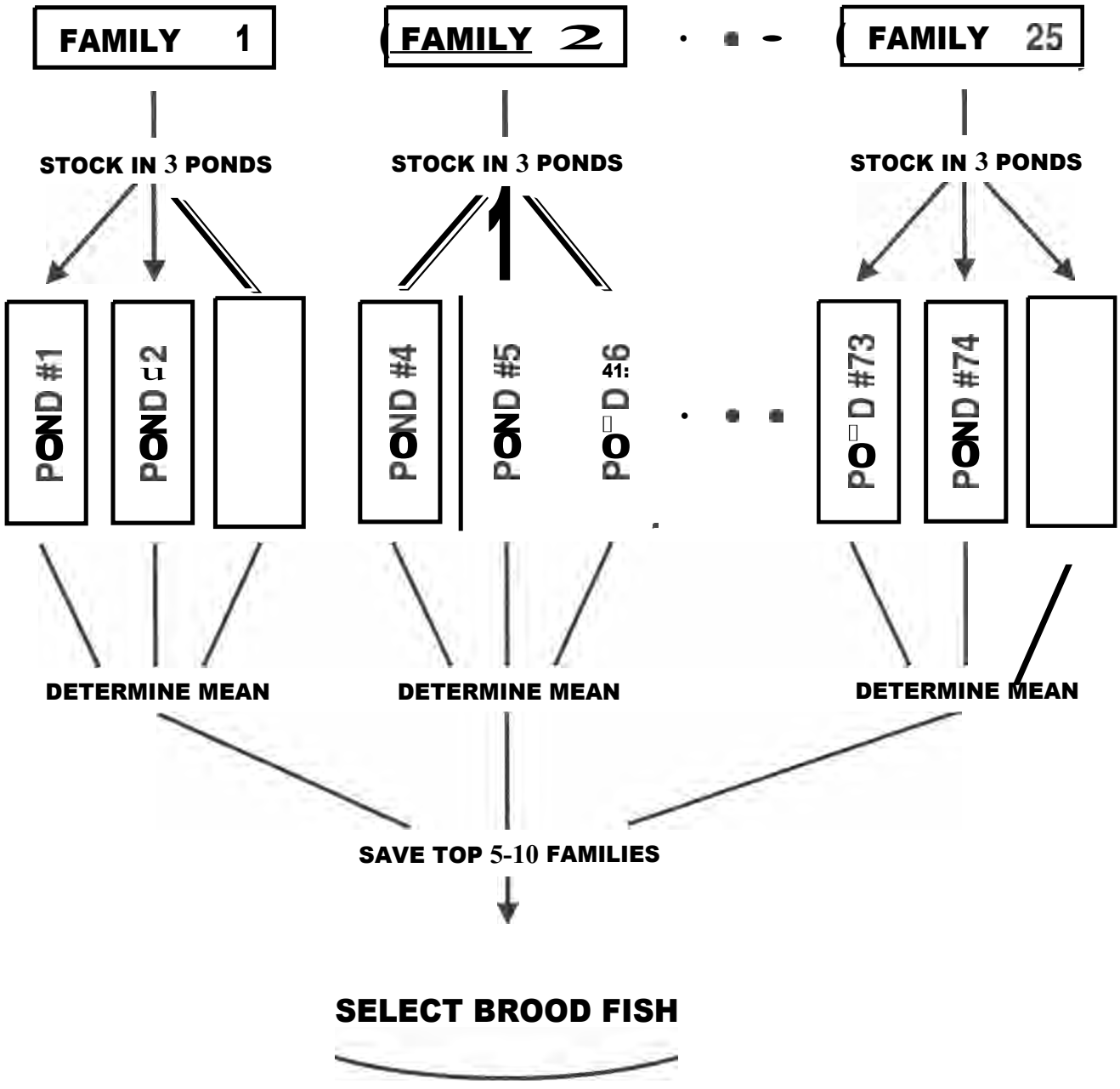


Figure 34. Schematic diagram of between-family selection to improve growth rate. A minimum of 25 families should be evaluated. Because family means are compared, each family must be grown in at least three ponds, and the overall mean of the three ponds is the value that determines whether a family is saved or culled. If the fish can be given family marks, they can be grown in a single pond, but the families must be segregated when they are measured and selected. The fate of the culled fish was described in Figure 29.

In general, between-family selection precludes selection for two or more phenotypes, because only those families whose means meet or exceeded two cut-off values would be saved, and it is unlikely that the top five families for one phenotype would also be the top five for a second. A farmer could improve' two phenotypes by using between-family selection to improve one phenotype and another type of selection to improve a second phenotype.

The select brood fish should be managed and spawned as was described for the within-family selective breeding programme. Again, because it is less expensive, most farmers should mix the select families and randomly spawn the select brood fish. However, if this is done, farmers should be aware of the fact that inbreeding will build to levels that will cause problems within a few generations. This occurs because between-family selection makes the breeding size of the population far smaller than the actual number of brood fish. This type of breeding programme is designed to save fish from only 5-10 families each generation, which means the breeding size of the P_1 generation is retroactively lowered to 10-20, and it is smaller thereafter.

