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Genetic Guidelines for Fisheries Management

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INTRODUCTION

This manual is a general reference for fishery and hatchery managers. Four major topics are covered: 1) the importance of proper management of the genetic resources of fishes, 2) biological principles underlying the genetics of fish, 3) genetic tools and their application to fish populations, and 4) genetic issues in fisheries management. Readers can find answers to specific questions by accessing the appropriate section of the text. A glossary of technical terms and a comprehensive index are also provided. Technical terms found in the glossary are highlighted in the text at their first usage.

WHY IS GENETICS IMPORTANT FOR FISHERIES MANAGEMENT?

Perpetuation of the resource is the common goal of all fisheries management programs. Genetic factors affect this goal because fish are the product of their genes, the environment, and of the interaction between the two. The genetics of fish, in connection with the environment, determine the quality and persistence of the fishery resource. Fisheries managers must realize that implementation of regulations, stocking strategies, and other management activities affect the genetic make-up of fish stocks. Management activities that impact the genetics of fish stocks include: 1) maintenance of a fishery with adequate natural reproduction, 2) enhancement of a fishery with marginal or inadequate natural reproduction by stocking, 3) rehabilitation of a depleted fishery by stocking or control of harvest, and 4) maintenance of a "put and take" fishery (one with no natural reproduction).

Traditionally, managers have concentrated on manipulation of non-genetic, environmental aspects of fisheries (e.g., harvest control, stocking, and pollution abatement). The problem with this approach is that management activities inadvertently affect the genetic make-up of fish stocks. Management costs due to the effects of management activities on the genetics of fish stocks have not been considered. This last point is particularly unfortunate because relatively small and inexpensive changes in management practices may produce substantial improvements in the genetic integrity of a stock.

Genetic variation is an important aspect of the genetic makeup of managed fish stocks. The long-term utility of genetic variation is that it enables populations to adapt to changing environments. The genetic diversity in a population is a finite resource that can be used up. Humans can "spend" the genetic diversity in populations to mitigate the impact of their own activities in the short-term. The long-term impact on the perpetuation of the populations is uncertain at best and detrimental at worst. It is important, therefore, to rationally integrate the conservation of genetic variation and the stewardship of fisheries resources. The material covered in this manual lays the foundation for this process.

CHAPTER ONE: GENETIC PRINCIPLES

OVERVIEW

In this section we describe the biology underlying the genetics of fish. Individual topics are explained in sufficient detail to allow subsequent discussion of genetic issues in fisheries and hatchery management. Individuals interested in a more complete treatment of any particular issue should consult a recent text. Gardner and Snustad (1981) provide good discussions of topics in molecular genetics. Hartl (1980) is useful for population genetics, and Falconer (1981) is a general reference for quantitative genetics and breeding. Kirpichnikov (1981) gives a thorough treatment of the genetics and breeding of fish. Areas of recent research are reviewed in Wilkins and Gosling (1983). The volume edited by Turner (1984) is a good reference for topics related to the evolutionary genetics of fish.

MOLECULAR GENETICS AND CYTOGENETICS

Molecular genetics and **cytogenetics** are foundations for the genetics of individuals and populations. Molecular genetics is the study of genetic processes at the molecular level. Cytogenetics is the study of genetics at the level of **chromosomes** in cells. The field of molecular genetics has grown tremendously in recent years and, as a result, many new techniques are available for study and manipulation of genes in fishes. Some familiarity with molecular genetics and cytogenetics is essential in order to understand genetic processes and to appreciate the new tools that are available.

DNA

All of the genetic information in an individual fish is contained in molecules of **deoxyribonucleic acid (DNA)**. Molecules of DNA are composed of subunits called **nucleotides**. Each nucleotide contains a compound called a **base**. There are four kinds of nucleotides in DNA because there are four different bases (adenine, guanine, thymine, and cytosine). DNA molecules, as shown in Figure 1, consist of a long ladder of paired nucleotides. A natural twist in the ladder gives the DNA molecule a **double helix** structure.

Nucleotides form **base pairs** in the double helix in a specific manner (Figure 1). Where thymine is found in one strand of the helix, only adenine will be found in the same position of the opposite strand. Similarly, where guanine is found in one strand, only cytosine will be found in the same position of the opposite strand. The two strands of the helix are said to be complementary because of the way nucleotides form base pairs.

Whenever a cell divides, the DNA must be replicated in order to provide each daughter cell with a complete set of genes. An advantage of complementary base pairing is evident during **replication** of the DNA molecule. During replication, the two strands of the DNA helix are separated by **enzymes** so that each strand is available to serve as a template for a new molecule (Figure 1). Individual nucleotides are affixed to each template. Two complete and identical DNA molecules result. The complementary pairing of bases ensures that the replication of DNA is essentially error free.

Figure 1

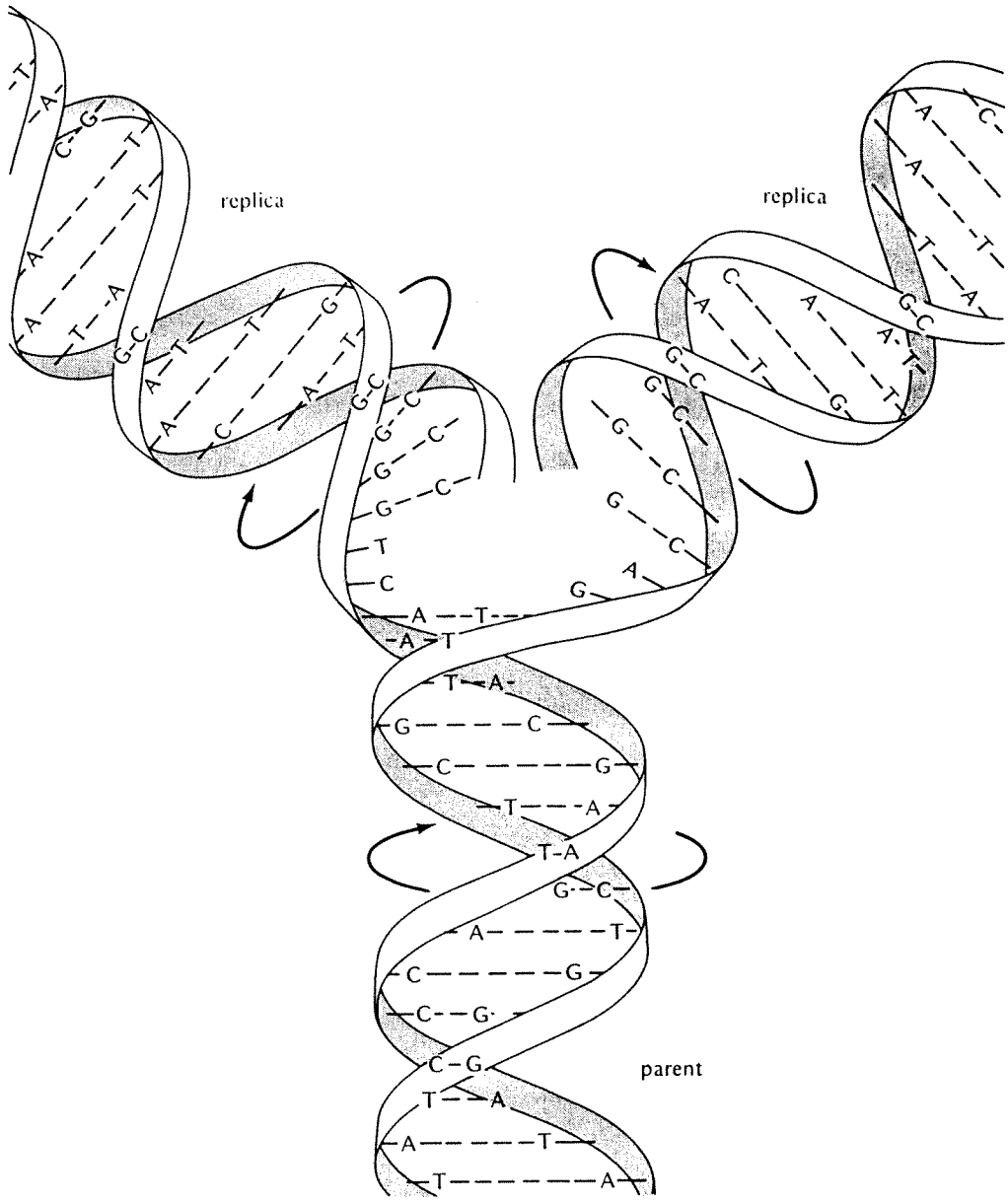


Figure 1. DNA. Nucleotides in one strand are paired with nucleotides in the opposite strand. Adenine (A) pairs only with thymine (T), and cytosine (C) pairs only with guanine (G). Together, the two strands form a double helix. During replication the strands unwind, and serve as templates for the synthesis of two new DNA molecules. (From Strickberger 1976.)

Expression of genes at the molecular level

A **gene** is a sequence of nucleotides occupying a specific position (**locus**) on a DNA molecule. There are three classes of genes including: 1) **structural genes** that code for proteins, 2) genes that code for molecules that are involved in protein synthesis, and 3) **regulatory genes** that do not code for a specific molecule but regulate the functioning of other genes. The immediate product of a structural gene is a specific chain of **amino acids** called a **protein**. The **one gene - one protein concept** provides another useful definition for a structural gene: a structural gene is the DNA that codes for a single protein.

The genetic code

Sequences of nucleotides in structural genes are the templates for amino acids in proteins. The genetic code is a **triplet code** because nucleotide triplets code for individual amino acids. A triplet of nucleotides is called a **codon**. The same genetic code is shared by almost all organisms.

Figure 2 illustrates the correspondence between nucleotides, codons, and amino acids in proteins. Note that the order of amino acids in the protein is the same as the order of the respective codons in the DNA molecule.

Protein synthesis

Genetic control of biological processes begins with the synthesis of proteins. An intermediate molecule (**messenger RNA**) and two processes (**transcription** and **translation**) are involved (Figure 2). Messenger RNA (**mRNA**) is a chain of nucleotides in a single strand, much like a single strand of the DNA helix. During transcription, a strand of RNA is produced which is complementary to one strand in the DNA helix; all of the information in the DNA is transferred to RNA. This property makes RNA an appropriate template for protein synthesis. During translation, enzymes link individual amino acids together using the mRNA as a template. The resulting chain of amino acids is shaped by other enzymes to form the final protein product.

Organization of genetic information in cells

Two types of DNA are found in cells: **nuclear** and **cytoplasmic DNA**. Nuclear DNA is found in chromosomes that are located in the **nucleus** of a cell. Cytoplasmic DNA is found outside of the nucleus in various **organelles** (e.g., **mitochondria**) within the **cytoplasm** of the cell. All of the cytoplasmic DNA in an individual fish is thought to originate from the mother through the cytoplasm of the egg. The sperm of the male is thought to contribute no cytoplasm to the fertilized egg. Most genetic tools and issues of interest to hatchery and fisheries managers involve nuclear DNA. Information about cytoplasmic DNA should not be neglected, however. New techniques, particularly for stock identification, are being developed that make use of cytoplasmic DNA. Furthermore, the suitability of an organism for a particular environment depends on both its nuclear and cytoplasmic DNA.

Chromosomes - structure

Most of the DNA in fish is packaged in chromosomes that reside in the cell nucleus. Each chromosome contains a single strand of DNA. Prior to and during cell division, the chromosomes are condensed. The DNA in **condensed chromosomes** is coiled so that the chromosomes assume a characteristic form and occupy a minimal amount of space. Condensed chromosomes are relatively easy to see using a light microscope.

Heterochromatin are regions of a condensed chromosome that stain more darkly than other regions when chromosomes are prepared for microscopic examination. Heterochromatin gives stained chromosomes a banded appearance with alternating dark (heterochromatin) and light bands (Figure 3). Heterochromatin bands can be useful as markers for stock identification.

Figure 2

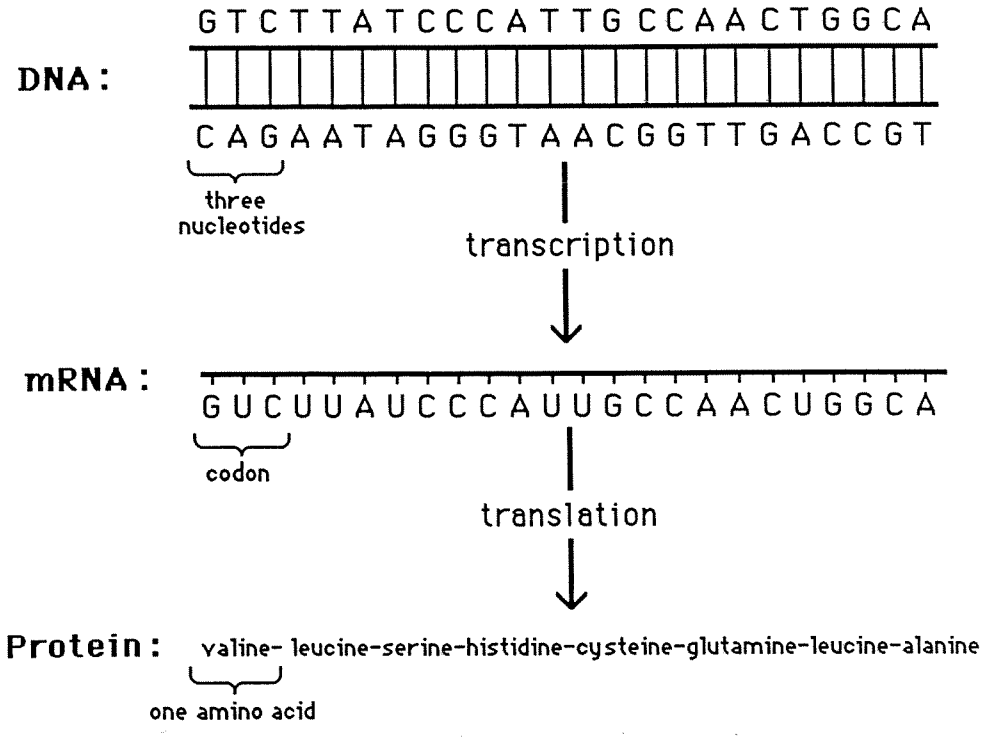


Figure 2. Transcription and translation, a diagrammatic illustration of how genetic information passes from DNA to mRNA to protein. DNA is used as a template for transcription of mRNA. The mRNA is used as a template for protein synthesis during translation. Three nucleotides in DNA specify one codon in mRNA and one amino-acid in the final protein. (After Strickberger 1976.)

Figure 3

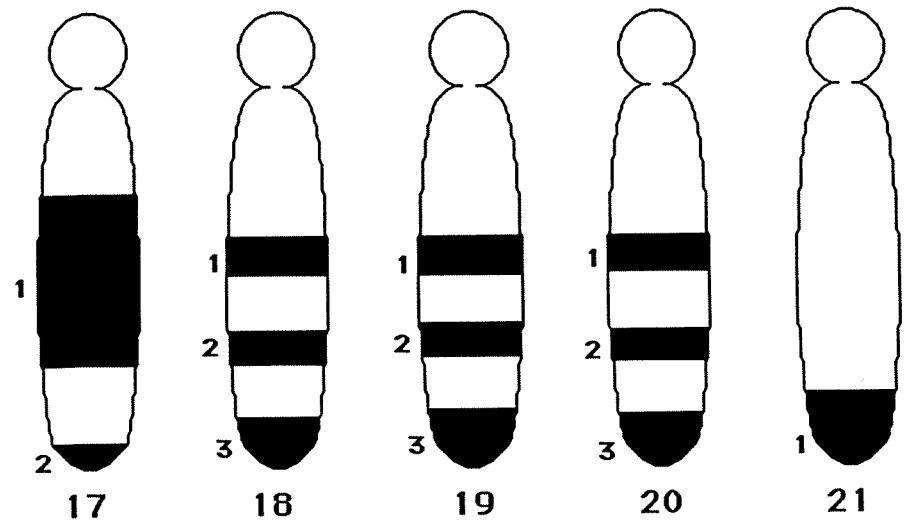


Figure 3. Diagram of chromosomes 17 - 21 of chinook salmon showing location and relative size of quinacrine stained Q bands. The banding patterns may vary between individuals and between populations. (From Phillips et al. 1985.)

Chromosomes - number

The number of chromosomes in **somatic cells** (cells that are not eggs or sperm) differs widely among species but is relatively constant among individuals of the same species. The number of chromosomes in a cell is normally an even number (denoted *2n*) because both parents contribute an equal number of chromosomes to their progeny. The number of chromosomes contributed by each parent through either the egg or sperm is called the **haploid** number and is denoted by *n*. Normal individuals of most species are said to be **diploid** because they have *2n* chromosomes in each somatic cell.

The chromosomes in a haploid cell (egg or sperm) differ from one another in size, shape, banding patterns, and in the genes they carry. In a cell of a diploid individual, pairs of **homologous chromosomes** are distinguishable. Homologous chromosomes originate from the **gametes** (eggs and sperm) of different parents but have the same general shape and carry the same genes.