A combinational approach that is often used is to combine between-family and within-family selection. If this combination is used to improve two phenotypes, the first step is to improve growth rate via between-family selection. The second step is to use within-family selection to improve the second phenotype. Of course, between-family and within-family selection can be combined in a two-step selection programme to improve only growth rate. A logical approach, and one that has been successfully used with rainbow trout and coho salmon, is to use between-family selection at the fingerling phase of selection and to use within-family selection at harvest.

If the between-family selection and within-family selection combination is used, it will be expensive. It will combine all of the costs of between-family selection with some of the costs of within-family selection.

Record keeping

Selective breeding programmes work only when farmers keep records. It is probably the least appreciated but most necessary aspect of any breeding programme. Without records, there is no way a cut-off value can be determined, so it is impossible to create a population of select brood fish. Without records, there is no way to determine if a selective breeding programme is succeeding. Without records, a farmer will not know which ponds contain select fish, which ponds contain select brood fish, which ponds contain control fish, and which ponds contain fish that are being grown for market.

Farming is one occupation where record keeping should be considered an integral part of everyday life. Farmers should gather information about spawning success, the stocking rates used, mean size at stocking, the amount of fertilizer used, the amount of feed used, percent survival, mean weight at harvest, yield, etc. If a farmer has this information, he knows what is going on and does not rely on guesses. He knows if yields decreased because of bad weather, and he knows how much they decreased. He knows if yields increased because he used a better quality fertilizer, and he knows how much they increased. If there are no records, he can only guess.

Farmers should keep records of these parameters for every pond. Ponds have individual personalities. Records will indicate which ponds are bad and which are good. This information can also be used to customize management for each pond.

Many farmers do not want to or are unable to keep accurate records. These farmers probably should not be encouraged to conduct a selective breeding programme. If a farmer will not gather the data that are needed to evaluate a programme, he probably will not conduct the programme properly. This could be detrimental on a regional basis because the farmer might tell his neighbors that selective breeding is a waste of time--he will not tell them that it did not work because he did not conduct it properly.

Extension agents could provide record keeping services for hard-working, reliable farmers who are unable to keep records. If selective breeding programmes are kept relatively simple, an extension agent could provide this service for a number of farmers. The only drawback to this approach is that these farmers will become totally dependent upon the extension agent and often will move from one phase of their programme to another only when the extension agent appears. If the extension agent is transferred to another region or retires, the selective breeding programmes could collapse if the new extension agent has other priorities.

What kind of data should a farmer take and what kinds of records should he keep if he is going to conduct a selective breeding programme to improve growth rate or other quantitative phenotypes? First and foremost, a farmer must be able to describe the phenotype he is going to improve via selection. This means he must be able to measure it accurately and quickly and without stressing the fish.

Farmers who take data routinely will be able to incorporate what is needed into everyday management. In fact, if a farmer already records the kind of information that was mentioned earlier in this section, he may be recording these data routinely, so there will be little extra work.

If a farmer is going to conduct a selective breeding programme to improve growth rate by individual selection, he must obtain and maintain data on: the number of fish that spawned, the number of families that were produced, and the dates the families were produced; the families that contributed offspring to the selective breeding programme; the number of fry from each family that were grown; when the fish were stocked; where the fish were stocked; when the fish were harvested; when the fish were measured; phenotypic values; the cut-off value; the spawning success of the select brood fish; the performance of the F_1 select generation, as well as that of the control population. This process is then repeated for the second generation of selection, etc. In addition, a farmer should maintain data about normal, everyday management for every pond used in the selective breeding programme.

Examples of data tables that can be used to gather the information needed to conduct a selective breeding programme by individual selection are presented in Tables 15, 16, 17, 18, 19, and 22 and Figure 20 (in Chapter 4); data tables that can be used to record normal, everyday management will not be presented. The data tables illustrated in this chapter are not immutable. They are simply presented as examples. Any permutation may be used, as long as it is well organized and as long as the data are easily accessible.

Tables 15 and 16 are examples of data tables that can be used to record spawning information for each generation of individual selection. Table 15 is a data table that can be used to record data for a simple selective breeding programme, where the species can be spawned synchronously and where the fish will be grown in a single pond. Table 16 is a data table that can be used to record data for a selective breeding programme where the species cannot be spawned synchronously, and where the fish will be raised and selected in cohorts. Both data tables provide data on the date each spawn was produced, the size of each family, the number of fish from each family that was used in the selective breeding programme, the pond where each family was stocked, and the date the pond was stocked.

Tables 17 and 18 are examples of data tables that can be used to record phenotypic values for individual selection. Table 17 is for a selective breeding programme that will select for only one phenotype, and Table 18 is for one that will incorporate two phenotypes. The tables include information about the group of fish: when the group of fish was produced, when it was stocked, and when the fish were measured (so the age can be determined); the pond in which the population was stocked; the number of families that contributed fish to the population. Both tables are designed for species that do not exhibit sexual dimorphism. If a species exhibits sexual dimorphism and if separate cut-off values will be used for each sex, the tables can be divided into male and female sections or separate tables can be kept for each sex.

Table 15. Example of part of a data table that can be used to record spawning data for a selective breeding programme that will improve growth rate by individual selection; the fish will be stocked in a single pond. The table also includes data on the number of fish stocked per family, the pond in which they were stocked, and the stocking date.

Dates: May 1- May 15, 1995
Pond Nos.: 1, 2, and 3

Stocked on: April 30, 1995

Species: Any fish species
Generation: P, generation. Fish grown will be selected to become F_1 select brood fish.

Date	Spawn	Pond	Weight egg mass (g)	Number of eggs	Number hatched	Number of fry	Used in breeding programme?	Number stocked	Pond stocked	Dated stocked
5/1	1	2	310	9,300	8,370	7,533	no	0		
5/3	2	1	262	7,860	6,681	5,946	yes	150	8	5/8
5/3	3	1	138	4,140	3,643	3,169	yes	150	8	5/8
5/3	4	1	152	4,560	4,332	4,115	yes	150	8	5/8
5/3	5	1	147	4,410	3,175	2,889	yes	150	8	5/8
5/3	6	2	25	750	325	145	no	0		
5/3	7	2	273	8,190	6,879	5,641	yes	150	8	5/8

Table 16. Example of a data table that can be used to record spawning data for a selective breeding programme that will improve growth rate by individual selection; the population will be divided into age cohorts. The table also includes data on the number of families in the cohort, the number of fish stocked from each family, the pond in which the cohort was stocked, and the stocking date.

Dates: May 5- May 15, 1995
Pond Nos.: 3, 4, and 5

Stocked on: May 1, 1995

Species: Any fish species
Generation: P, generation. Cohort A.
Fish grown to become F_1 select brood fish.

Date	Spawn	Pond	Weight egg mass (g)	Number of eggs	Number hatched	Number of fry	Number stocked	Pond stocked	Dated stocked
5/5	1	3	413	12,390	11,151	9,924	200	12	5/10
5/5	2	3	352	10,560	8,976	8,257	200	12	5/10
5/5	3	4	238	7,140	5,640	4,906	200	12	5/10
5/5	4	4	252	7,560	6,350	5,715	200	12	5/10
5/5	5	4	136	4,080	3,876	3,565	200	12	5/10
5/5	6	5	251	7,530	5,647	5,251	200	12	5/10

Table **17.** Example of a data table that can be used to record length measurements at harvest. This data table is designed for a species that does not exhibit sexual dimorphism. In this example, only 30 lengths are recorded.

Harvest Length

Species: Any fish species
Date: October 1, 1995
Stocking Date: March 1, 1995
Number stocked: 1,000 fingerlings

Pond: 23
Spawned: April 20, 1994
Number of families: 27

Lengths in mm

345	354	327	355	330	341	361	357	348	328
329	355	359	369	340	351	349	344	348	345
352	331	333	336	338	342	347	343	344	355

mean: to be calculated

Table 18. Example of a data table that can be used to record harvest data for two quantitative phenotypes. This data table is designed for a species that does not exhibit sexual dimorphism for body size. In this example, length and body depth are recorded for only 4 fish.

Harvest Length and Body Depth
Species: Any fish species
Date: October 3, 1995
Stocking date: March 4, 1995
No. stocked: 1,230 fingerlings
Pond: 25
Spawned: April 2, 1994
Number of families: 29

Fish No.	Length (mm)	Body depth (mm)
1	259	127
2	265	135
3	263	133
4	278	139
Means	= to be calculated	= to be calculated

The data tables illustrated in Tables 17 and 18 record harvest data. These data tables can be used to record data at any time, from stocking to harvest. In the examples, Tables 17 and 18 were used to record **phenotypic values from the sample of fish that were measured to** determine the cut-off value(s). The phenotypic values in Tables 17 and 18 would be transferred to the data table illustrated in Figure 20 to determine the phenotypic value(s) that corresponds to the desired cut-off percentage.

Table 19 is a table that takes the means from Tables 17 and 18 at harvest (or at any other time if selection is done prior to harvest) and records the progress that is being made by the selective breeding programme. Mean lengths for the select population and control population, as well as the genetic gain can be recorded in Table 19.

Tables 19-23 are examples of data tables that can be used to record data from selective breeding programmes that use family selection. Some of the data tables can be used for both individual and family selection, but those illustrated in Tables 20, 21, and 23 are specific for family selection.

Table 19. Example of a data table that can be used to record the mean lengths for each generation, and the progress that is made as a result of selection. This data table can be used for both individual and family selection. In this example, only the first two years' data are recorded.

Selective breeding programme to improve growth rate in: Any fish species

Date	Generation	Original mean	Select population mean	Control population mean	Genetic gain
1994	P_1	315 mm			
1995	F_1		330 mm	321 mm	9 mm

Table 20. Example of a data table that can be used to record spawning data for a selective breeding programme that will improve growth rate by within-family selection. The table also includes information on the pond where each family was stocked, the number of fry stocked in the pond, and when the pond was stocked. Ponds 13 and 15 are smaller than the others, so they were stocked with fewer fish.

Dates: May 1 - May 15, 1995
Pond Nos.: 1, 2, and 3

Stocked on: April 30, 1995

Species: Any fish species
Generation: P_1 generation. Fish grown will be selected to become F_1 select brood fish.