Variation in the ploidy of individuals is common but is usually associated with reduced viability and fertility. Individuals with a single haploid complement of chromosomes are haploid or **monoploid**; those with more than two haploid complements are **polyploid**. There are various types of polyploids. **Triploids**, for example, have *3n* chromosomes and **tetraploids** have *4n* chromosomes.

Triploid individuals are usually sterile because the triploid genome cannot be split into two parts with equal numbers of chromosomes; inviable gametes result. Tetraploid genomes can be split into two equal parts (each with *2n* chromosomes) and viable tetraploid species of fish are common. Tetraploidy is thought to have played an important part in salmonid evolution (Turner 1984).

Aneuploidy is another kind of variation in chromosome number where there are extra or too few copies of a single chromosome. Individuals with three copies of a particular chromosome are said to be **trisomic**; those with four copies are said to be **tetrasomic**. Aneuploidy in animals usually results in deformity, sterility, and loss of viability.

Sex chromosomes

Sex chromosomes are the major determinants of sex in fish. Chromosomes that are not principal determinants of sex are called **autosomes**. Most fish have a pair of sex chromosomes.

Chromosome aberrations

Chromosome abnormalities occur when chromosomes break and reunite at the broken ends. Multiple breaks may occur on the same chromosome, resulting in deficiencies (loss of chromosome segments), inversions (inverted segments of chromosomes), and duplications (presence of multiple copies of a segment). Multiple breaks on different chromosomes may result in a translocation (a segment of a chromosome inserted into the body of another, nonhomologous chromosome). Duplications and deficiencies of chromosome segments are usually lethal. Translocations and inversions, as in sockeye salmon (Thorgaard 1978), are not necessarily detrimental.

Chromosomes during growth, gametogenesis, and fertilization

Chromosomes are the vehicles of genes. Consequently, the behavior of chromosomes during the life cycle of an organism is very important.

Growth

Cells must divide to replace senescent cells or increase in number. Cell division for growth involves duplication (rather than splitting) of whole chromosome sets because daughter cells are diploid and genetically identical to each other and their precursor.

Mitosis is the division of the cell nucleus. **Cytokinesis** is the division of the actual cell, including the cytoplasm. **Chromosome duplication** is completed before mitosis begins. Figure 4 shows the sequential stages of mitosis: **interphase**, **prophase**, **metaphase**, **anaphase**, and **telophase.**

Figure 4

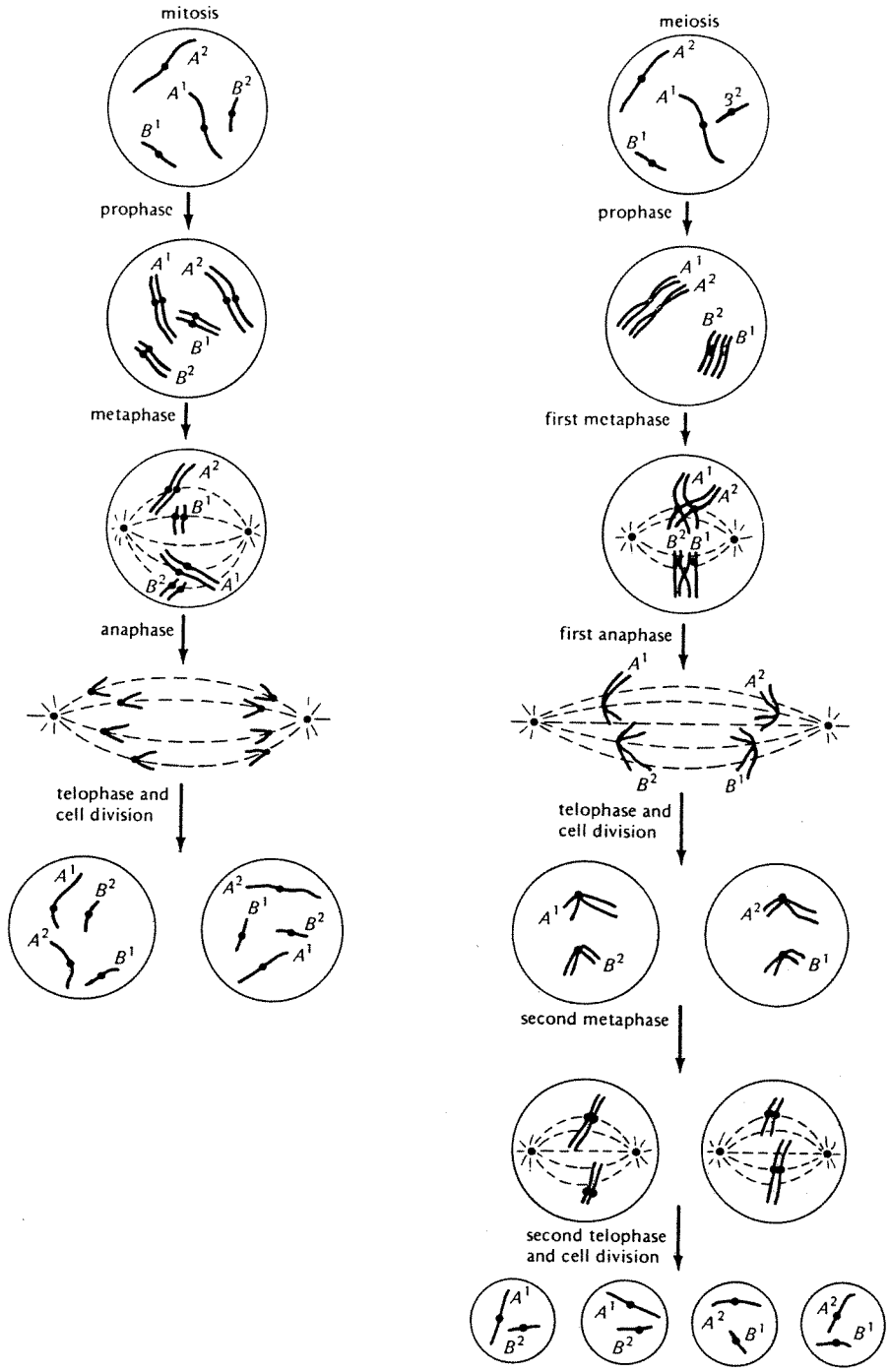


Figure 4. Mitosis and meiosis. Mitosis produces normal diploid (*2n*) somatic cells. Meiosis produces haploid (*n*) germ cells that mature into gametes (eggs and sperm). An important feature of meiosis is that homologous chromosomes form pairs that may cross over at the first metaphase. Chromosome number is reduced from *2n* to *n* after the first meiotic metaphase. (From Strickberger 1976.)

Gametogenesis - segregation and independent assortment

Gametogenesis is the production of gametes. In gametogenesis, the diploid *(2n)* number of chromosomes in somatic cells is reduced to the haploid (*n*) number. Reduction in the number of chromosomes is accomplished through **meiosis**. Two meiotic cell divisions are required (Figure 4). The chromosome number is reduced during the first meiotic division. The second meiotic division results in mature eggs or sperm. Gametogenesis has two important consequences, **segregation** and **independent assortment**, that are known as **Mendel's principles**. The two products of the first meiotic division each contain a single chromosome from every homologous pair found in the parent cell. Homologous chromosomes and their respective genes are said to segregate during gametogenesis because pairs of homologous chromosomes separate into different daughter cells. Independent assortment means that non-homologous chromosomes of maternal and paternal origin segregate randomly so that each gamete receives a mixture of maternal and paternal chromosomes. Because of segregation and independent assortment, the chromosomes in a single germ cell are a complete haploid set and are random mixtures of maternal and paternal chromosomes.

Crossing over

During **crossing over** (also called **recombination**), pieces of chromosomes are exchanged between homologous chromosomes (Figure 5). Crossing over is an important source of genetic variation because genes of maternal and paternal origin come to reside on the same chromosome. Chromosomes in an individual's gametes may differ substantially from chromosomes in the individual's somatic cells because of recombination.

Fertilization

The genetic composition of an organism is determined at **fertilization** when the egg and sperm unite. At fertilization, the diploid *(2n)* condition is normally restored and the cytoplasmic DNA of the egg becomes the cytoplasmic DNA of the offspring. An abnormal chromosome number after fertilization may result from: 1) union of an unreduced germ cell *(2n)* with a normal germ cell *(n)* resulting in a triploid *(3n)*, and 2) hybridization between two species, one with haploid number *n* and the other with haploid number *n'*, producing an offspring with *n+n'* chromosomes.

GENETICS OF INDIVIDUAL ORGANISMS

Genetics at the molecular and cellular level is the foundation of genetics in individual organisms. Similarly, the genetics of individual fish is the foundation for the genetics of broodstocks and populations.

Phenotype and genotype

Every individual has both a **phenotype** and a **genotype**. The genotype is the specific set of genes carried by the individual. The phenotype is the set of characteristics (e.g., morphological, physiological, behavioral) expressed by the individual. The phenotype is produced by the genotype in combination with the environment.

Description of the genotype

There are two representatives of every gene (called **alleles**) in a normal diploid individual because alleles of the same gene occupy the same place (**locus**) on both homologous chromosomes. The genotype is the set of alleles an organism carries at one or more loci in an organism.

Consider a fictitious gene with two alleles denoted *A* and *a*. Three genotypes are possible in a diploid individual: *AA*, *Aa*, and *aa*. Individuals with two copies of the same allele (i.e., those with *AA* or *aa*) are **homozygous** while those with different alleles (Aa) are **heterozygous**. In a triploid individual the number of potential genotypes is larger than in a diploid because all possible combinations of the two alleles taken three at a time (e.g., *aaa* , *aaA* , *aAA* , etc.) must be counted.

Figure 5

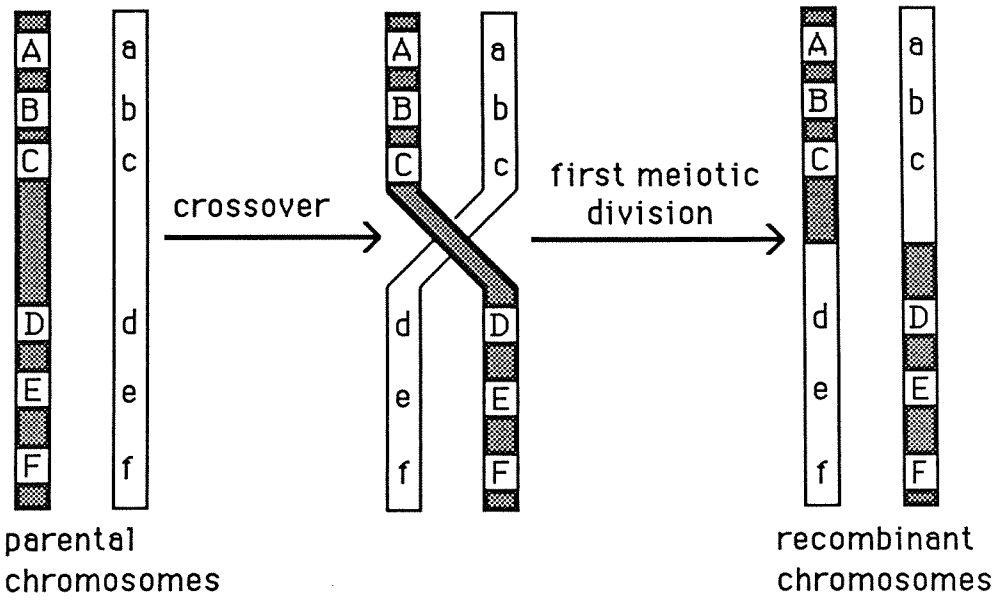


Figure 5. Crossing over between homologous chromosomes during meiosis results in new combinations of alleles on individual chromosomes. (After Strickberger 1976.)

There may be any number of different alleles for a single gene. The number of possible genotypes depends on the number of alleles. For example, with three alleles (*A, a, a'*) there are six possible genotypes in a diploid: *AA, Aa, Aa', aa , a'a'*, and aa'.

We can describe the genotype of a single individual at several loci. Consider two loci, each with two alleles (*A* and *a* at one locus, *B* and *b* at the other locus). There are nine possible genotypes: *AABB, AABb, AAbb, AaBB, AaBb, Aabb, aaBB, aaBb*, and *aabb*. It is apparent that relatively few alleles at only a few loci can generate an enormous amount of genetic diversity. The potential for genetic diversity increases as either the number of heterozygous loci, number of alleles, or ploidy of an organism increases.

Description of the phenotype

The phenotype of an organism is some detectable attribute. The attribute or **trait** may be physical (e.g., size), physiological (e.g., ability to osmoregulate in salt water), or behavioral (e.g., water temperature preference). The attribute of interest may be a **qualitative trait** or a **quantitative trait**. A qualitative trait can be described without measurement, e.g., albinism, presence or absence of dorsal spines, and sex. Quantitative traits are described by a count or measurement, e.g., number of scales in the lateral line or total weight of a fish.

Phenotype, genotype, and the environment

Geneticists study phenotypic variation in order to make inferences about genotypic variation. However, it must be remembered that the phenotype is the product of the environment, the genotype, and the interaction between the two. A particular trait in an organism may or may not be determined primarily by the genotype. For example, a fish that is starved cannot express its genetically determined potential for growth.

Qualitative traits

Qualitative traits are often controlled by a relatively small number of loci and alleles. Furthermore, different genotypes may produce distinct phenotypes so that phenotypic variation among individuals can be attributed easily to variation in genotype. It is often possible to learn how a qualitative trait is inherited because the underlying genetics are relatively simple. Qualitative traits that have a simple genetic basis are called **Mendelian traits**.

Phenotypic expression of qualitative traits

Consider a fictitious locus that controls the presence or absence of dorsal fin rays (a qualitative trait) in a fish. There are two alleles: *D*, associated with normal development of dorsal fin rays and *d*, associated with absence of dorsal fin rays. The three possible genotypes are *DD, Dd*, and *dd*. The phenotypic expression of these genotypes depend on **dominance** (interaction between alleles at the same locus), **epistasis** (interactions between genes at different loci), **penetrance**, and **expressivity**.

Dominance relationships

A **dominant** allele is one that is always expressed phenotypically, regardless of the genotype. A **recessive** allele is one that is expressed only in individuals who are homozygotes for the recessive allele. A locus with two alleles and complete dominance produces only two phenotypes. For example, if allele *D* was dominant to allele *d*, then development of fin rays would be normal in individuals with genotype *DD* or *Dd*. Fin rays would fail to develop only in individuals with the homozygous recessive genotype *dd*.

Codominant alleles are expressed equally in the heterozygote. With **semidominance**, or **incomplete dominance** both alleles are expressed in the heterozygote but not to the same extent. If alleles *D* and *d* were codominant or allele *D* was semidominant, then we would expect normal development for individuals with genotype *DD*, absence of fin rays with *dd*, and an intermediate phenotype (perhaps abnormally small fin rays) in heterozygotes.

Penetrance and expressivity

Genotypes that are not always expressed phenotypically have incomplete or partial penetrance. Genotypes that are expressed to different degrees in different individuals have variable expressivity. For example, the genotype *dd* would have partial penetrance if some individuals with genotype *dd* developed normal dorsal fin rays. If the fin ray development of individuals with genotype *dd* ranged from normal to abnormal to absent, then the genotype *dd* would have variable expressivity.

Inheritance: independent assortment and segregation

The principles of independent assortment and segregation (Mendel's principles) govern the inheritance of all genes but these principles are particularly evident in the inheritance of qualitative traits. Consider two loci each with two alleles. The first locus controls development of dorsal fin rays as in the previous example. The second locus controls pigmentation where allele *P* is associated with normal pigmentation and allele *p* with albinism.

Each haploid gamete gets one complete set of chromosomes and therefore, one complete set of alleles because homologous chromosomes and alleles segregate during gametogenesis. The principle of segregation asserts that an individual with genotype *Aa* produces equal numbers of two types of gametes, one containing *A* and the other containing *a*.

The principle of independent assortment asserts that alleles of different loci assort independently when gametes are produced. Consider an individual with genotype *AaPp*. If alleles at the two loci assort independently, then equal number of gametes with **haplotypes** *AP*, *Ap*, *aP*, and *ap* will be produced. Independent assortment of genes on different chromosomes should come as no surprise. It is surprising, however, that the principle of independent assortment holds generally for genes on the same chromosome.

Genes on the same chromosome which do not assort in a completely independent manner are **linked** and the strength of the linkage is measured by the degree to which independent assortment is observed. Consider two linked genes carried by an individual with genotype *AaPp* (*AP* on one homologous chromosome and *ap* on the other homologous chromosome). Independent assortment (no linkage) would result in gametes with equal numbers of each haplotype listed above. Gametes with only two haplotypes (*AP* and *ap*) would be produced in the complete absence of independent assortment (complete linkage). With incomplete linkage all four haplotypes would be produced but with an excess of *AP* and *ap* and a deficiency of *Ap* and *aP*.