Date	Spawn	Pond	Weight egg mass (g)	Number of eggs	Number hatched	Number of fry	Family	Number stocked	Pond stocked	Dated stocked
5/1	1	1	285	8,550	7,609	6,772	A	200	10	5/7
5/2	2	2	234	7,020	6,458	5,812	B	200	11	5/8
5/2	3	2	27	810	310	175	not used			
5/2	4	2	224	6,720	5,644	4,458	C	200	12	5/8
5/2	5	2	174	5,220	3,915	3,719	D	190	13	5/8
5/3	6	3	157	4,710	4,050	3,523	E	200	14	5/9
5/3	7	3	270	8,100	6,053	5,447	F	185	15	5/9

Tables 20 and 21 are data tables that can be used to record spawning information for each generation of family selection. Table 20 is for within-family selection, and Table 21 is for between-family selection. The information recorded on these data tables are similar; however, they are organized differently.

The data tables presented in Tables 17 and 18 and Figure 20 can be used to record phenotypic values for selective breeding programmes that use family selection. The only difference would be that the data tables would record the family that is being measured.

The data table presented in Table 19 can also be used to record yearly means from a breeding programme that uses family selection. If desired, a separate table can be used to record data about every family.

Finally, the data tables illustrated in Tables 22 and 23 can be used to record the number of fish that spawned each generation. Table 22 is for individual and within-family selection, and Table 23 is for between-family selection.

Table 21. Example of a data table that can be used to record spawning data for a selective breeding programme that will improve growth rate by between-family selection. The table also includes information on the ponds where each family was stocked, the number of fry stocked in the pond, and when the pond was stocked. The table is only partially completed.

Dates: May 5 - May 20, 1995
Pond Nos.: 4, 5, and 6
Stocked on: May 1, 1995

Species: Any fish species
Generation: P_1 generation. Fish grown will be selected to become F_1 **select** brood fish.

Date	Spawn	Pond	Weight egg mass (g)	Number eggs	Number hatched	Number of fry	Family	Number stocked	Pond stocked	Date stocked
5/5	1	4	224	6,720	5,690	5,438	A	200	17	5/12
							A	200	23	5/12
							A	200	8	5/12
5/5	2	4	174	5,520	4,055	3,867	B	200	12	5/12
							B	200	20	5/12
							B	200	11	5/12

Table 22. Example of a data table that can be used to record the number of fish that are spawned each generation for a selective breeding programme that uses individual and within-family selection. In this example, only two years' data are recorded.

Selective breeding programme to improve growth rate in: Any fish species

Date	Number of fish spawned			Number of families used	Number of brood fish contributing offspring	
	Females	Males	Total		Females	Males
1994	27	27	54	25	25	25
1995	35	25	60	34	34	25

Table 23. Example of a data table that can be used to record the number of fish that are spawned each generation, the number of families that are used, and the number of families that are saved for a selective breeding programme that uses between-family selection. In this example, only two years' data are recorded.

Selective breeding programme to improve growth rate in: Any fish species

Date	Number of fish spawned			Number of families used	Number of families saved	Number of brood fish contributing offspring	
	Females	Males	Total			Females	Males
1994	27	27	54	26	10	5	5
1995	35	25	60	32	10	5	4

Conclusion

The selective breeding programmes outlined in this chapter demonstrate that growth rate and other quantitative phenotypes can be improved by relatively simple and inexpensive selective breeding programmes. If possible, individual selection should be used because it is the easiest and least expensive. If fish can be spawned synchronously, a selective breeding programme to improve growth rate can be conducted in only one or two ponds, and it will have little effect on normal farming operations. Even if the species cannot be spawned synchronously, if several age cohorts can be produced, the selective breeding programme will still be relatively simple and inexpensive, and it will have minimal impact on normal farming operations.

If a farmer cannot control spawning behaviour and if he cannot develop age cohorts or if the phenotype that the farmer wants to improve has a small heritability and is strongly influenced by environmental variables, he must use family selection to improve the phenotype. If possible, within-family selection should be used because it is easier and less expensive than between-family selection. However, the most appropriate type of selective breeding programme is determined by the biology of the species, by the phenotype's heritability, and by the type of environmental factors that influence phenotypic expression, not by a farmer's desire to have an inexpensive breeding programme.

The complexity of a selective breeding programme depends on a number of factors: First and foremost is the number of phenotypes that will be improved. Virtually all selective breeding programmes should attempt to improve growth rate. This is the most important phenotype, because faster-growing fish take less time to reach market and faster-growing fish increase yields. Other phenotypes can be added, but a farmer must add only those traits that are truly important, because the rate of improvement for growth rate will be inversely related to the number of phenotypes that he incorporates into the selective breeding programme. At most, a farmer should add only one or two additional phenotypes.

Secondly, the complexity and cost of the selective breeding programme is determined by the way the fish are produced: a single-phase growing system, where fry are stocked in a pond and grown to market; a two-phase system, where fry are grown to fingerlings in one pond and where fingerlings are then grown to market size in a second pond. If fish are produced under a single-phase production system, selective breeding programmes will be easier and less expensive because fewer ponds will be needed. On the other hand, if fish are produced under a two-phase system, selection can occur twice, which means greater gains can be achieved.

Finally, the complexity of the selective breeding programme is partially determined by whether the species exhibits sexual dimorphism for body size. If it does, cut-off values will have to be created for each sex, which means each fish must be sexed in addition to being measured. This doubles the cost of measurement and increases record keeping slightly.

One of the end goals of a selective breeding programme should be to save 100-200 select brood fish each generation. This will ensure that a farmer will be able to spawn at least 25 males and 25 females each generation. If this is done, inbreeding-related problems should be minimized for 5 generations. A farmer also needs to save enough select brood

fish in order to produce sufficient offspring for the next generation of selection. Although this can be a major concern on large farms, it should be of little concern on medium-sized farms.

If the programme is conducted properly, it can be integrated with and can complement normal farming operations. This is important because if there is a conflict, the selective breeding programme will usually be neglected or abandoned; a farmer's top priority is going to be food production.

If there are enough select brood fish, they can be used to produce offspring for both the selection programme and for the production ponds. This will enable a farmer to transfer the genetic gain from the selective breeding programme to the production ponds immediately.

If the select brood fish cannot produce enough offspring for both purposes, they must be used to create the next generation of select fish; any surplus offspring can be stocked in the production ponds. In this case, culls from the selective breeding programme or the previous generation's select brood fish (beginning with the **F2** generation of selection) can be used to produce the production fish. This approach will transfer genetic gain from the selective breeding programme to the production ponds, but the transfer will be delayed; in the extreme, the transfer will be with a one-generation delay. This means a farmer must maintain two sets of brood fish: those used to produce the select generation, and those used to produce the fish stocked in the production ponds. Even if the transfer of genetic gain is delayed by one generation, the mean growth rate and yields that are obtained in the selective breeding programme will allow a farmer to predict the growth rates and yields that he will be able to achieve in his production ponds in the future. Additionally, these data will demonstrate that selective breeding is improving his fish and will also enable him to realize that his selective breeding programme is going to create better fish, larger harvests, and greater profits.

GLOSSARY

Additive gene action - The type of gene action whereby each of two alleles contributes equally to the production of qualitative phenotypes; neither allele is dominant. The heterozygous genotype produces a phenotype that is intermediate between those produced by the homozygous genotypes.

Additive genetic variance (V_A) - The portion of phenotypic variance for a quantitative phenotype that is due to the additive effects of all alleles across all loci. This is the heritable component of variance, and it is exploited by selection. The proportionate amount of phenotypic variance due to additive genetic variance is called "heritability."

Allele - An alternate form of a gene.

Autosomal gene - A gene located on an autosome, which are the non-sex chromosomes.

Autosomal phenotype - A qualitative phenotype produced by an autosomal gene. Autosomal phenotypes are expressed identically in males and females, unless a sex hormone is needed for phenotypic expression.

Autosome - A non-sex chromosome. The autosomes are the pairs of chromosomes that are the same in males and females.

Between-family selection - A selective breeding programme for quantitative phenotypes where selection occurs at the family rather than at the individual level. In this type of selective breeding programme, whole families are either culled or saved, and that decision is based on family means.

Chromosomal manipulation - Biotechnical manipulation of eggs, sperm, or zygotes by temperature or pressure shocks or with chemicals either to alter chromosome set number or to create fish with only a single parent. This is used to create triploid (3N) **or** tetraploid (4N) fish and to create fish that have only a mother (gynogens) or only **a** father (androgens). The creation of triploids is done to produce a population of sterile fish.

Chromosome - The structure on which the genes are located. Chromosomes reside in the nucleus of each cell and, in most species, they occur in pairs. There are two types of chromosomes: autosomes and sex chromosomes.

Cohort - A sub-population. If a population is divided into several groups based on spawning date, the population is divided into age cohorts.

Common phenotype - The normal qualitative phenotype. This is the phenotype that most individual's have. A common phenotype is also called a "wild-type phenotype."

Complete dominant gene action - A type of gene action whereby one allele is expressed more strongly than the other in the production of qualitative phenotypes: the allele that is expressed more strongly is called the "dominant allele," and the other is called the "recessive allele." A gene that exhibits complete dominance produces two qualitative phenotypes: a dominant phenotype and a recessive phenotype. The dominant allele always produces the dominant phenotype and suppresses phenotypic expression by the recessive allele in the heterozygous state; consequently, homozygous dominant and

heterozygous genotypes both produce the dominant phenotype. The recessive phenotype is produced only when a fish is homozygous recessive.

Control population - A population of fish where no selection occurs. The select population is compared to this population to quantify the gain that occurred as a result of selection.

Crossbreeding - A breeding programme where fish from different populations or species are mated to produce hybrids. Crossbreeding is used to exploit dominance genetic variance. In some cases, it can be used to produce monosex populations (e.g., tilapia) or sterile populations (e.g., baitfish). The terms "crossbreeding" and "hybridization" are synonymous.

Crossing over - The exchange of sections of chromosomes (and thus genes) during meiosis. This occurs during tetrad formation.