Independent assortment of genes on the same chromosome depends on the exchange of alleles between homologous chromosomes (recombination) during the first meiotic division of gametogenesis. The probability of crossover and the degree of linkage between two genes depends on the distance between them on the chromosome. With greater distance between genes, the probability of crossover is increased and the degree of linkage is decreased.

Sex linked genes

Sex linked genes are located on sex chromosomes. An allele for a sex linked gene is found on a particular sex chromosome so that the genotype of an individual at a sex linked locus can be predicted once the sex of the individual is known.

Sex determination

Sex determination in fishes is **polygenic**, that is, controlled by more than one gene (Kallman 1985). Two types of genes are involved. The first type, called **superior sex genes**, are found on sex chromosomes. The second type, called **male factors** and **female factors**, are found on either autosomes or sex chromosomes and are less important than superior sex genes in the determination of sex.

Superior sex genes are the principal determinants of gender. The sex of an individual can usually be predicted from the combination of sex chromosomes that it carries. Certain combinations of male or female factors, however, may overwhelm the influence of the superior sex genes, thus reversing the sex of an individual. Interactions among male factors, female factors, and superior sex genes result in the diverse array of sexual phenotypes exhibited by fish (e.g., **sex reversal** and **hermaphroditism**).

Quantitative traits

Quantitative traits are described by a count or measurement. Traits that can be described by a simple count, such as the number of dorsal fin rays on a fish, are **meristic traits**. Variation among individuals in a meristic trait is discrete. A fish, for example, may have seven or eight dorsal fin rays but cannot have 7.5 dorsal fin rays. Quantitative traits described by a measurement, such as body weight, are continuously variable. For example, a fish may weigh 7.0, 8.0, or 7.5 grams. Most of the important traits in fish are continuously variable.

Genetic control of quantitative traits

Genetic control of quantitative traits differs from the genetic control of qualitative traits in at least four ways: 1) a large number of genes typically control a single quantitative trait, 2) environmental influences can have substantial effects on the phenotype so that differences in the environments of individuals with the same genotype may result in different phenotypes, 3) the effect of any single gene is usually small, and 4) single genes may affect more than one trait (**pleiotropy**). The number of genes that affect a quantitative trait is so large that it is not feasible to consider them individually.

Phenotypic and genotypic value

It is usually impossible to specify the genotype or genotypes that produce a particular quantitative trait. Genotypes and phenotypes for quantitative traits are linked so loosely that geneticists distinguish between the **genotypic value** and **phenotypic value** of an individual. The phenotypic value of an individual is determined by taking a measurement. For example, the phenotypic value for body weight of a 250 gram catfish is 250 grams. The genotypic value of an individual is the mean phenotypic value of individuals with the same genotype. By averaging over a large number of individuals with the same genotype, extraneous sources of environmental and genetic variation are controlled. Genotypic value is an estimate of the phenotypic value conferred, on average, by a particular genotype.

Phenotypic expression of quantitative traits

The phenotypic value of an individual for a quantitative trait is determined by genes, the environment, and the interaction of genes with the environment. The relative importance of each of these factors varies from trait to trait.

The phenotypic value of an individual can be represented by the sum of genetic, environmental, and interaction effects:

$$P = G + E + GxE,$$

where P is the phenotypic value, G is the genotypic value, E is the **environmental effect**, and GxE is the **genotype-environment interaction**. The interaction term *(GxE)* arises from the possibilities that the same environment will have different effects on different genotypes or that the same genotype may be expressed differently (have different phenotypes) in different environments.

The genotypic value *(G)* can be broken down further into **additive** *(A)* and **non-additive** components. The non-additive components are due to dominance *(D)*, and epistasis *(I)*:

$$G = A + D + I,$$

so that:

$$P = A + D + I + E + GxE.$$

Additive effects result from the cumulative contribution of alleles at all the loci governing a quantitative trait. **Dominance effects** result from interaction among alleles at the same locus. Epistatic effects are due to interactions among loci.

Additive effects

Additive effects of individual alleles are important because they contribute to the breeding value of individuals and are passed to progeny in a predictable manner. The **breeding value** of an individual is judged by the mean phenotypic value of its progeny (Falconer 1981). It is impossible to determine the additive effect of an allele by examining a single individual because the effect is obscured by the other factors that contribute to the phenotype.

Non-additive genetic effects

Non-additive genetic effects include the dominance relationships described above for qualitative traits, **overdominance**, and epistasis. Dominance and epistatic effects are not passed from parents to progeny because the diploid genotypes of parents are dismantled when haploid gametes are produced. Non-additive effects in the progeny will depend only on the diploid genotype and environment of the progeny; they cannot be predicted from non-additive effects observed in the parents.

Overdominance

Overdominance (or **heterozygote advantage**) occurs when the **phenotypic value** of heterozygotes is greater than the phenotypic value of homozygotes. Consider a fictitious locus with two alleles that controls growth rate in a fish. If the growth rate of one homozygote is 10 units while the growth rate of the other homozygote is 20 units, then the predicted growth rate of the heterozygote would be between 10 and 20 units. With overdominance, the actual growth rate of the heterozygote would be greater than 20 units.

Mechanisms for introduction of genetic diversity

Genetic diversity can be induced by **mutation**, recombination, variation in chromosome number, and **hybridization**. Mutation is a change in the DNA resulting from exposure to **mutagens** (e.g., radiation and chemicals) or an error in replication during cell division. Recombination creates new combinations of alleles for genes on the same chromosome. Variation introduced by recombination may be important when genes are linked so that sets of alleles are inherited as a unit and the alleles interact strongly with one another. Variation in chromosome number was an important event in the evolution of the salmonids (Allendorf and Thorgaard 1984). Hybridization, the union of gametes from two different species, results in a new organism. This mechanism for introduction of genetic diversity is useful when management requires organisms with novel characteristics such as sterility (Chevassus 1983).

GENETICS OF POPULATIONS AND STOCKS

The rational management of hatcheries or fisheries requires an understanding of the genetics of groups (**populations** and **stocks**) of fish. In the following section we discuss the genetics of qualitative and quantitative traits in populations. Most of the concepts are explained in the context of **idealized populations**. Managers will note that real stocks of fish differ substantially from these idealized populations. The principles developed for idealized populations, however, can be applied to real stocks. It is easier to discuss genetic issues that relate to real stocks after considering those same issues in the context of idealized populations. The characteristics of an idealized population are: 1) infinite size, 2) random mating, 3) non-overlapping generations (individuals born in one generation do not mate with individuals born in another generation), 4) equal numbers of males and females, 5) no migration into or out of the population, and 6) no mutation or **natural selection**.

Genotypic frequencies

The genetic constitution of a population could be described if the genotype of every individual in the population were known. Consider a fictitious population of 100 individuals and just one locus with two alleles (*A* and *a*). If 25 individuals were *AA*, 50 individuals were *Aa*, and 25 individuals were *aa*, then the **genotypic frequencies** of *AA*, *Aa*, and *aa* would be 0.25, 0.5, and 0.25, respectively.

The description is more complicated when more than one loci or more than two alleles are included. Consider an additional loci with just two alleles (*B* and *b*) and the same genotypic frequencies. The following example completely describes the genotypes at both loci in the population.

genotype	frequency
AABB	0.0625
AABb	0.125
AAbb	0.0625
AaBB	0.125
AaBb	0.25
Aabb	0.125
aaBB	0.0625
aaBb	0.125
aabb	0.0625
	total = 1.000

Note that the loci in this example exhibit independent assortment because the frequency of a combined genotype is the product of the frequencies of the genotypes at each locus. For example, the frequency of *AABB* (0.0625) is the product of the frequency of *AA* (0.25) and the frequency of *BB* (0.25)

The last example included nine combined genotypes because there were two loci, each with three individual genotypes. If there were three alleles at each loci, then there would be six individual genotypes for each locus and 36 combined genotypes. The number of possible combinations for a large number of alleles and loci is staggering. Epistatic interactions among the many combinations of alleles at many loci are one of the important sources of genetic variation in populations.

Allelic frequencies

Allelic frequencies are easily obtained from genotypic frequencies. Consider the genotypes *AA*, *Aa*, and *aa* in the last example. There are 25 individuals with *AA* (50 *A* alleles), 50 individuals with *Aa* (50 *A* alleles and 50 *a* alleles), and 25 individuals with *aa* (50 *a* alleles). There are 200 alleles in total, 100 of *A* and 100 of *a*. The allelic frequency of *A* is 100 / 200 or 0.5 and the frequency of *a* is 100 / 200 or 0.5.

Hardy-Weinberg equilibrium law

Genotypic frequencies in real populations can be predicted from the allelic frequencies only under the conditions of **Hardy-Weinberg equilibrium**. Consider a large idealized population of diploid organisms and a single locus with two alleles, *A* and *a*. The frequencies of *A* and *a* in the population are *p* and *q*, respectively.

According to the Hardy-Weinberg law, the frequency of any genotype in the population after one generation of random mating is the product of the parental allelic frequencies. Genotypic frequencies after one generation of random mating are given by terms in the expansion of $(p + q)^2 = p^2 + 2pq + q^2$. For example, the frequency of the genotype *AA* is the probability that a sperm with allele *A* will find an egg with allele *A*. The probability that a particular sperm or egg carries allele *A* is *p* (the frequency of *A*) so that the probability of a union between two gametes with *A* is $p \times p = p^2$. The frequency of the other genotypes are obtained in the same way. There are two ways to get the genotype *Aa*, either a sperm with allele *A* finds an egg with allele *a* (with probability $p \times q$) or a sperm with allele *a* finds an egg with allele *A* (with probability $q \times p$). The genotypic frequency for heterozygotes is the sum of the two probabilities is $(p \times q) + (q \times p) = 2pq$.

Allelic frequencies in an idealized population do not change from one generation to the next. Genotypic frequencies also remain constant after the first generation of random mating and are said to be in Hardy-Weinberg equilibrium.

The Hardy-Weinberg law holds for loci with more than two alleles. If alleles *A*, *a*, and *a'* have frequencies *p*, *q*, and *r*, respectively than the frequencies of all possible genotypes are given by terms in the expansion of $(p + q + r)^2$.

Changes in allelic and genotypic frequencies

In contrast to idealized populations at Hardy-Weinberg equilibrium, real stocks and populations of fish experience changes in allelic and genotypic frequencies. Two types of processes cause these changes: **dispersive processes** (**inbreeding** and **genetic drift**) and **systematic processes** (mutation, **migration**, and **selection**). Dispersive processes cause changes in allelic and genotypic frequencies that are random in amount and direction of change. Systematic processes cause changes that are consistent and predictable. The allelic frequencies of any population are due to the combined effects of inbreeding, genetic drift, mutation, migration, and selection.

Dispersive and systematic processes have different effects on the genetics of populations. Dispersive processes cause loss of alleles, increased homozygosity, and loss of genetic diversity. Two of the systematic processes (mutation and migration) increase genetic diversity in populations and counteract the loss of genetic diversity by dispersive processes.

Dispersive processes

The allelic frequencies of real populations, especially small populations, do not remain the same from one generation to the next, even in the absence of natural or artificial selection, because of genetic drift and inbreeding. In this section of the manual, the term inbreeding does not imply conscious inbreeding by an animal breeder. Rather, inbreeding refers to matings between related individuals which occur by chance in randomly mating populations.

The consequences of genetic drift and inbreeding are always loss of alleles and genetic diversity and increased homozygosity. The average rate at which alleles are lost depends on the size of the population. In large populations the effects of genetic drift and inbreeding may be counteracted by systematic processes that increase genetic diversity, i.e., mutation and immigration. In small populations the effects of genetic drift and inbreeding overwhelm systematic processes. Theoretically, inbreeding and genetic drift could convert a small population into a single family of homozygous individuals. Another important consequence of genetic drift and inbreeding is genetic differentiation among subpopulations derived from a single, larger population. The allelic frequencies for the subpopulations will diverge over time as inbreeding and genetic drift operate independently in each subpopulation (Figure 6).

Genetic drift

It is easy to illustrate genetic drift with an extremely small, fictitious population. Consider a single locus with two alleles (*A* and *a*) and a population with four members, two females and two males. One male and one female are *AA* while the other male and female are *aa*. The initial frequency of allele *A* is $p = 0.5$ and the initial frequency of *a* is $q = 0.5$. If the male with genotype *aa* died before mating and only the female with genotype *A A* managed to rear her young, all the progeny would arise from the mating between the *AA* male and the *AA* female. Allelic frequencies for the progeny would be $p = 1.0$ and $q = 0$; the progeny would be composed of homozygous individuals belonging to just one family. The loss of one male and one female was very significant in the fictitous population of only four individuals; the same loss would generate a much smaller effect in a population of several thousand individuals.

Inbreeding

In a real population, some families may fail to breed or fail to successfully rear their young so that entire families are eventually lost. As families are lost, the probability of a mating between related individuals increases and the population becomes increasingly inbred. Alleles and genetic diversity are also lost as families are lost.

Systematic processes

Mutation, migration, and selection are systematic processes that change allelic frequencies. The rates and direction of allelic frequency changes can be predicted quantitatively if certain information (e.g.,

Figure 6

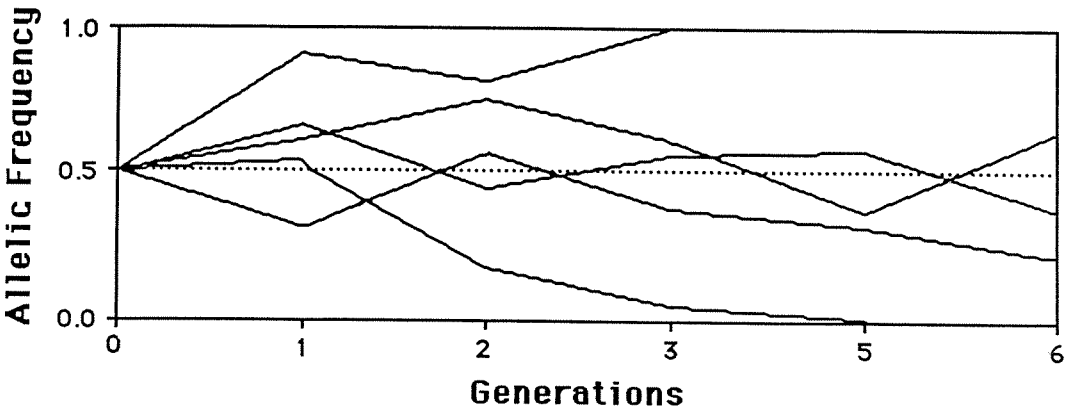


Figure 6. Genetic drift in five fictitious lake trout populations over six generations. Five populations were derived from a single hatchery population by stocking over five separate reefs. The initial frequencies of both alleles at the fictitious locus were 0.5. The y-axis in the figure shows the frequency of one of the alleles. Allelic frequencies diverge over time as genetic drift and inbreeding operate independently in each population. Note that the allele shown becomes fixed (frequency = 1) in one population and is completely lost (frequency = 0) in another. (After Falconer 1981.)

mutation and migration rates) is available. In the absence of such detailed information, the qualitative results of systematic processes can be predicted.

Mutation

Mutation is the source of new alleles. A new allele may be entirely novel or it may be the same as some other allele that previously existed or already exists in the population.

Migration

Movement of individuals between populations with different allelic frequencies can affect the allelic frequencies of the populations involved. Immigration of reproductive adults into very small populations can counteract the loss of genetic diversity due to inbreeding and genetic drift by contributing new or rare alleles to the recipient population. The effects of migration on genetic drift depend on the number of individuals exchanged between populations, not on the proportions of the populations that migrate (Allendorf and Phelps 1981). An exchange of twenty migrants between two populations of 50 individuals, for example, will result in the same rate of genetic drift as an exchange of twenty migrants between two populations of 5000 individuals. A relatively low rate of immigration (about one individual per generation) is sufficient to prevent genetic differentiation (i.e., loss of alleles from one population but not from another) among populations that are exchanging migrants (Allendorf and Phelps 1983). The impact of immigration on genetic diversity is an important issue for fisheries management because stocking and transplantation of fish are artificial forms of immigration.

Selection

Selection occurs whenever reproductive success depends on genotype. Individuals with certain genotypes produce more progeny than do individuals with other genotypes so that genes of the former group increase in frequency with each generation. **Natural selection** is operating if the environmental factors affecting reproductive success (e.g., predation, disease, temperature) are not controlled by humans. **Artificial selection** occurs whenever humans select the individuals that will breed successfully. Selection, whether natural or artificial, can cause changes in allelic and genotypic frequencies.