Cryopreservation - The freezing and storage of gametes (usually sperm) so they can be used at a later date.

Cull - The removal of fish from the population during selection. Culled fish are not allowed to spawn.

Cut-off value - The minimum acceptable phenotypic value during selection for a quantitative phenotype. Fish that meet or exceed the cut-off value are saved; those that fall below the cut-off value are culled.

Diploid (2N) - A fish or cell where chromosomes occur in pairs. Although there are naturally occurring triploid (3N) and tetraploid (4N) species, all fish are considered to be diploids is this manual.

Domestication - The selection process by which the farm (the culture environment and the management programme) and the farmer alter the genetic and phenotypic make-up of a population. This unplanned, non-directed process usually produces faster growing, healthier, calmer, and less aggressive animals that are easier to raise.

Dominance genetic variance (V_D) - The portion of phenotypic variance for a quantitative phenotype that is due to the interaction between the two alleles at all loci. This portion of genetic variance is not heritable because it is destroyed during meiosis; instead, it is recreated in new and in different combinations every generation at fertilization. It is exploited by crossbreeding.

Dominant allele - An allele that is expressed more strongly than its partner allele. When the mode of gene action is complete dominance, the dominant allele completely suppresses the recessive allele in the heterozygous state. When the mode of gene action is incomplete dominance, the dominant allele only partially suppresses the recessive allele in the heterozygous state.

Dominant gene action - The type of gene action whereby one allele is expressed more strongly than the other. There are two types: complete dominant gene action and incomplete dominant gene action.

Dominant phenotype - The qualitative phenotype produced by the dominant allele.

Environmental variance (V_E) - The portion of phenotypic variance for a quantitative phenotype that is due to environmental factors (e.g., spawning date, age of mother, temperature).

Epistasis - A type of gene action where one gene suppresses or alters the qualitative phenotypes produced by a second gene. This interaction usually results in the production of new qualitative phenotypes.

Epistatic genetic variance (V_I) - The portion of phenotypic variance for a quantitative phenotype that is due to the interactions of alleles across loci. This portion of genetic variance is difficult to exploit, and most is non-heritable as a result of the reduction division during meiosis; consequently, it is usually ignored.

Equational division - The division of the replicated homologs that exist in the secondary gametocytes into the gametes. This is final step of meiosis.

F_1, F_2, etc. - The names of the generations that are produced during a breeding programme. The F_1 generation is the first generation of select brood fish, which are chosen from the P_1 generation; F_1-generation select fish are the offspring that are produced by the initial (F_1) generation of select brood fish. The **F2** generation (second generation of selection) is the descendants of the F_1 generation, etc.

Family - A group of fish that have the same mother and father.

Family selection - A selective breeding programme for quantitative phenotypes where selection occurs at the family, rather than at the individual level. Selection is based on family means rather than on individual values. There are two types of family selection: between-family selection and within-family selection.

Fix - **To** make the frequency 100%. The goal of a selective breeding programme that works with qualitative phenotypes is to fix the desired phenotype by fixing the allele that produces it. This will produce a true-breeding population.

Gamete - An egg or a sperm. Gametes are haploid (N).

Gametogenesis - The process by which gametes are produced. The portion of gametogenesis that deals with the reduction of the chromosome complement from the diploid (2N) to the haploid (N) state is called "meiosis."

Gene - The basic unit of inheritance. Genes contain the blueprints that determine the production of phenotypes. Genes are located on chromosomes.

Generation - **The** length of time it takes to replace brood fish with their offspring. In nature, it is the time it takes fish to become sexually mature and spawn. In aquaculture, this time period can be lengthened or shortened, either by retaining the brood fish for a longer period before they are replaced or by speeding up maturity in the offspring via culture techniques. Progress, in terms of gain per year, is partially determined by the generation interval.

Genetic-environmental interaction variance ($V_{G,E}$) - The portion of phenotypic variance for a quantitative phenotype that is due to the interactions between the fish's genes and the environment. It is due to genes that are expressed differently in different environments.

Genetic variance (V_G) - The portion of phenotypic variance for a quantitative phenotype that is due to the genes. There are three sub-components of genetic variance: additive genetic variance (V_A), dominance genetic variance (V_D), and epistatic genetic variance (V_I).

Genome - A fish's entire genetic make-up.

Genotype - The genetic make-up of a fish at the locus (or loci) that produces a specific phenotype. Fish are either homozygous or heterozygous at each locus.

Haploid (N) - A fish or cell that contains only one chromosome from each chromosome pair. Gametes are haploid. Haploid fish will not survive, but they can be created by chromosomal manipulation.

Heritability (h^2) - The portion of phenotypic variance for a quantitative phenotype in a given environment that is due to additive genetic variance ($h^2 = V_A/V_P$). Heritability describes the percentage of phenotypic variance that is heritable. Phenotypes with heritabilities ≥ 0.25 can be improved efficiently by individual selection; those with heritabilities < 0.15 are difficult to improve by individual selection, and family selection is usually used. A heritability > 0.3 is considered to be large.

Heritable - Something that is transmitted from a parent to its offspring.

Heterozygote - A fish with two different alleles at a locus.

Heterozygous - The genotype that occurs when the pair of alleles at a locus are not identical.

Heterozygous phenotype - The qualitative phenotype produced by the heterozygous genotype. A heterozygous phenotype can be produced when the mode of gene action is incomplete dominance or additive.

Homologues - The two chromosomes that combine to form a chromosome pair. One of the homologues comes from the father, while the other comes from the mother.

Homozygote - A fish with an identical pair of alleles at a locus.

Homozygous - The genotype that occurs when the pair of alleles at a locus are identical.

Homozygous phenotype - The qualitative phenotype produced by the homozygous genotype. When the mode of gene action is complete dominance, the recessive phenotype is the homozygous phenotype. When the mode of gene action is incomplete dominance or additive, there are two homozygous phenotypes.

Hybridization - A synonym for crossbreeding. See crossbreeding.

Importance factor - A value derived by dividing the phenotypic mean by the relative importance of the phenotype. Importance factors are used in a modified selection index

to establish the I value (the breeding value) for a fish when conducting a selective breeding programme that incorporates two or more quantitative phenotypes.

Inbreeding - The mating of relatives.

Inbreeding depression - Declines in growth rate, fecundity, etc. and an increase in the percentage of deformed/abnormal fish that occur when inbreeding reaches certain levels.

Incomplete dominant gene action - A type of gene action whereby one allele is expressed more strongly than the other during the production of qualitative phenotypes, but the dominant allele cannot suppress the recessive allele in the heterozygous state. Two copies of the dominant allele are needed to produce the dominant phenotype. Because the recessive allele is able to function in the heterozygous state, that genotype produces a phenotype (the heterozygous phenotype) that is marginally different from the dominant phenotype. The recessive allele produces a third phenotype (the recessive phenotype) when the fish is homozygous recessive.

Independent assortment - The segregation of homologues of each chromosome pair (and the genes on these chromosomes) into the secondary spermatocytes or into the secondary oocyte and the first polar body. The segregation of each chromosome pair is independent of that which occurs in all other chromosome pairs. This process destroys all dominance genetic variance and most epistatic genetic variance.

Independent culling - A selective breeding programme that is used to simultaneously select for two or more quantitative phenotypes. Cut-off values are created for all phenotypes, and a fish must meet or exceed all cut-off values in order to be saved.

Indirect selection - A breeding programme that improves one phenotype by selecting for another. This occurs because the two phenotypes have a positive genetic correlation.

Individual selection - A selective breeding programme for quantitative phenotypes where selection is based on individual merit. An individual whose phenotypic value is equal to or exceeds the cut-off value is saved, while those whose phenotypic value falls below the cut-off value are culled. Family relationships are ignored. Individual selection is also called "mass selection."

Locus (plural = loci) - The location of a gene on a chromosome. The terms "gene" and "locus" are often used interchangeably, and they are used synonymously in this manual.

Mass selection - A synonym for individual selection. <u>See</u> Individual selection.

Mean - The arithmetic average.

Meiosis - The process by which the diploid (2N) complement of chromosomes is reduced to the haploid (N) state during qametogenesis. Heritable mutations, crossing over, and independent assortment occur during meiosis.

Modified independent culling - A variation of independent culling. In modified independent culling, fish that are superior for one trait can be saved, even if their other phenotype's value falls below the cut-off value.

Monosex population - A population composed only of males or only of females.

Mutant allele - An allele that is created when a portion of a chromosome is replicated incorrectly during meiosis.

Mutant phenotype - **A** qualitative phenotype that is produced by a mutant allele; a qualitative phenotype that is different from the normal or common phenotype.

Mutation - **A** mistake that occurs during chromosomal replication. When a mutation occurs, a gene is incorrectly replicated on the new chromosome. This new allele may be capable of producing a different (mutant) phenotype. Many mutant alleles produce lethal or sub-viable phenotypes. The mutation rate for each gene is very low.

P_1 - The parental generation. F_1 select brood fish are chosen from the parental generation.

Phenotype - The physical expression of a fish's genotype. There are two phenotypic categories: qualitative phenotypes, which are described; quantitative phenotypes, which are measured. The terms "phenotype" and "trait" are used interchangeably.

Phenotypic variance (V_P) - The variance that is measured for a quantitative phenotype in a population. It is the sum of genetic variance, environmental variance, and genetic-environmental interaction variance.

Pleiotropy - Secondary effects that occur when fish have a particular qualitative phenotype. Many alleles that control the production of qualitative phenotypes can also affect traits such as growth and survival. **If** growth and survival are affected, the pleiotropic effects can be of greater economic importance than the phenotype (colour or scale pattern) itself.

Population - A group of fish at a fish farm that have a common background.

Progeny testing - A breeding programme that is used to decipher a fish's genotype by examining it offspring's phenotypes.

Qualitative phenotypes - Phenotypes that are described: for example, colour, scale pattern, and sex.

Quantitative phenotypes - Phenotypes that are measured: for example, weight, length, eggs/kg female, and dressing percentage.

Recessive allele - An allele whose phenotype is only expressed when an individual has two copies of the allele (homozygous recessive).

Recessive phenotype - The qualitative phenotype produced by the recessive allele.