Effective population size

The **effective population size** of a real population is the size of an ideal population that would experience genetic drift and inbreeding at the same rate as the real population. In an ideal population (i.e., with random mating, no migration, no selection, balanced sex ratio, and non-overlapping generations) the rates of inbreeding and genetic drift depend on the number of individuals in the population. In any real population, however, the reproductive success of individuals varies. For example, some individuals will be too young or old to breed, some females may be more fecund than others, some individuals may not mate, and some progeny will not be viable. These inequities in reproductive success make the effective population size smaller than the number of individuals in the real population.

Inbreeding coefficients

Inbreeding coefficients (also called *F*-statistics) measure the extent and rate of inbreeding and genetic drift (divergence) in wild and hatchery populations of fish. Inbreeding coefficients (denoted *F*) are related to the probability that uniting gametes contain identical alleles derived from a common ancestor. This probability increases (the value of *F* increases) as alleles are lost from the population by inbreeding or genetic drift. Values of *F* can range from zero (no inbreeding or divergence) to one (complete inbreeding or divergence). A stock with an inbreeding coefficient of zero, has maximum heterozygosity. A stock with a coefficient of one is completely homozygous.

Inbreeding coefficients measure the current level of inbreeding and genetic drift relative to a base population, usually the condition of the population at some previous time. The inbreeding coefficient in the base population is assumed to be zero. The base population must be specified by the investigator and should reflect the history of the population and the management objective. If, for example, the objective is to monitor loss of genetic diversity in hatchery broodstock, the condition of the broodstock at

the time it was established in the hatchery is the appropriate base population. The inbreeding coefficient at the time the broodstock was established would be zero and inbreeding coefficients would be calculated to determine how much inbreeding and drift had occurred since the broodstock was established.

A different base population is required to determine how much genetic divergence had occurred between subpopulations of fish that were derived from the same broodstock but planted into different lakes at about the same time. In this case, the condition of the broodstock at the time the lakes were stocked is the appropriate baseline. The inbreeding coefficient would measure how much divergence due to genetic drift and inbreeding had occurred since the subpopulations were established.

The rate of inbreeding and genetic drift is the amount of new inbreeding or genetic drift that occurs in each generation. Not surprisingly, the rate of inbreeding (ΔF) depends on the population size:

$$\Delta F = 1 / (2N_e),$$

where N_e is the effective population size.

Fitness

Fitness is a measure of the reproductive success of individuals or populations. Fitness is a quantitative trait that is the product of many genes and the environment interacting throughout the lifetime of an individual. **Fitness related traits** are traits that have important effects on reproductive success (e.g., survival, growth rate, size at sexual maturity, and disease resistance). The environment can have tremendous influence over fitness. Examples of environmental factors that affect fitness of wild fish populations include availability of suitable forage, predator-prey interactions, fishing mortality rates, and availability of suitable spawning habitat. The fitness of a hatchery population is affected by environmental factors also (e.g., water quality, temperature regimes, loading densities, and feed quality).

Individual fitness

An individual's fitness can be measured by the number of its progeny that survive to reproduction in the next generation. Individuals in real populations have different levels of fitness due to differences in viability, fecundity, and other factors.

Population fitness

The fitness of a population is determined by the fitness of all members of the population. The mean of individual fitness levels is the most common measure of population fitness. Kapuscinski and Lannan (1986) suggest, however, that the probability distribution (the mean as well as the variance) of individual fitness levels in a population is a more appropriate measure of population fitness. The variance of individual fitness levels reflects genetic variation and, therefore, long-term adaptability of the population. They suggest that the shape of the probability distribution can be determined from life history characteristics (e.g., age-structure, fecundity, migration).

Population fitness is generally used as a relative measure. The fitness distributions of two populations can be compared to determine the relative health or vigor of the populations. The distribution of individual fitness levels in a single population may change over time so it may be useful to compare the fitness distributions of a single population at two points in time. The fitness of a population depends on the environment so the fitness of a hatchery or wild stock may change when the fish are planted in new habitats, when harvest methods change, or when major changes occur in the environment.

Inbreeding depression

Inbreeding depression is loss of fitness associated with inbreeding. The loss of fitness is due to decreased heterozygosity (with reduced overdominance) and **fixation** of **deleterious alleles**. Deleterious alleles have a negative effect on fitness; an allele is fixed when every individual in the population is homozygous for that allele. Inbreeding depression is difficult to demonstrate in natural populations but is commonly observed in domestic animals and laboratory populations that are extremely inbred.

Heterosis

Greatest fitness is often observed in populations that have a high level of heterozygosity. A high level of fitness due to heterozygosity is called **heterosis** or **hybrid vigor** and is usually attributed to overdominance at many loci. Hybrid vigor is the increased value of a quantitative trait (e.g., growth rate) in hybrid progeny relative to the two parental lines.

Quantitative genetics of populations

The description of a quantitative trait for an entire population involves taking a measurement from every member of the population or from a representative sample. The distribution of phenotypes in the population can then be described by the mean and variance of the measurements. The mean and variance of a quantitative trait in a population are fundamental values in quantitative genetics.

Components of variance

Analysis of phenotypic variance is essential to understanding and managing the genetics of quantitative traits in populations. Phenotypic variance in a population is due to the same factors that determine the phenotypes of individuals. Consequently, phenotypic variance can be partitioned into genetic and environmental components:

$$V_P = V_G + V_E + V_{GxE},$$

where the total phenotypic variance in the population is V_P, the phenotypic variance due to purely genetic differences among individuals is V_G, the component of variance due to environmental differences among individuals is V_E, and variance due to the interaction between genetic and environmental differences is V_{GxE}. The term V_{GxE} is sometimes assumed to be zero for the sake of simplicity.

The genetic component arises entirely from differences in the genotypes of individuals. The ratio V_G / V_P is a measure of how much of the total phenotypic variation in a population is due to genotypic differences among individuals.

It is useful to partition the genetic component of phenotypic variance into parts due to additive, dominance, and epistatic effects:

$$V_G = V_A + V_D + V_I,$$

where V_A is additive variance, V_D is dominance variance, and V_I is variance due to interactions among genes (epistatic effects).

The term for additive genetic variance describes how much of the total phenotypic variation is passed from one generation to the next in a predictable manner. Additive genetic variance is the property most often exploited by plant and animal breeders in artificial selection programs. The ratio V_A / V_P is called the **heritability** of a phenotypic trait.

Heritability

Heritability (V_A / V_P), denoted h^2, describes the contribution of additive genetic effects to the phenotypic variance of a trait in a population. Heritability values can be used to predict the phenotypic values of progeny from the phenotypic values of the parents because additive genetic effects are passed from one generation to the next. Values of h^2 may range from zero, when there is no additive variance, to one when the phenotypic variance is due entirely to additive effects ($V_A = V_P$). The higher the heritability, the greater will be the resemblance among parents, progeny, and other related individuals.

Heritabilities measured in one environment may not apply in another. The heritability of a particular

trait in a single population depends on the environment (because $h^2 = V_A / V_P$ and $V_P = V_G + V_E + V_{GxE}$). For example, if an environmental change causes an increase in phenotypic variance, then the heritability will decrease because $h^2 = V_A / V_P$ will be smaller. The heritability of a trait in one environment may be different from the heritability for the same trait and the same population after an environmental change. It would be unwise, for example, to formulate a breeding program for largemouth bass in Minnesota on the basis of heritabilities that were estimated in Florida.

Estimation of variance components and heritability

The heritability and variance components for a trait can be estimated in a number of ways. Most methods involve comparison of related individuals (e.g., parent and offspring, mean of both parents and offspring, half-sibs or full-sibs) in an analysis of variance. The details vary among procedures but the ideas underlying the various methods are similar (Falconer 1981; Becker 1984).

Selective Breeding

Selection, response to selection, and heritability are discussed most often in the context of intentional breeding programs. It is important to remember, however, that these concepts apply equally well to natural selection.

Individuals used for breeding in artificial selection programs are usually obtained by breeding all individuals with phenotypic values greater than or less than some cutoff value. The difference between the mean value of the individuals selected for breeding and the mean of the original population is the **selection differential** *(S)*. The predicted response to one generation of artificial selection is easy to calculate once the heritability and selection differential are known:

$$R = h^2 \, S,$$

where R is the **expected response**, h^2 is the heritability, and S is the selection differential. The actual response to selection will differ from the predicted value due to chance, errors in estimation of h^2, changes in environmental conditions, and inbreeding.

CHAPTER TWO: GENETIC TOOLS FOR FISHERIES APPLICATIONS

OVERVIEW

Three categories of genetic tools and techniques that are useful in the management of fisheries and fish hatcheries are described. Tools in the first category are used for stock identification; those in the second category are used for breeding and management of hatchery broodstocks. The third category includes biotechnological tools for creation of fish with novel genotypes.

Each tool is described, along with applications and limitations, in general terms. Readers who want a more thorough description of any particular tool should consult the references cited.

TOOLS FOR STOCK IDENTIFICATION

Description - general

All of the genetic tools for stock identification discussed in this manual involve **genetic markers** of some kind. Genetic markers are phenotypic characteristics (e.g., proteins, chromosome bands, sequences of nucleotides) that can be used to infer the genotype of individuals. Immunological characteristics have been used for stock identification (Ihssen et al. 1981) but are not discussed in this manual because the genetic basis for immunological markers is usually uncertain (Hodgins 1972). Typically, samples of fish from two or more alleged stocks are obtained. The sample frequency of each marker is determined and the frequencies for different samples are compared statistically, for example, by a chi-square test. If there are significant differences in marker frequencies between samples, then there is evidence that the samples were drawn from different populations.

Another common statistical approach is to compute the **genetic distance** between all pairs of samples (Wright 1978). A **cluster analysis** (Sneath and Sokal 1973) of the genetic distance measurements is then used to group together the samples that are similar and to separate the samples that are dissimilar. Samples assigned to the same group may belong to the same or similar populations. The results of such an analysis are usually summarized in a figure called a **dendrogram** (Figure 7).

Verification of genetic markers

Verification of the genetic basis for markers used in a population identification study is important. Investigators usually assume that variation in markers is due to genetic variation. Breeding studies can and should be used to establish the genetic basis of markers used in population identification studies. Other criteria, such as experience with related species, can be applied when breeding studies are too expensive or difficult (Allendorf and Utter 1979). Without breeding studies, however, it is difficult to be sure that variation observed in markers is genetic and not due to environmental differences, developmental stage of fish in the samples, or treatment of samples.

Advantages - general

The tools described in this section will sometimes allow managers to determine if samples of fish are from different populations and to determine the relative contribution of stocks to a mixed stock fishery.

Figure 7

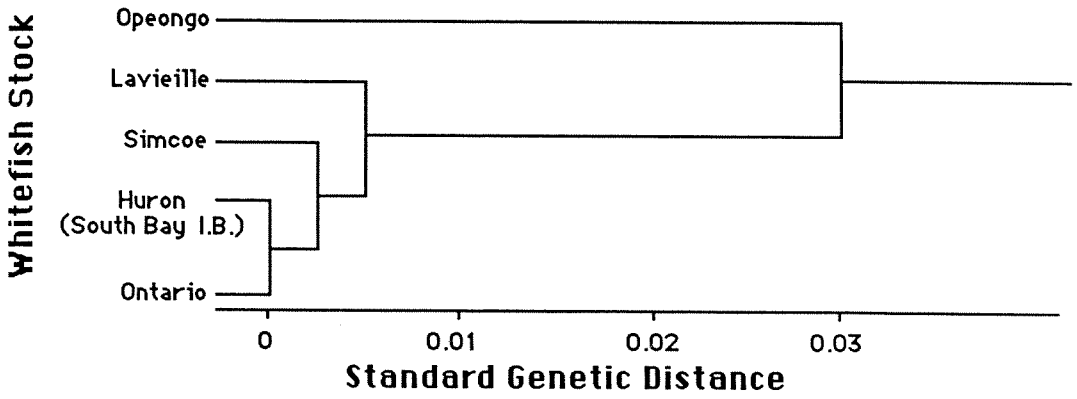


Figure 7. A dendrogram of the standard genetic distances for five southern Ontario lake whitefish stocks, produced by cluster analysis of electrophoretic data. The Huron and Ontario stocks are most closely related. The Opeongo stock is the most genetically divergent stock of the group. (From Ihssen et al. 1981.)

The information obtained using genetic tools can be used in connection with information obtained by other means, such as tagging experiments and analysis of morphological and meristic data (Fournier et al. 1984). Genetic markers occur naturally and are passed from one generation to the next without human intervention so that it is not necessary to tag fish. Genetic markers do not increase the probability of capture by nets as physical tags do.

Limitations - general

None of the tools described in this section allow managers to determine if samples of fish are from the same population. Consider, for example, samples of fish from two different lakes. The samples must be from different populations. It may happen, however, that the samples are indistinguishable on the basis of genetic markers. This example shows how unwise it is to assert that two samples are from the same population just because they cannot be proven different. Genetical techniques for population identification rely on the existence of observable genetic differences between populations. In the absence of observable genetic differences these techniques provide no information about stock structure. There may be an absence of observable differences because only a few genetic markers were examined.

Tools described in this section are not generally useful for determining if a particular population is well adapted to a particular environment. It is usually difficult to determine the adaptive significance of a particular marker.

Genetic markers used in stock identification studies may be difficult to find or expensive to observe. Unlike the tags that can be applied to fish for mark-recapture studies, genetic markers are not unique; many individuals in a stock bear the same mark.

Statistical considerations

Genetic tools for stock identification are plagued by lack of **statistical power** (ability to discriminate between different stocks) in the statistical tests used to determine if samples are from different populations. Statistical power is particularly low when sample sizes are small and marker frequencies are similar (Lewontin 1984; Fairbairn and Roff 1980). Consequently, it may be difficult to reject the null hypothesis that samples were drawn from a single stock.

Allendorf and Phelps (1981) stress that statistically significant differences in the frequencies of genetic markers can exist among stocks even when there is considerable migration between the stocks. A manager cannot be certain that there is no migration between stocks that can be distinguished electrophoretically.

Sampling

Results of stock identification studies can be extremely misleading if samples are not representative of the populations from which they were taken. Consider a sampling program that involved capture of fry emerging from spawning grounds. Very large samples might be obtained that consisted of the progeny of just one or a few matings. Statistically significant differences in marker frequencies among the samples would then be due to differences among a few families, not due to differences among populations (Allendorf and Phelps 1981; Jacobson et al. 1984).

Assumption of selective neutrality

Investigators usually assume that the genetic variation used in stock identification studies is **selectively neutral**, meaning that the markers used have no effect on the fitness of individual fish. This assumption makes interpretation of genetic data easier because differences in the frequencies of genetic markers among samples can be attributed to population differences, not to natural selection. In most cases, the assumption of selective neutrality is probably justifiable, at least as a first approximation (Ihssen et al. 1981). It appears, however, that not all markers are selectively neutral (Gaffney and Scott 1984). Gauldie (1984) argues that the assumption of selective neutrality in connection with **electrophoretic markers** is often unjustified. This issue is the subject of much ongoing debate. Managers should be aware that uncertainty regarding the selective neutrality of genetic markers makes interpretation of genetic data difficult.

Electrophoretic techniques

Electrophoretic tools for stock identification use **polymorphic** proteins as genetic markers. Polymorphic proteins are proteins that serve the same function but differ slightly in chemical structure; **monomorphic** proteins have a single structure. Differences in molecular structure are often due to differences between alleles at one locus; each version of the protein is the product of one particular allele. The proteins used most often in electrophoretic studies are enzymes. Polymorphic enzymes that are products of different alleles at the same locus are called **allozymes**. Often there will be two or more loci in the same organism that produce enzymes with the same general function but have different chemical structures. Polymorphic enzymes that have the same function but are products of different loci are called **isozymes**.

Electrophoresis involves separation of the proteins from a tissue sample in a slab-like gel that is subjected to an electrical field. The proteins are separated on the basis of small differences in electrical charge and molecular size. After the proteins have been separated, they can be stained in such a way that isozymes and allozymes are clearly visible on the gel as bands. Genotypes of individual fish can be easily determined by examining the banding patterns.

Consider a fictitious system of two isozymes, one polymorphic and the other monomorphic (Figure 8) in a sample of four fish that has been analyzed electrophoretically. There are no differences among individuals in the banding patterns on the gel for isozyme one because the isozyme is monomorphic. We can infer that all of the individuals in the sample are homozygous at the first locus.

The differences among individuals in the banding patterns for isozyme two are due to genetic differences among individuals. We note three distinct bands in the patterns for isozyme two and infer that there are three alleles (say *a*, *a'*, and *a")* at the locus in question. Individuals with just one band must be homozygotes because both alleles produce the same band. Individuals with two bands must be heterozygotes because each allele produces a different band. We could expect to see the banding patterns characteristic of all possible genotypes *(aa, a'a', a"a", aa', aa", a'a")* in sufficiently large samples .

Data are obtained by simply counting the numbers of alleles and genotypes observed. Allelic and genotypic frequencies for a sample are the counts for each allele and genotype divided by the total number of alleles or individuals in the sample (Figure 8). The sample frequencies are estimates of the frequencies in the population from which the sample was drawn.

Advantages

Electrophoretic studies enjoy many advantages. A large number of loci and individual fish can be examined in a relatively short time and at moderate expense. Environmental effects on banding patterns are usually unimportant. Genotypic and allelic frequencies can be readily inferred from banding patterns. Workers have accumulated tremendous experience with interpretation of electrophoretic patterns and analysis of electrophoretic data.

Limitations

Conventional electrophoretic techniques (especially those using starch gels) fail to reveal all of the genetic variation that exists. Some proteins that appear to be monomorphic on electrophoresis gels are actually polymorphic proteins that could be resolved using a more efficient technique for separation. Genes that do not produce proteins (e.g., regulatory genes) usually cannot be detected using conventional electrophoretic techniques. This problem amounts to a waste of information since unresolved proteins or other gene products contain information relevant to the problem of stock identification.

Restriction enzyme analysis

Certain enzymes (**restriction endonucleases**) cleave DNA at specific locations called **recognition sites**. Each restriction enzyme cleaves DNA at a single and characteristic recognition point.

Mitochondrial DNA (**mtDNA**) is often used in restriction enzyme analysis because it is relatively easy to obtain from tissue samples and can be compared across taxa. Furthermore, the rate of

Figure 8

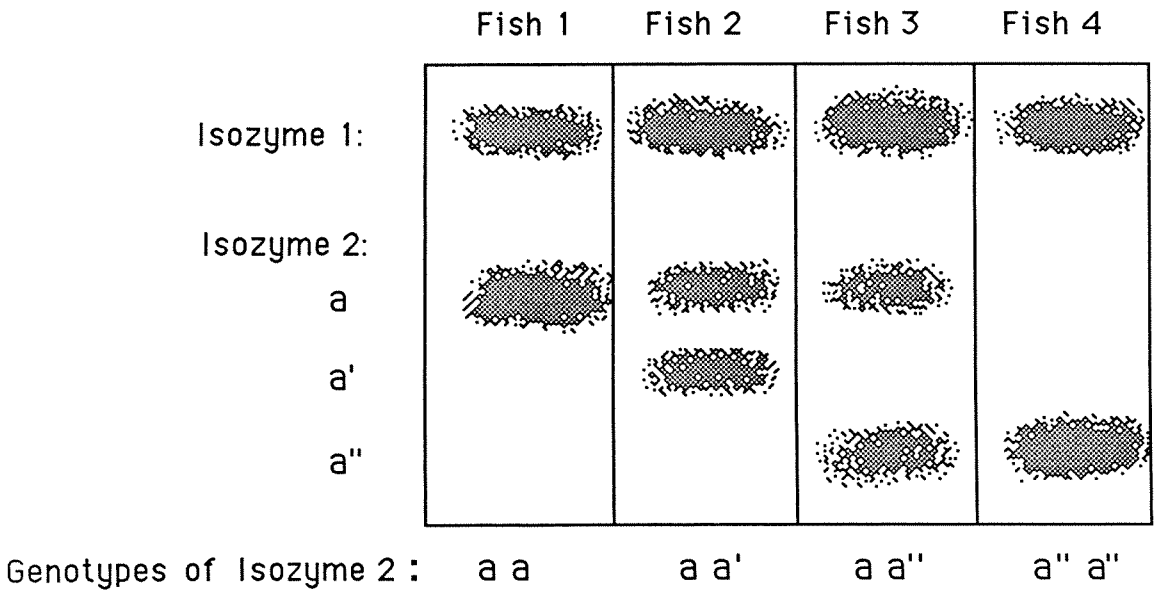


Figure 8. An illustrative example of gel electrophoresis. Isozyme 1 is monomorphic; all four fish are homozygous for one allele. Isozyme 2 is polymorphic; three different alleles (*a, a',* and *a"*) are present. Fish 1 is homozygous *a a* , fish 2 is heterozygous *a a'* , fish 3 is heterozygous *a a"*, and fish 4 is homozygous *a" a"*.

certain mutations is five to ten times more rapid in mtDNA than in nuclear DNA so that genetic differences useful for stock identification are more likely to exist.

Recognition sites can be used as genetic markers because there are differences in recognition sites among individuals and stocks (Avise and Saunders 1984). The mtDNA is extracted from soft tissues and purified. One or more restriction enzymes are then applied and the mtDNA is cleaved. The number and length (number of base pairs) of each of the resulting fragments are determined. Differences in fragmentation patterns reflect genetic differences among samples. For example, if there are four cleavage sites, then the mtDNA, which is a circular molecule, will be broken into four fragments. A single mutation within one of the cleavage sites will prevent cleavage at that site and result in only three fragments after treatment with the same restriction enzyme. Appropriate statistical techniques for data analysis have been developed (e.g., Nei and Li 1979).

Advantages

The most important advantage of restriction enzyme analysis is that it provides additional genetic markers for stock identification. Restriction enzyme analysis deals directly with DNA so that investigators can be sure of the genetic basis for the markers used. The number of polymorphic markers available is potentially large because there are many restriction enzymes and because the rate of mutation in mtDNA is high.

The transfer of mtDNA from mother to progeny with no contribution from the father may be an advantage. It may be relatively easy to find unique markers for individual stocks using restriction enzyme analysis of mtDNA because reproduction by immigrant males will not result in mixtures of markers from different stocks. Additionally, it should prove easy to intentionally mark large numbers of fish (such as those used in stocking programs) in hatcheries because related females can be used to pass the same mtDNA markers to an entire yearclass of progeny.

Limitations

Restriction enzyme analysis is expensive and requires special laboratories and trained personnel. The biology and inheritance of mtDNA are not fully understood. Furthermore, although a good deal is known about differences in mtDNA among populations and taxa of certain animals, very little is known about variation within populations. Many of these limitations are due to the relative infancy of the technique and should disappear as experience accumulates.

Cytogenetic tools

Cytogenetic tools for population identification involve morphological characteristics of chromosomes (usually banding patterns) as genetic markers. Morphological features of chromosomes, like genes, are passed from one generation to the next in a Mendelian fashion. To date, cytogenetic tools have been seldom used for population identification (Ihssen et al. 1981; Thorgaard 1983) but new techniques for staining heterochromatin bands on chromosomes are making cytogenetic tools more useful (Phillips et al. 1985).

The use of cytogenetic tools requires examination of individual chromosomes. Metaphase chromosomes are usually used for cytogenetic analysis because they are condensed, have distinct shapes and can be obtained readily from rapidly growing tissues. Chromosomes from cells are stained to make the bands visible and then examined under a light microscope. Data from cytogenetic investigations (e.g., frequencies of banding patterns in samples) are analyzed in the same manner as allelic frequencies obtained from electrophoresis.

Advantages

The principal advantage of cytogenetic methods is the possibility of additional genetic markers for population identification. Cytogenetic tools may make an important contribution when genetic markers are difficult to find by other means.

Limitations

Time, difficulty, and expense involved in sample preparation and data collection are the principal limitations of cytogenetic methods. The use of cytogenetic tools for population identification is

complicated by the fact that chromosomes of fish tend to be smaller and more numerous than the chromosomes of other vertebrates. Ihssen et al. (1981) review the limitations associated with cytogenetic analysis and suggest ways to avoid them.

TOOLS FOR BREEDERS AND HATCHERY MANAGERS

Tools discussed in this section are the classic breeding techniques for improvement of quantitative traits in animals. These tools are of greatest use in aquaculture and hatcheries. Many of the tools (e.g., **mass selection**, **family selection**, **multiple trait selection**) make use of additive genetic variation for improvement of fish strains. Others (e.g., **hybridization**) make use of nonadditive genetic variation. Several techniques (e.g., **rotational line crossing**, **outcrossing**) can be used to lessen inbreeding in broodstocks. Some techniques (e.g., **indirect selection**, **sib selection, progeny selection**) can be used when the phenotype is difficult to measure or, as in the case of dressed weight, cannot be measured without killing the fish. The tools described in this section can be applied to the improvement of one phenotypic trait or to the simultaneous improvement of several traits (multiple trait selection).

Estimation of heritability

Artificial selection programs that make use of additive genetic variance require heritability estimates for the traits involved. Heritability estimates allow breeders to estimate the response to a selection program as well as time and cost required to reach the desired goals.

One of the easiest methods for estimating the heritability of a trait is to compare the mean phenotypic value of **full-sibs** (individuals that have the same two parents) to the mean phenotypic value of their parents (**mid-parent mean**) in a regression analysis. In a randomly mating population the slope of the line obtained from a regression of full-sib means on mid-parent means is exactly h^2, the heritability (Figure 9).

Heritabilities for many commercially important and fitness related traits in fish have been calculated and are reviewed by Gjedrem (1983) and Kinghorn (1983). Generally, heritabilities are lower in fish than in domestic animals and poultry.

Mass selection

Mass selection (also called **individual selection**) is the simplest form of artificial selection. The best individuals are selected from a population for breeding and the remaining individuals are discarded. The progeny of the selected individuals are usually better, on average, than the original population. Mass selection can be repeated in each new generation until the desired change in the mean phenotypic value of the population is obtained.

Predicting the response to mass selection

Improvement due to mass selection is predictable (Figure 10). The difference between the mean phenotypic value of the population and the mean phenotypic value of the individuals selected from the population for breeding is called the selection differential. Note that the selection differential can be either positive or negative, depending on whether selection is for increased or decreased phenotypic value. The **intensity of selection** is a standardized measure of the selection differential. The intensity of selection is computed by dividing the selection differential by the standard deviation from the original population. In general, the number of individuals that can be used for breeding decreases as the selection differential increases or the size of the population decreases.

Figure 9

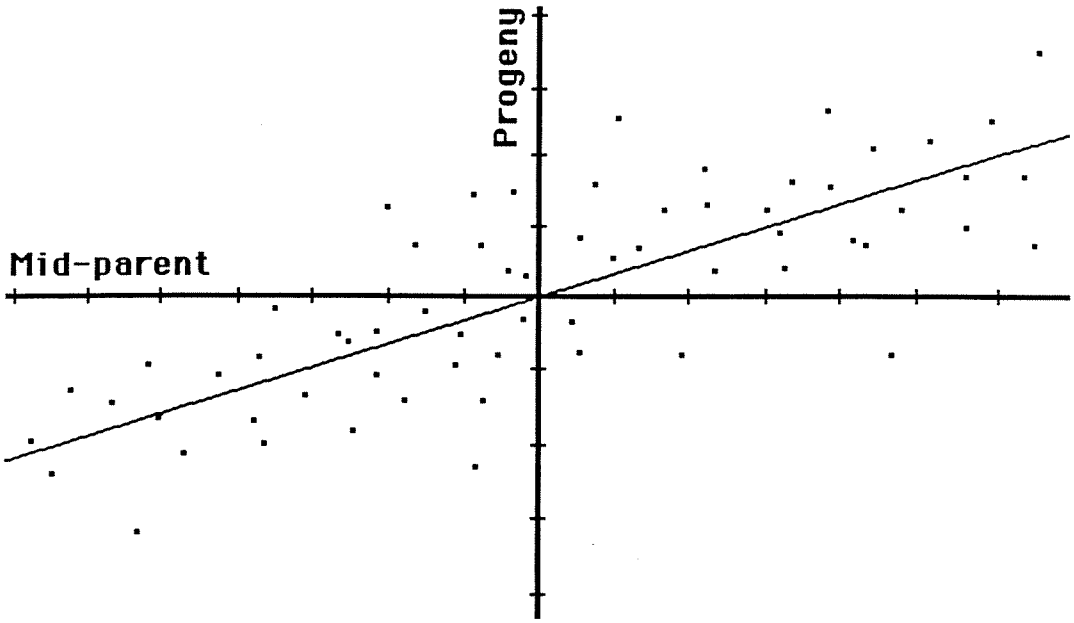
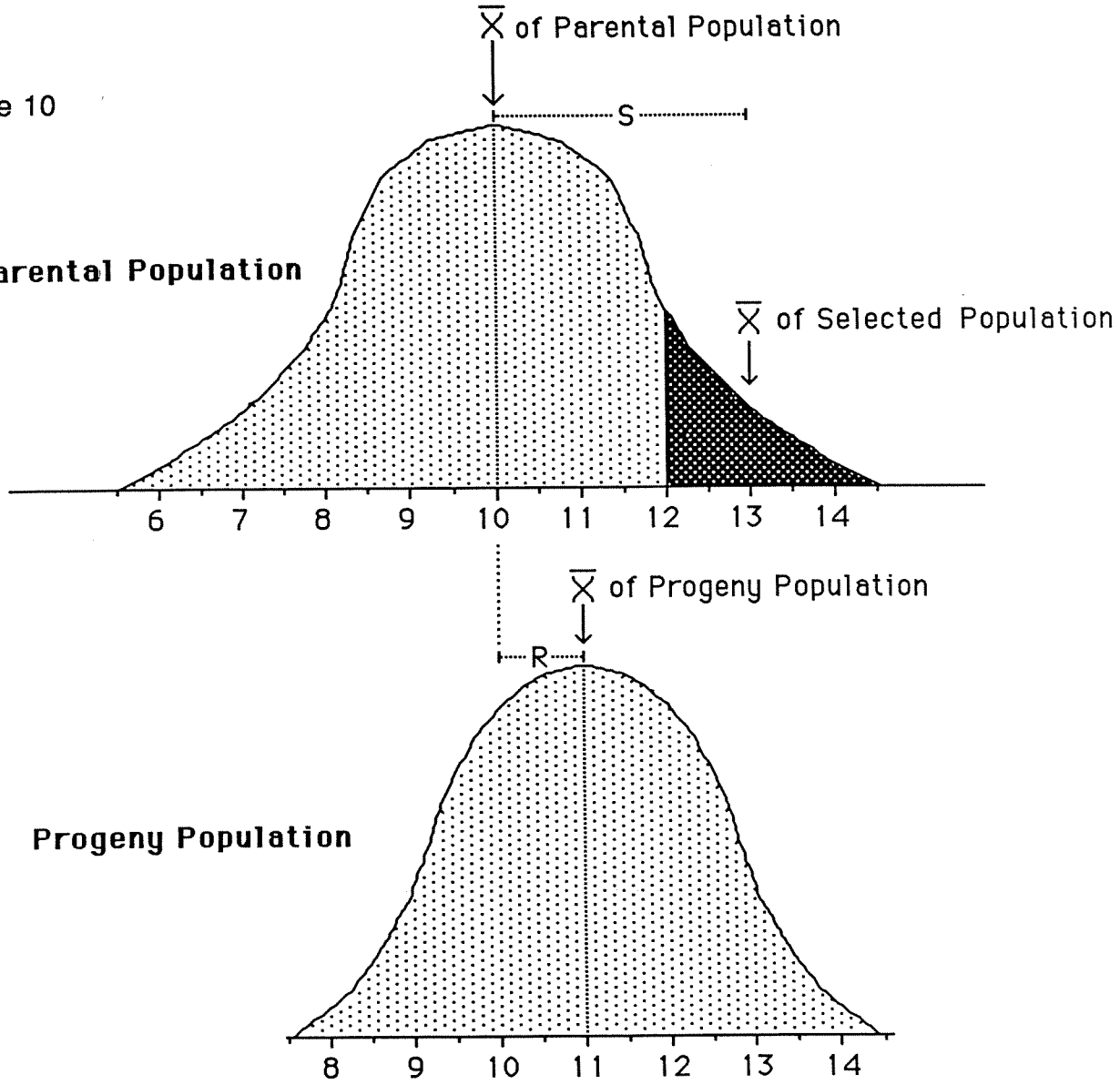


Figure 9. Estimation of heritability by regression of the phenotypic value of the progeny on the mean phenotypic value of the parents (mid-parent mean). In this fictitious example, the heritability (h^2) of six month weight in a hatchery population of lake trout is estimated by the slope (b) of the regression line; $b = h^2 = 0.33$. (After Falconer 1981.)

Figure 10



Selection Differential = S = 13 - 10 = 3 grams

Heritability = h^2 = 0.33

Response = $S \times h^2$ = 3 x 0.33 = 1 gram

Figure 10. An illustrative example of response to mass selection. A population of lake trout had a mean weight of 10 grams at six months of age. The adults selected for breeding (the dark section of the parental distribution) had a mean weight of 13 grams at six months of age. The selection differential S = 13 - 10 = 3 grams. The heritability for weight at six months of age is 0.33, so the predicted response to one generation of mass selection is $R = S h^2$ = 3 x 0.33 = 1 gram.

The **response to selection** is the difference between the mean of the progeny from the selected parents and the mean of the original population. The expected response to one generation of selection is given by the product of the selection differential and the heritability:

$$R = S\,h^2,$$

where R is the response to selection, S is the selection differential and h^2 is the heritability. If one generation requires x years then the expected response to breeding is R/x units per year. Note that the sign and direction of R is the same as the sign and direction of S. Note also that the response to selection is always less than the selection differential because h^2 is always less than one.