Reduction division - The separation (segregation) of homologues of each chromosome pair during the creation of the secondary spermatocytes or of the secondary oocyte and the first polar body during meiosis. This phase of meiosis destroys all dominance genetic variance and most epistatic genetic variance.

Select population - The population that is created by selection.

Selection - A breeding programme whereby a breeder saves only those individuals or families that meet or exceed predetermined phenotypic criteria for quantitative phenotypes or those individuals that exhibit the desired qualitative phenotype. Fish that do not meet these criteria are culled.

Selection differential - The difference between the mean of the select brood fish and the mean of the population from which they were chosen.

Selection index - A selective breeding programme that can be used to simultaneously select for two or more quantitative phenotypes. A selection index assigns a numerical value to each fish (I), based on the individual's phenotypic values relative to the population means and on how important the phenotypes are. Once each fish has received its overall numerical value, the fish are ranked, and selection is based only on these values.

Sex chromosome - The chromosomes that determine sex. They can be morphologically different in males and females, but in most species of fish there is no obvious morphological difference.

Sex-linked gene - A gene located on a sex chromosome. These genes are inherited and expressed differently in males and females.

Sex-linked phenotype - A qualitative phenotype produced by a sex-linked gene.

Sex-reversed - Fish that are one sex phenotypically but the other genetically. Sex-reversed fish are created by feeding sex hormones to sexually undifferentiated fry. Sex-reversed fish can be used to produce monosex populations.

Sexual dimorphism - This occurs when there are marked phenotypic differences between the sexes. The differences can be qualitative in that phenotypes are present or absent, such as colour or breeding tubercles; or they can be quantitative, in that one sex grows faster and is larger. If sexual dimorphism exists for body size, selection for growth rate must be conducted independently in males and females.

Sibs - Brothers and sisters. Fish that have the same mother and father are full-sibs. Fish that have the same mother or the same father, but not both, are half-sibs.

Standard deviation - The square root of the variance. The standard deviation is a value that describes how phenotypic values are disbursed about the mean. When combined with the mean, it is the best way to describe a quantitative phenotype.

Tandem selection - A selective breeding programme that can be used to improve two or more quantitative phenotypes. Initially, you select for only one phenotype for several generations; then you stop selecting for that phenotype and select for the second phenotype.

Test fish - A fish whose genotype is known. Test fish are mated to fish whose genotypes are to be deciphered during a progeny test. Test fish are usually homozygous recessive.

Tetrad - **A** bundle of four chromosomes. Tetrads occur when the homologues of each chromosome pair replicate and then pair-up during the early stages of meiosis.

Trait - A synonym for phenotype. See Phenotype.

Triploid (3N) - A fish or cell where each chromosome occurs in triplicate (the cells contain three sets of chromosomes). Triploids are usually created by temperature or pressure shocks; this type of breeding programme is used to produce sterile fish.

True-breeding - A population that is capable of producing only one qualitative phenotype, because only one allele exists at the locus in question. When working with qualitative phenotypes, the goal of a selective breeding programme is to produce a true-breeding population.

Variance - The average squared deviation of phenotypic values from the mean. It is a value that describes how phenotypes are disbursed about the mean. The square root of the variance is called the "standard deviation."

Wild-type phenotype - A synonym for common phenotype. See Common phenotype.

Within-family selection - A selective breeding programme for quantitative phenotypes, whereby selection occurs at the family rather than at the individual level. In within-family selection, each family is considered to be a sub-population, and selection occurs independently within each family.

Zygote - The cell that is created when a sperm fertilizes an egg. This is often called a "fertilized egg."

RECOMMENDED READING

General textbooks on fish genetics:

Kirpichnikov, V.S. 1981. Genetic Bases of Fish Selection. Springer-Verlag, New York, New York

This textbook contains valuable information about most aspects of fish genetics. The bibliography contains over 2,000 references, and is especially rich in Russian and Eastern European literature. However, the book is written in a highly technical manner for scientists, especially those working with fish genetics.

Tave, D. 1993. Genetics for Fish Hatchery Managers, 2nd ed. Van Nostrand Reinhold, New York, New York.

This textbook is written for extension specialists, government hatchery personnel, and fish farmers. It contains sections on all aspects of fish breeding and includes examples of successful selective breeding programmes with fish. There is a bibliography of over 800 references and a table that lists over 400 heritabilities in fish.

Paper that describes the discovery of a mutant phenotype in a hatchery population of cultured food fish, the studies that were conducted to determine the cause of the deformity, and the breeding programme that was used to cull the phenotype and produce a true-breeding population.

Tave, D., J.E. Bartels, and R.O. Smitherman. 1983. Saddleback: a dominant lethal gene in Sarotherodon aureus (Steindachner) (= Tilapia aurea). Journal of Fish Diseases 6:59-73.

Papers that describe selective breeding programmes that have been conducted to improve quantitative phenotypes in populations of farmed fish. These papers are highly technical, but they provide examples of selective breeding programmes that have been conducted in an attempt to improve growth rate, disease resistance, age of spawning, survival, and other quantitative phenotypes. Some of the programmes were successful, but some were not.

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