Pitfalls in the prediction of response

It is important to remember that the expected response to a unit of selection differential will change if the heritability changes. Heritability (V_A / V_P) will change if the environment (which contributes to the total phenotypic variance, V_P) or the amount of additive genetic variation (V_A) in the population changes. Estimates of the heritability for a trait are usually obtained under experimental conditions that are unlike the environmental conditions in a production scale hatchery or rearing facility. Consequently, estimates of heritability obtained under experimentally controlled conditions may not apply in the environment of a hatchery or rearing facility. If the heritability estimate is inappropriate, then calculation of the expected response to selection will be misleading. Changes in the environment of the production facility (e.g., water temperature, feeding) will also affect heritability and the response to selection.

A final note of caution is that heritabilities are population specific. The amount of additive variance, phenotypic variance, and the heritability for a trait varies from population to population. The predicted response to selection for a population may be unreliable if the heritability estimate was obtained from a different population.

Advantages

Mass selection is simple and works well when the heritability is high (> 0.3) and the population is large so that large selection differentials can be employed.

Limitations

Mass selection is ineffective when the heritability is low (< 0.3) or the population size and selection differential are small. Large selection differentials cannot be used with small populations because few individuals would be used as parents and inbreeding would result. Under circumstances of low heritability and small populations, other breeding schemes (e.g., family selection) perform better.

Family selection

Family selection is used when the heritability for mass selection is low. Family selection involves choosing entire families, usually groups of full-sibs or **half-sibs** (half-sibs are individuals that share one parent), rather than individuals for breeding. Families are selected on the basis of their mean phenotypic value. Phenotypic values of individuals are ignored except in calculation of the means for families.

The heritability for family selection is often larger than the heritability for mass selection because most of the variance among family means is genetic variance. Environmental variance among family means is reduced by raising the families in similar environments and by averaging over a large number of individuals in calculation of the family mean.

The predicted response to one generation of family selection is given by a familiar looking formula:

$$R = S'\,h^{2\prime},$$

where R is the response, S' is the selection differential between the mean of the selected families and the mean of the population, and $h^{2\prime}$ is the heritability for family selection.

The number of families that a breeder can maintain is usually small so the families used for breeding must be selected from a relatively small group. Consequently, selection differentials used in family selection programs are usually smaller than those used in mass selection programs. The increased heritability is usually sufficient to offset the reduction in selection differential.

Advantages

Family selection can produce an acceptable response to selection when the heritability for individual selection is low.

Limitations

Increased complexity and the resources required to rear a large number of families are the principal limitations of family selection. Detailed records must be kept and families of fish must be maintained separately. Inbreeding may be an obstacle if the effective size of individual families is small.

Progeny and sib selection

Progeny and sib selection are variations of family selection. Progeny selection involves selection of individuals for breeding on the basis of the mean phenotypic value of their progeny. The "families" in the case of progeny selection are groups of progeny (either full- of half-sibs). The principal advantage of progeny selection is that relatively small families can be used to determine which families should be used for broodstock. After the families are selected, the size of the best families can be increased by allowing the original parents to continue breeding. The principle disadvantage of progeny selection is lack of speed. The response to selection per unit of time is low because of the time required to breed and evaluate families.

Sib selection is useful when the phenotypic value of an individual (e.g., carcass weight) cannot be determined without destroying the fish. Sib selection involves the selection of broodstock on the basis of the mean phenotypic value of full- or half-sibs. The difference between family selection and sib selection is that the phenotypic value of individuals selected as parents in sib selection are not included in calculations of the family mean.

Within family selection

Within family selection is useful when phenotypic differences among families are due primarily to environmental factors, rather than genetic differences among families. The mean phenotypic values of families are ignored for within family selection. Instead, the best individuals from each family are selected and used as broodstock.

Advantages

Within family selection allows breeders to make use of information about families when the variation among families is due largely to environmental factors. For example, consider families of fish in a hatchery raised at different water temperatures. The average size of families in the coldest water would be smaller than the average size for those in warm water. Most of the variation in average size among families would be due to environmental differences (i.e., water temperature) rather than genetic differences. Another advantage is that inbreeding is minimized. Consider an example involving a number of families and within family selection. In every generation, two breeders are obtained from each family so there is very little chance that any family will fail to contribute progeny to the next generation. The rate of inbreeding is decreased because the probability of losing any particular family is reduced. Within family selection effectively doubles the effective size of the population (Falconer 1981). Consequently, only half as much space is required to maintain a population with a given effective population size under a program of within family selection.

Limitations

Heritabilities for within family selection are usually lower than for mass selection. It is possible to combine family selection and within family selection in a program of **combined selection** in which only the best individuals from the best families are bred. The advantage of combined selection is increased response because the additive variance among individuals as well as within families is exploited.

Selection involving multiple traits: index selection and selection for merit

The **breeding value** of an individual in an artificial selection program is determined from the mean phenotypic value of its progeny. The simplest estimate of breeding value is based on a single trait. Additional information about the breeding value of an individual can be obtained from traits that are **genetically correlated** with the trait under selection as well as from relatives. Two traits, say *X* and *Y*, are genetically correlated if the breeding value of an individual for trait *X* is correlated with the breeding value of the individual for trait *Y*. Genetic correlation results, in part, from pleiotropy (single genes that affect more than one trait). Information from genetically correlated traits as well as from relatives can be combined to form an index that is used to decide whether or not an individual should be kept for breeding.

Index selection

An index is the weighted sum of all the available information about breeding value:

$$I(i) = b_1 P_1(i) + b_2 P_2(i) + b_3 P_3(i) + ...,$$

where $I(i)$ is the index for the value of individual i, $P_j(i)$ is the phenotypic value for the j*th* correlated character or relative, and b_j is a weighting factor that reflects the importance of the j*th* character in the index. The weighting factors are estimated in such a way that the correlation between the index for individuals and their breeding values is maximized (Becker 1984; Falconer 1981).

Selection for merit

Breeders often want to improve several traits simultaneously. The relative importance of each trait can be used to construct an index for merit that takes each of the important traits into account. The merit of an individual can be used to determine its value in a breeding program.

For example, if three traits affect the commercial value of a fish, then a reasonable expression for merit would be:

$$M(i) = a_1 C_1(i) + a_2 C_2(i) + a_3 C_3(i),$$

where $M(i)$ is the merit of individual i and $C_j(i)$ is the breeding value of individual i for the j*th* trait. The weights a_j reflect the relative economic gain to be expected from an improvement of one unit in trait j.

Index selection and selection for merit can be combined:

$$a_1 C_1(i) + a_2 C_2(i) + a_3 C_3(i) + ... = b_1 P_1(i) + b_2 P_2(i) + b_3 P_3(i) + ...$$

The weights b_j are chosen so that the correlation between the index on the right side of the equation and breeding value for merit on the left side of the equation is maximized.

Advantages

Index selection uses all available and relevant information. The standard deviation of index values and selection intensity can be used to predict the response to selection.

Selection for merit can be used to improve a number of characteristics simultaneously. The effort devoted to improving any single trait is proportional to its relative importance. Merit can be expressed in

any units that are convenient and meaningful to the breeder. For example, merit can be expressed in dollars if all of the characteristics considered affect economic value.

Limitations

The determination of the traits to include in an index and the estimation of coefficients for the index are complex tasks that require a large amount of information. The coefficients for an index can change as selection proceeds, gene frequencies are altered, and the genetic correlations between characters change. Coefficients for merit can change as the breeding goals or market conditions change.

Selection involving multiple traits: other methods

Independent culling and **tandem selection**, like selection for merit, are breeding techniques that can be used to improve two or more traits in a single breeding program. Independent culling and tandem selection are simpler than index selection but not as efficient. **Indirect selection**, like index selection, allows breeders to choose individuals for breeding on the basis of a genetically correlated trait.

Independent culling

Independent culling involves choosing individuals for breeding on the basis of a set of independent cutoff values; a different cutoff value is used for each trait under selection. For example, consider a breeding program designed to improve three phenotypic traits in a fish stock: age at maturity, body weight at maturity, and fat content of flesh. The breeder might decide to discard fish that mature at ages greater than one year, weigh less than 0.5 kg at maturity, and have less than 5% fat content. A fish that failed to meet any one of these criteria would be discarded, even though that fish might exceed the cutoff values for the other two traits. A disadvantage of independent culling is that all of the traits are assumed to have equal importance.

Tandem selection

Tandem selection involves selection for one trait in the first generation, a second trait in the second generation, a third trait in the third generation and so on. A breeding program that requires five generations of selection for each of three traits would take at least 5 x 3 = 15 generations to complete. If the generation time is two years then a total of 5 x 3 x 2 = 30 years will be required. The principal disadvantage of tandem selection is a slow rate of progress.

Indirect Selection

Indirect selection is a simple form of index selection based on a pair of genetically correlated traits. Individuals are selected for breeding on the basis of their phenotypic value for one trait, called a **secondary character**, in order to affect improvement in another, genetically correlated trait. Indirect selection is efficient when the heritability of the secondary character and the genetic correlation between the secondary and primary characters are high.

Indirect selection is useful when the heritability of the primary character is low, the primary character is difficult or expensive to measure, or is expressed in only one sex. A breeder may, for example, wish to increase fecundity in a population of fish. Fecundity cannot be determined for males and can only be determined in mature, relatively old females. If the breeder knows that another character, say growth rate, is genetically correlated with fecundity, then males as well as females can be selected for breeding and the selection process can occur while the fish are relatively young.

Intentional inbreeding

The purpose of inbreeding is to increase homozygosity and decrease heterozygosity. Individuals in completely inbred strains are homozygous and genetically identical. Inbred lines are genetically stable; allelic frequencies remain the same from one generation to the next even when effective population size is small because virtually all of the genetic variation has been eliminated. Breeders use inbreeding primarily to generate lines for use in the production of hybrids (see below). Inbred lines (e.g., white mice) are used in scientific work when genetic uniformity is important.

Advantages

Intentional inbreeding is a traditional and well understood method for production of lines with reduced heterozygosity. Inbreeding combined with artificial selection can be used to minimize inbreeding depression.

Limitations

Inbreeding programs require careful design and control and many years if the generation time is long. It may be difficult or impossible to completely avoid inbreeding depression. Inbred lines are often more susceptible to environmental variation than are non-inbred lines.

Hybridization

Hybrids are the progeny of parents from different lines, strains (intraspecific hybrids), or species (interspecific hybrids). The mean phenotypic value of hybrids is often greater than the value of either parental line. Breeders cross lines in order to produce superior hybrid individuals. Superiority of hybrids is called hybrid vigor or heterosis and is due to overdominance and heterozygosity at many loci. Interspecific hybrids are often sterile and usually do not display hybrid vigor (Blanc and Chevassus 1979).

The primary genetic characteristics of hybrid lines are high levels of heterozygosity and genetic uniformity. When two completely inbred (homozygous) lines that differ at every locus are crossed, the progeny are completely heterozygous and genetically identical. Phenotypic uniformity, due to underlying genetic uniformity, is an important characteristic of hybrids .

The characteristics of hybrids depend on the parental lines. The best parental lines differ widely in genetic composition, are vigorous themselves, and yield superior hybrids when crossed. A great deal of effort is often devoted to the breeding of parental lines used for production of hybrids.

Combining ability

The **combining ability** of a line is a measure of the quality of the hybrids that can be expected when the line is used in a cross. **General combining ability** is the mean value of the progeny obtained when the line is crossed to a large number of other lines. **Specific combining ability** is a measure of the value of the hybrids obtained when two specific lines are crossed. General combining ability is an estimate of the additive genetic variation (V_A) present in the line for the given trait; specific combining ability estimates the nonadditive component of the genetic variation (Falconer 1981).

Reciprocal crosses

A **reciprocal cross** involves mating the females of line *A* with the males from line *B* and mating the males of line *A* with the females from line *B* (the former cross is the reciprocal of the latter). The phenotypic value of the hybrids will often depend on which reciprocal cross was employed. Differences between the hybrids obtained from reciprocal crosses depend on the parental line that was the source of the females because of **maternal effects**. Maternal effects on progeny depend on the mother, not on the genotype of the progeny. Egg size and quality are examples of important maternal effects in many fish species. Maternal effects may be due to environmental causes (e.g., differences in nutrition) or to genetic causes (e.g., genes for large eggs).

The hybrids produced by females of one line might be better, on average, than the hybrids obtained from the reciprocal cross. Therefore, it is possible to consider the combining ability (general or specific) of males and females separately. If the combining abilities of males and females differ, a breeder may decide to cross females of one strain with males of another but not vice-versa.

Advantages

Advantages of hybridization include increased vigor and phenotypic uniformity in the crossbred progeny. It is not necessary to maintain hybrid strains because they can be produced at any time as long as the parent strains exist.

Limitations

Hybridization is an optimum breeding program only when hybrids show heterosis. Heterosis depends on nonadditive genetic variation (due primarily to overdominance at many loci). Consider a breeder who wants to improve the commercial value of a fish stock and can maintain several lines derived from the base population. The breeder could select for combining ability in the lines and market hybrids (a hybrid breeding program) or select for phenotypic value within lines and market surplus stock (a line breeding program). If nonadditive genetic variance in the original population was negligible, then the hybrid breeding program would give poorer results than the line breeding program. Conversely, if there was a great deal of nonadditive genetic variance and little additive genetic variance in the base population, then the hybrid breeding program would perform better than the line breeding program. Hybrid breeding programs may be useful for fish because genetic variation for body weight, length and viability is mostly nonadditive in the cyprinids and salmonids studied to date (Gjedrem 1983).

Hybrid lines cannot be maintained by allowing hybrids to reproduce; they must be produced from parental lines in every generation. Consider a fictitious population of identical hybrids with genotype *Aa* at one locus. If the hybrids were allowed to reproduce, then the progeny would have genotypes *AA*, *Aa*, and *aa* in the proportions 0.25, 0.5, and 0.25, respectively. The genetic uniformity and extreme heterozygosity of hybrids is lost after a single generation of random mating.

Outcrossing

Outcrossing involves breeding individuals from one strain to superior individuals from unrelated lines or strains in order to bring new genes into a selection program. Outcrossing differs from hybridization in that progeny of crosses are used in the ongoing selective breeding program.

Advantages

This technique utilizes the additive genetic variation in both strains and any heterosis resulting from their combination. Additionally, new genes from the unrelated lines become available to the selection program and inbreeding is reduced.

Limitations

Outbreeding programs are necessarily larger in scope than simpler selection programs. Individuals from unrelated but suitable strains may not be available. It may be difficult to evaluate the suitability of unrelated strains of fish.

Rotational line crossing

Rotational line crossing involves sequential crosses among three or more separate lines. Figure 11 illustrates crosses involving three lines. In the first generation, females from line *A* are mated to males from line *C*, females of line *B* are mated to males of line *A*, and females of line *C* are mated to males of line *B*. This mating scheme is repeated in each succeeding generation. Specific recommendations for the implementation of rotational lines crosses in hatcheries are given by Kincaid (1977) and Hynes et al. (1981). The advantage of rotational line crossing is a reduction in the rate at which inbreeding accumulates within the strains. This advantage, however, depends on the presence of a high level of genetic diversity in the starting broodstock and on the maintenance of genetic diversity in subsequent generations. Kincaid (1977) suggests starting each line from different strains and using at least 50 fish of each sex to advance the generation for each line. The disadvantage in rotational line crossing is increased complexity in the handling of hatchery stock.

Figure 11

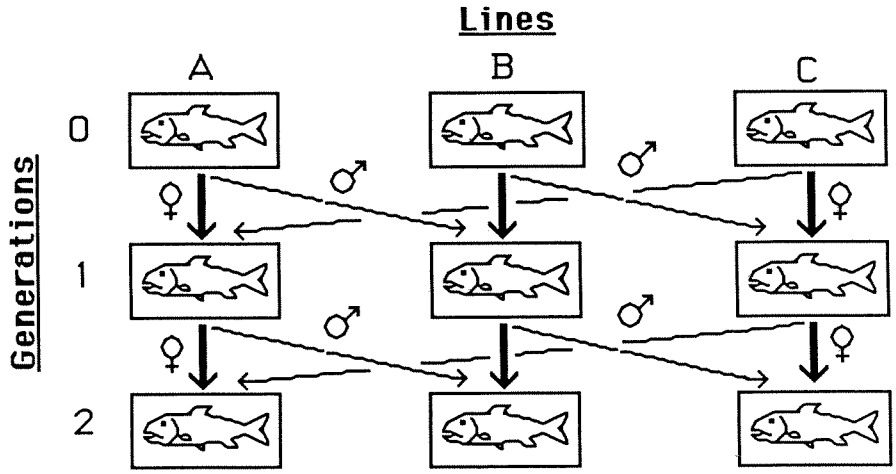


Figure 11. Rotational line-crossing scheme using three separate lines. Each box represents a group of fish from a separate line. Bold, vertical lines show the source of females used for breeding. Thin, diagonal lines show the source of males mated with those females. This scheme minimizes further inbreeding and genetic drift within the lines. (After Kincaid 1977.)

TOOLS FOR GENETIC ENGINEERING

Tools for genetic engineering in fish are based on recently developed techniques and are used for construction of fish with novel genotypes. These methods are the subject of an increasing amount of research; limitations, advantages, and applications are not yet clear. In the future, tools for genetic engineering will be used probably in connection with traditional techniques for improving the phenotypic value of fish, i.e., genetically engineered fish will be used in breeding programs.

There are potential hazards in the use of any tool that creates "new" fish. An important hazard is the possible effect of genetically engineered fish on wild fish populations and natural ecosystems. The first applications for genetically engineered fish should be in aquaculture where populations can be controlled with relative ease.

Gene transfer

Gene transfer involves insertion of the DNA for a gene into the DNA of a recipient organism. The purpose of gene transfer is to improve the recipient organism. The new gene may be derived from any species and might confer, for example, disease resistance or faster growth.

There are five steps in gene transfer. First, the gene must be identified and located in the organism in which it occurs naturally. Second, a copy of the DNA for the gene must be obtained (Sekine et al. 1985). Third, DNA for the gene is **cloned** (produced in large quantities, usually by **cell culture**). Fourth, copies of the gene are inserted into a **transfer vector,** usually a bacterial **plasmid**. Bacterial plasmids are circular "minichromosomes" derived from bacteria. The transfer vector is a segment of DNA that facilitates insertion and expression of the foreign DNA in the genome of the recipient. In the final step, the transfer vector and gene are applied to cells (usually eggs or sperm for fish) of the recipient organism. If the transfer is successful, at least one copy of the gene is integrated into the recipient's genome and expressed. Researchers expect that the inserted gene will be passed to future generations through the gametes of the recipient.

Induced polyploidy

The production of triploid fish is of interest to fisheries managers because triploids are sterile (Kinghorn 1983). Sterile fish do not divert energy to reproduction and thus grow to larger final size. It may be possible to use sterile fish for management purposes (e.g., weed control, control of overabundant forage fish) with little risk to the natural system because reproduction will not occur. There is interest in the production of interspecific triploid hybrids because they sometimes have higher survival rates than diploid interspecific hybrids (Chevassus et al. 1983; Scheerer and Thorgaard 1983).

Triploidy in fish is usually induced by treatment of fertilized eggs with temperature or pressure shocks just before the second meiotic division so that the maternal contribution to the embryo is *2n* chromosomes. The haploid sperm combines with the unreduced diploid eggs to produce triploid progeny. Another method is to mate tetraploid individuals (which are fertile) with diploid individuals to produce offspring that are triploid and sterile.

Not all of the fish produced using these techniques are sterile; some fertile diploids are usually produced as well. Furthermore, separation of the fertile and sterile individuals is difficult. This is a significant disadvantage when it is important to be sure that all fish are sterile. Survival rates of triploids may be lower than the survival rates for normal diploids at some life stages. This disadvantage may be offset by increased survival or faster growth at other life stages.

Gynogenesis and androgenesis

Gynogenesis is the production of viable progeny with all-maternal inheritance. Development of the embryo is initiated when irradiated sperm penetrate the egg. Radiation inactivates the DNA in the sperm so that the DNA in the progeny comes only from the mother. **Androgenesis** is the production of viable progeny with all-paternal inheritance. In the case of androgenesis, the DNA of the egg is inactivated

by radiation. These methods can be used to produce sterile triploids, as described above, or fertile diploids as described below.

Diploid gynogenesis

Diploid gynogenesis occurs in fish when sperm fertilize eggs but do not contribute DNA to the embryo. The progeny are diploid but all the genetic information in the developing embryo comes from the mother. Natural gynogenesis is rare. Induced gynogenesis is a recently developed genetic tool of potential use to fish breeders. Gynogenesis can be used to generate inbred lines of all female fish.

Diploid gynogenesis in fish can be induced by sperm in which the DNA has been deactivated by radiation. Development of a haploid embryo is initiated when a deactivated sperm penetrates an egg but does not fertilize it. A temperature or pressure shock is applied to the egg after development begins just prior to the second meiotic division. The shock prevents the second meiotic division from occurring so that the germ cell remains diploid. Another method of restoring the diploid state involves use of pressure shock to suppress the first mitotic division in haploid embryos. The remainder of development is normal if the treatments have been successful.

Diploid androgenesis

Diploid androgenesis occurs when the egg does not contribute DNA to the embryo; all of the genetic material in the embryo comes from the sperm. Development of a haploid embryo occurs when a nonirradiated sperm penetrates an irradiated egg. The diploid state is restored by using a pressure shock to block the first mitotic division in the haploid embryo. Androgenesis may have several advantages over gynogenesis for generating inbred lines of fish (Parsons and Thorgaard 1985). For example, less time may be required to produce inbred lines for species in which males mature earlier than females.

Production of monosex populations

Technologies that allow production of monosex populations are potentially useful because one sex may be more valuable than the other and because reproduction can be controlled in monosex populations. There are at least three ways to produce fish that are all one sex. The first method involves hybridization of two closely related species. The second method involves the use of **hormones** to artificially reverse sex (**sex-reversal**). The third method is induced gynogenesis (discussed above).

Hulata (1983) describes and reviews the production of monosex hybrid populations of tilapia. Crossing males from certain species of tilapia to females of certain other species produces progeny that are completely or predominantly of one sex. The advantage is that monosex culture is facilitated (fish need not be sorted by hand) and unwanted reproduction may be controlled. Unfortunately, these methods are imperfectly understood and have proven difficult to employ.

The work of Hunter et al. (1983) illustrates the use of sex-reversal to produce broods of completely female chinook salmon. Female chinook salmon are **homogametic** (homozygous for sex chromosomes, i.e., genotype *XX* where *X* is a sex chromosome), normal males are **heterogametic** (heterozygous for sex chromosomes, i.e., genotype *XY*). The sex of genetic females can be reversed by administration of male hormones in feed. The sex-reversed males are functionally male but remain genetically female. When these functional males are mated to normal females the progeny are all *XX*, that is genetically and functionally female. The monosex progeny produced in this manner have normal levels of heterozygosity, unlike the nearly homozygous progeny obtained using gynogenesis. Heterozygous progeny may be more useful in aquaculture than inbred, homozygous lines.

It is difficult to distinguish between normal and sex-reversed males when the sex-reversal process is begun with mixed sex populations. This problem may be circumvented by application of gynogenesis in the first generation (to give all female progeny), followed by sex-reversal (to give *XX* functional males). The sex-reversed males can be outcrossed to produce all female, heterozygous progeny.

CHAPTER THREE: GENETIC ISSUES IN FISHERIES MANAGEMENT

OVERVIEW

There are three categories of genetic issues in fisheries management. The first category involves intentional and unintentional alterations of the genetic makeup of hatchery stocks. The second involves inadvertent effects of management and exploitation on the genetics of wild stocks. The third category involves the use of technologies for genetic engineering in fisheries management. Information about genetic principles and techniques can be used by management to address these issues.

IMPACTS OF HATCHERY MANAGEMENT ON THE GENETICS AND FITNESS OF HATCHERY STOCKS

In this section, the effects of hatchery management on the genetics and fitness of fish are discussed. Mating techniques, intentional and inadvertent selection, domestication, and inbreeding all affect the genetics and fitness of fish and are discussed here.

Hatchery managers should, in general, try to preserve genetic variation in breeding populations while producing fish that are suitable for their intended use. The principal concerns are: 1) that hatchery practices may detrimentally alter survival, yield, or reproduction, and 2) small effective population sizes in hatcheries can lead to inbreeding and loss of genetic diversity.

How will the fish be used?

Concerns about the genetic impacts of hatchery management depend on the use intended for the hatchery fish. Hatchery bred fish may be stocked in an aquacultural facility for food production, in a natural environment, or in some captive setting as broodstock. The reproductive fitness of fish destined for slaughter is not important; in fact, reproduction is often undesirable. In contrast, the fitness of fish used as broodstock or for stocking in natural environments is of paramount importance because the fitness of future generations depends on genetic characteristics of the present generation. Improvements to the management of genetic resources in hatcheries will increase the benefits due to stocking hatchery fish.

Mating techniques

The rate at which genetic diversity is lost in a hatchery program due to inbreeding and genetic drift depends partly on how the fish are mated. For a fixed number of breeders, effective population size is maximized (inbreeding and genetic drift are minimized) when there are equal numbers of males and females and all breeders contribute equal numbers of progeny to the next generation. In addition to using a large number of parents, hatchery managers should employ mating techniques that: 1) use equal numbers of males and females, and 2) produce approximately equal numbers of progeny from each parent. It is difficult to ensure that all parents contribute equal numbers of progeny to each year-class. Differences in family sizes always occur and result in decreased effective population size. Fish culturists

should be aware of this problem in connection with the "dry fertilization" method for mating fish in which the milt of several males is added sequentially to eggs before water is added to activate the sperm. Gharrett and Shirley (1985) demonstrate substantial differences in potency among male pink salmon. Furthermore, it is known that the sperm of some fish species can fertilize eggs in ovarian fluid before the water is added (Rucker et al. 1960). Milt from the first male may fertilize a disproportionately large number of eggs. The mating scheme that Gharrett and Shirley (1985) suggest to alleviate these problems involves the use of males in overlapping pairs to fertilize eggs. Milt of two males is mixed immediately before addition to the eggs of a single female.

Selection

Selection in a hatchery may be intentional (a deliberate selection program designed to change some characteristic of the population) or inadvertent (a side effect of some sampling procedure). The consequences of either type of selection in hatcheries are greatest when selection acts on traits related to fitness.

Fitness related traits (e.g., fertility, disease resistance, and growth rate) are primary determinants of the survival and reproductive success of an individual fish. Fitness related traits show little additive genetic variance (the sort of variation most easily utilized by breeders) in populations already well adapted to their environments. According to theory, heritabilities for fitness related traits are low because natural selection has "used up" the additive genetic variance. This means it is difficult to improve the fitness of a population through artificial selection.

The fitness of an individual or population depends on its environment as well as its genetic makeup. A management program designed to improve the fitness of a hatchery population in one environment may decrease the fitness of the population in other environments. A particularly relevant example is the contrast between the fitness of domesticated strains of fish in hatcheries and their fitness when they are placed in a natural environment.

Intentional selection

Artificial selection involving captive populations (populations used for aquaculture) and artificial selection involving fish used for stocking in natural environments are different issues. This discussion addresses only genetic issues that are related to artificial selection of fish used in stocking programs. Hynes et al. (1981) review artificial selection and hybridization programs that improve hatchery populations and enhance the management of fisheries. Important points that are relevant to these issues follow:

1) It is difficult to increase the fitness of a population that is already well adapted to its environment.

2) Selection programs designed to affect one trait may unintentionally and adversely affect other genetically correlated traits, particularly those traits that are fitness related.

3) Improperly designed selection programs invariably reduce the effective population size and encourage inbreeding and loss of genetic diversity.

4) Artificial selection is difficult and inefficient for species with complex life histories (e.g., anandromous fish) because they cannot be maintained in a hatchery during their entire life cycle.

5) Many generations of selection and hatchery culture are usually necessary to effect substantial change in a population. Detrimental effects due to culture in an artificial environment (domestication and inadvertent selection) accumulate with time.

6) It is hard to obtain large selection differentials and responses to selection when spawners must be selected from relatively small hatchery populations.

Inadvertent selection

Inadvertent selection is unintentional artificial selection in hatcheries and is closely related to the issue of domestication. The potential for inadvertent selection exists whenever spawners used in a hatchery are not a random sample of the population from which they were obtained. A good, though incompletely documented example, is that of run timing in pink salmon. The time of spawning is a heritable trait in pink salmon. Selection of spawners by hatchery personnel from the early part of the spawning run may result in a change in the mean time of the spawning run in the next generation (Smoker 1985). Inadvertent selection may occur if the average size, age, spawning times, or spawning locations of the spawners used in hatcheries are different than the averages for the entire population. This possibility is the basis for recommendations that spawners used in hatcheries should be either a random sample from the spawning population or should "cover the range of sizes, ages, spawning times, and sites of the spawning parents" (Hynes et al. 1981). Practical problems with crossing large numbers of fish from different age groups, size groups, spawning sites, and spawning locations are not trivial. **Cryopreservation** of gametes obtained at various times and locations may be of some use (Hynes et al. 1981).

The issue of inadvertent selection is not restricted to Pacific salmon. Potential for inadvertent selection exists, for example, when lake trout gametes are taken from wild populations in the Great Lakes for culture in hatcheries.

Domestication

Doyle (1983) describes domestication as "natural selection for traits which affect survival and reproduction in a human-controlled (domestic) environment." He suggests that domestication is unavoidable in stocks held in hatcheries for many generations because hatchery fish evolve so their fitness in the hatchery environment increases. Domestication may be desirable in fish that are used for aquaculture but it is almost certainly undesirable in fish destined for stocking in the wild.

Doyle (1983) reviews an experiment by Bagenal (1969) in which a reduction in the ration fed to brown trout inadvertently selected for faster growth rate. This example illustrates the difficulties in avoiding the effects of domestication.

Inbreeding

Inbreeding is the most important genetic concern in hatchery management. In this section, inbreeding denotes unintentional inbreeding which occurs in all populations of finite size. Inbreeding results in loss of genetic diversity (loss of alleles) and increased homozygosity. The consequence of reduced genetic diversity is, potentially, inbreeding depression. The rate of inbreeding in a population depends on the effective size of the population; it is low in large populations and high in small populations. The rate of inbreeding (amount of inbreeding per generation) is given by:

$$\Delta F = 1 / (2 N_e),$$

where ΔF is the rate of inbreeding per generation and N_e is the effective population size. Inbreeding is cumulative because it increases from one generation to the next.

Certain hatchery practices reduce the effective size of populations and accelerate inbreeding. We have seen, for example, how a standard technique for breeding fish (the dry fertilization method) reduces effective population size.

Factors that affect inbreeding and effective population size

The principal factors affecting inbreeding and effective size of hatchery populations are the number of individuals in the population, the sex ratio, variation in the reproductive success of individual spawners, and effective population size during previous generations.

Population size (numbers of individuals)

In an idealized population (infinitely large, no variation in reproductive success, non-overlapping generations, and balanced sex ratio) the effective size is simply the number of individuals in the population. In real populations the effective size is always less than the number of individuals in the population. The first requirement, therefore, for the reduction of inbreeding in hatcheries is the capability to hold large numbers of spawners. There is no guarantee that inbreeding will be minimized in large populations, however, because the effective population size also depends on other factors that are discussed below.

Sex ratio

Consider a population with N_m males and N_f females where the number of males does not necessarily equal the number of females. The effective population size and the rate of inbreeding are given approximately by:

$$1/N_e = 1/(4N_m) + 1/(4N_f),$$

$$\Delta F = 1/(2N_e) = 1/(8N_m) + 1/(8N_f).$$

Note that $1/N_e = 1/N$ and $\Delta F = 1/(2N)$ when the sex ratio is balanced ($N_m = N_f$). An unfortunate consequence of these relationships is that unbalanced sex ratios have large effects on N_e and ΔF. Consider two hatchery populations of 50 individuals. In the first population (with equal numbers of males and females) the effective population size and rate of inbreeding for the population are 50 and 1%, respectively; in the second population (with 40 females and 10 males) the effective size and rate of inbreeding for the population are 32 and 1.6%, respectively. The unbalanced sex ratio reduced the effective population size by 36% and increased the rate of inbreeding by 60%.

Variation in reproductive success

Variation among individuals in reproductive success can be due to differences in fecundity, fertility, longevity (fish that live longer have more opportunities to reproduce), and accidents in the hatchery (e.g., fungus infections). Falconer (1981) states that differences in reproductive success are "the most important cause of N_e being less than N" in real populations.

Temporal variability in effective population size

Inbreeding and loss of genetic diversity accumulate with each new generation so the degree to which a population is inbred depends on the effective population size during each of the previous generations. It is important to consider how temporary reductions in the effective population size (**population bottlenecks**) affect the loss of genetic diversity in the long-term. The mean effective population size of a population over a period of n generations can be calculated (approximately) as the harmonic mean of the effective population sizes during each of the generations:

$$1/N_e = (1/N_1 + 1/N_2 + \ldots + 1/N_n)/n$$

where N_e is the mean effective size and N_i is the effective size for generation i. The mean rate of inbreeding can be obtained from N_e in the usual way. It is important to realize that population bottlenecks (small values of N_i) have large effects on N_e, inbreeding, and the loss of genetic diversity. Consider a population with the following effective population sizes during ten consecutive generations: 100, 50, 10, 50, 100, 100, 100, 100, 100, 100. The mean effective size and mean rate of inbreeding are 47.6 and 1%, respectively. With no population bottleneck, the effective size and mean rate of inbreeding would have been 100 and 0.5%, respectively. A population bottleneck that lasted only three generations reduced the mean effective size by 54% and doubled the mean rate of inbreeding.

Recommendations for effective size of hatchery populations

The effective size of hatchery populations should be as large as possible in order to minimize loss of genetic diversity. Recommended values for N_e reflect compromises involving the value of the genetic diversity in a population (which is very difficult to measure), the rate at which genetic diversity is lost and the costs of raising fish and managing a hatchery. Recommendations in the fisheries literature for the minimum effective population size of hatchery populations vary tremendously. Gharrett and Shirley (1985), for example, cite values ranging from 60 to 200. This variability results from uncertainty about the minimum amount of genetic variation required for populations to persist in unpredictable natural environments. Domestic animals seem to tolerate inbreeding at the rate of about one percent per generation (equivalent to $N_e = 50$) without showing inbreeding depression. The figure $N_e = 50$ is thus an extreme lower bound on the acceptable values of N_e for populations used in aquaculture. Acceptable values for hatchery populations used in stocking programs are higher. Kincaid (1983), for example, suggests that the effective size of a breeding population should be at least 100 (equivalent to $\Delta F = 0.5\%$). This recommendation should be regarded as a minimum acceptable value for hatchery populations that are used for enhancement of wild stocks.

New developments in fisheries genetics research are likely to change recommendations for minimum effective population sizes. Kapuscinski and Lannan (1986) suggest that no single value of N_e is appropriate for all stocks. They propose using life history data to determine the appropriate effective population size and recommend minimum effective population sizes of more than 100 for hatchery fish.

As we have seen, the effective size of a population is always less (and often much less) than the number of fish in the spawning population. How many fish are required to insure that the effective size of a population is at least some specified value? The answer is not simple and will depend on the sex ratio of the stock, the breeding technique used, the means by which spawners are selected, etc. When the sex ratio is balanced and all spawners enjoy equal reproductive success, fewer fish will be required to obtain a given value of effective population size.

Techniques for minimizing inbreeding in hatchery populations

There are two general approaches to minimizing inbreeding in hatchery populations (Kincaid 1983). The first and simplest approach is to make random matings and to use large breeding populations. The second approach is to employ a line crossing scheme such as rotational line crossing (Kincaid 1977) that minimizes matings between related individuals.

IMPACTS OF STOCKED AND TRANSPLANTED FISH ON THE GENETICS OF WILD STOCKS

It is possible that the fitness of stocked fish will be less than the fitness of the wild population residing at a particular location (in this context, stocked fish are hatchery raised or transplanted from a different locality). Stocked fish could, for this reason, affect the fitness and long-term adaptability of the population. Fitness will be reduced if the stocked fish are poorly adapted to the environment in which they are stocked and if the number of fish stocked is large relative to the number of fish produced by natural reproduction. Stocking carefully selected fish strains may be the only way, however, to restore fitness and insure persistence of a depleted wild population.

Recommendations

Whenever possible, manage wild populations so that stocking is unnecessary. When stocking is necessary, try to stock fish that are well adapted to the local environment.

The best way to insure that stocked fish will have high fitness in a particular environment is to use wild fish from the same environment as broodstock (Krueger et al. 1981). If this is not practical, then broodstock should be obtained from environments as similar as possible to the environment into which fish will be planted. In some cases, wild broodstock are too scarce to achieve minimum effective population sizes. In such a case, stocking of wild x hatchery hybrids warrants consideration; a number of

studies have shown hybrid vigor for performance in natural waters. Wohlfarth (1986) recommends preliminary evaluation of hybrids in small isolated bodies of water. Another approach, when native broodstock are nonexistent or scarce, is to collect gametes from many wild populations, perform all possible crosses among the sources and then stock the progeny (Krueger et al. 1981). The rationale for this approach is to maximize genetic variation in the progeny and then to let the natural environment select for the most fit individuals.

A number of other methods can be used to help insure that stocked fish have high fitness. Broodstock should be obtained by sampling randomly from spawners in a wild population in order to avoid inadvertent selection for body size, spawning time, etc. Mating schemes and hatchery management should aim to maximize effective population size. The hatchery rearing period for broodstock and production stock should be minimized because consequences of hatchery culture (i.e., domestication, inadvertent selection and inbreeding) accumulate with time. This applies to broodstock used for routine stocking as well as for rehabilitation of severely depressed fish populations. Problems with stocking for rehabilitation are more pronounced, however, because it may be impossible to obtain broodstock from native populations (Krueger et al. 1981).

IMPACTS OF HARVEST MANAGEMENT ON THE GENETICS OF WILD FISH STOCKS

Harvest management affects the genetics of wild fish stocks in at least two ways. First, high exploitation rates reduce the effective size of a stock so that the rates of genetic drift and inbreeding are increased. Second, fishing methods that "select" individual fish for harvest on the basis of some characteristic (e.g., size selectivity in a gillnet fishery) amount to artificial selection programs that can cause genetic changes in the stock over time.

Harvest management and effective population size

Overharvest leads to reduced effective population size because the number of fish that survive to reproduction is reduced. This phenomenon is called "recruitment overfishing" or "reproductive overfishing" in the terminology of population dynamics. Rates of genetic drift and inbreeding increase when the effective size of a stock is decreased. Increased genetic drift and inbreeding result in loss of genetic diversity, increased homozygosity and, ultimately, may result in reduced population fitness. The effective size of a population is always less than the number of individuals in the population. Consequently, severe reductions in the effective size of a stock due to overharvest can occur before the number of fish in the stock is drastically reduced, particularly when the sex ratio is unbalanced or when the reproductive success of many individuals is low.

Many exploited fish stocks show tremendous variation in abundance from one year to the next. For these stocks, it is important to remember that short periods of low effective population size are population bottlenecks that can accelerate the loss of genetic diversity. Long periods of high abundance do not make up for the losses incurred during short periods of low abundance. Harvest management that increases variability in abundance can affect genetic diversity in a population.

Harvest management and effective population size in mixed stock fisheries

A potential for reproductive overfishing exists in mixed stock fisheries when some stocks are more productive than others. Ricker (1973) shows that the abundance of less productive stocks is depressed in mixed stock fisheries when there are high levels of exploitation. Appropriate levels of exploitation for the productive stocks in a mixed stock fishery may result in decreased effective population size and loss of genetic diversity in the less productive stocks. This is a potential problem whenever stocks are aggregated for management purposes; different stocks need not be caught at exactly the same location. Consider two fictitious lake trout stocks in the same statistical district or quota zone. The first stock is large, productive, and capable of withstanding a considerable amount of fishing pressure. The second stock is small, unproductive, and incapable of withstanding even a moderate fishery. Catch quotas applied to the entire statistical district will likely be set at levels that take advantage of the productivity of the first stock but

overexploit the second stock. Consequently the effective size of the second stock will remain low and genetic diversity will be lost. Management of genetic resources in mixed stock fisheries should take into account different productivities of the stocks. The most conservative approach to management of a mixed stock fishery is to set harvest rates low enough to protect the least productive stocks. Ideally, mixed stock fisheries should be avoided; terminal fisheries, for example, can be used to harvest returning adult salmon.

Exploited populations that contain a large number of stocked fish are, in essence, mixed stock fisheries. It may happen, as with lake trout in the Great Lakes, that the stocked fish are a significant fraction of the total population but may contribute relatively little to natural reproduction. Consequently, the effective size of the breeding population is much smaller than the number of individuals in the population. Recruitment of wild fish depends on the abundance of wild spawners in the population and may be depressed at high levels of exploitation. Recruitment of stocked fish depends only on stocking levels and is independent of the rate of exploitation. At high levels of exploitation, stocked fish are more productive, in a sense, than are wild fish. Consequently, abundance and effective size of the wild fish population may be severely depressed even though the total number of fish in the stock is not low.

Harvest management and unintentional selection

Many fisheries amount to artificial selection programs that act on fitness related traits or traits genetically correlated with fitness. Fish taken by a fishery are seldom a random sample from the population because fishing techniques and gear select individuals with certain characteristics. Consequently, fish that survive the fishery and live to spawn will be different, on average, than fish in the population before exploitation. If the differences are heritable, then the next generation will be genetically and phenotypically different from the previous generation. This process can occur in every generation until substantial changes have occurred in the population. It is possible that inadvertent artificial selection will produce a stock of fish with inferior commercial value or reduced fitness.

Inadvertent selection has been cited repeatedly in connection with size selective gillnet fisheries. Gillnets are usually designed to select individuals larger then some minimum size, consequently fish that survive to spawn are relatively small. Growth rate is a heritable characteristic and reduced growth rates have been observed in several stocks following exploitation (Handford et al. 1977; Ricker 1981). Traits genetically correlated with growth rate, such as average age at sexual maturity, may also change in response to selection by the fishery (Beacham 1983; Ricker 1981). Inadvertent selection is not limited to commercial gillnet fisheries. Favro et al. (1979) discusses the genetic effects of inadvertent selection due to size limits in a recreational trout stream fishery.

EFFECTS OF HABITAT ALTERATION ON THE GENETICS OF WILD STOCKS

Changes in the environment can affect the genetics of wild populations in two familiar ways: 1) by depressing the effective size of the population, which causes a loss of genetic diversity; and 2) by natural selection for increased fitness in the new environment, which may decrease the value of the resource.

Depression of effective population size (leading to increased inbreeding, increased genetic drift, and loss of genetic diversity) is a certain consequence of environmental changes that reduce habitat size (e.g., obstruction of spawning streams), kill fish (e.g., pollution) or limit reproductive success (e.g., acid rain).

Population fitness may be reduced by a major change in habitat because characteristics that maximize fitness in the old environment may not maximize fitness in the new environment. Natural selection for increased fitness in the new environment is, for this reason, a certain consequence of major habitat alterations. This is a natural and constructive response of the population to an environmental change. A number of related consequences, however, should be kept in mind. Fish adapted to the new environment (e.g., tolerant of polluted water) may not be desirable for human consumption. Productivity of the population may remain low even after the population adapts to the new environment. Many

generations might elapse before the population adapts to the new environment because the response to natural selection may be slow. The population may never adapt if the environment continues to change.

GENETIC ENGINEERING: EMERGING ISSUES

Genetic engineering (e.g., the development of fish with novel genomes and production of monosex populations) is an important development in fisheries management and aquaculture. With promise, however, come uncertainty and peril.

Aquaculture vs. management of wild stocks

The use of genetically engineered fish for aquaculture is less risky than their use in management of wild populations because the effects of genetically engineered fish on wild stocks, communities, and ecosystems are unknown. Genetically engineered fish will require careful evaluation before their introduction into natural environments is considered. Biological characteristics (e.g., growth, food consumption rates, fertility, behavior and longevity) of genetically engineered fish should be determined. Extensive field tests in carefully controlled environments will be required in order to determine the ecological interactions between genetically engineered fish and natural communities. The effects of genetic manipulations on fitness should be understood. Genetically engineered fish that are released into natural environments should be sterile, at least until the biological and ecological uncertainties are resolved. In some cases, the effort and expense required to evaluate genetically engineered fish may preclude their use in natural environments.

Genetically engineered fish used for aquaculture will also require extensive evaluation. Of particular interest are the effects of genetic manipulations on fitness and commercially important characteristics (e.g., growth rate, food consumption and disease resistance).

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GLOSSARY

ADDITIVE COMPONENT (V_A)–the portion of the total phenotypic variance in a population that is due to the additive effects of genes.

ALLELE–one of the alternative forms of the same gene; alleles for the same gene occur at the same locus.

ALLOZYME–an enzyme produced by one allele at a locus; allozymes are produced by different alleles at the same locus.

ALLELE–one of two or more alternative forms of the same gene.

ALLOZYME–an enzyme produced by one allele at a locus; different allozymes are produced by different alleles.

AMINO ACID–a molecule that is one of the building blocks of proteins.

ANAPHASE–the third stage in the division of a cell nucleus during mitosis or meiosis when the chromosomes migrate toward opposite ends of the cell.

ANDROGENESIS–production of offspring having all paternal inheritance (all chromosomes and genes obtained from the father).

ANEUPLOIDY–the condition in which cells have extra copies of one or more chromosomes.

ARTIFICIAL SELECTION–the process of choosing parents on the basis of a trait in order to obtain a phenotypic and genetic change in the next generation.

AUTOSOME–any chromosome that is not a sex chromosome.

BASE–one of five molecules (guanosine, cytidine, thymidine, adenosine, and uracil) that are the building blocks of DNA and RNA.

BASE PAIR–a pair of nucleotides containing bases (adenosine with thymidine or guanosine with cytidine) that are linked together; chains of base pairs form the double helix of DNA.

BREEDING VALUE–the value of an individual as a breeder in an artificial selection program as judged from the mean phenotypic value of its progeny.

CELL CULTURE–the process of growing living cells under artificial conditions.

CHROMOSOME–a structure that contains DNA, carries genes, and is found in the nuclei of cells.

CHROMOSOME DUPLICATION–a mutation in which parts of a chromosome are duplicated.

CLONE–a group of genetically identical organisms descended from one common ancestor; genetically engineered replicas of a DNA sequence.

CLUSTER ANALYSIS–a statistical procedure that assigns similar units or samples to the same group or cluster.

CODOMINANT–the condition in which both alleles at a locus are expressed phenotypically to the same degree.

CODON–a group of three adjacent nucleotides in DNA or RNA that code for a specific amino-acid in a protein.

COMBINED SELECTION–an artificial selection program that combines individual and family selection.

COMBINING ABILITY–the value of a particular line in the production of hybrids (see general combining ability and specific combining ability).

CONDENSED CHROMOSOME–the state of chromosomes during division of the cell nucleus; condensed chromosomes have a characteristic shape and are visible under a light microscope.

CROSSING OVER–the process in which arms of homologous chromosomes cross over and exchange DNA during production of eggs and sperm (meiosis).

CRYOPRESERVATION OF GAMETES–the preservation of live gametes (e.g., fish sperm) by rapid freezing at very low temperatures in chemical solutions that prevent cellular damage.

CYTOGENETICS–the study of genetics at the level of individual chromosomes and cells.

CYTOKINESIS–the last stage of cell division in which the cytoplasm of a mother cell splits into two daughter cells.

CYTOPLASM–all living material inside a cell except the nucleus.

CYTOPLASMIC DNA–DNA found in the cytoplasm of a cell (not in the nucleus) in connection with organelles (e.g., mitochondria); DNA not found in chromosomes within the nucleus.

DELETERIOUS ALLELE–an allele that has a deleterious effect on an organism.

DENDROGRAM–a type of graph or chart that resembles a tree (with trunk and branches) and is used to illustrate similarity or relatedness among units or samples.

DEOXYRIBONUCLEIC ACID (DNA)–the chemical used to store genetic information in most organisms.

DIPLOID–a cell or organism that has two complete sets of chromosomes.

DIPLOID GYNOGENESIS–production of gynogenetic diploids; see gynogenesis.

DISPERSIVE PROCESS–a process (either genetic drift or inbreeding) that causes random changes in allelic frequencies and loss of genetic diversity in populations over time.

DNA–see deoxyribonucleic acid.

DOMINANCE–the property of an allele that suppresses expression of other alleles at the same locus; a dominant allele is the only allele expressed phenotypically in a heterozygote.

DOMINANCE EFFECT–the effect of dominance at one or more loci on the phenotype of an individual or mean phenotype of a population.

DOUBLE HELIX–the shape of a DNA molecule; a chain of base pairs twisted in a spiral.

EFFECTIVE POPULATION SIZE–the size of an ideal population that would experience genetic drift and inbreeding at the same rate as the real population under consideration.

ELECTROPHORESIS–a laboratory procedure for the separation and observation of proteins (usually enzymes) that can be used as genetic markers.

ELECTROPHORETIC MARKER–a polymorphic protein (usually an enzyme) that is used as a genetic marker and is identified electrophoretically.

ENVIRONMENTAL EFFECT–the influence of the environment on the phenotype of an individual or mean phenotype of a poulation.

ENZYME–a protein produced in living cells that speeds up a particular chemical reaction.

EPISTASIS–interaction between genes at different loci such that one gene affects the phenotypic expression of the other.

EXPECTED RESPONSE–the predicted response to one generation of artificial selection; calculated as the product of the selection differential (S) and the heritability (h^2).

EXPRESSIVITY–the intensity with which a gene is expressed phenotypically in different individuals.

FAMILY SELECTION–an artificial selection program in which superior families rather than superior individuals are chosen for breeding.

FEMALE FACTOR–a gene not found on a sex chromosome that promotes female characteristics.

FERTILIZATION–the fusion of an egg and sperm to initiate development of an embryo.

FITNESS–a measure of the reproductive success of an individual; the frequency distribution of reproductive success for a population of sexually mature individuals.

FITNESS RELATED TRAITS–quantitative traits that directly affect the fitness of an individual.

FIXATION–the loss from a population of all but one of the alleles at a locus due to inbreeding or genetic drift.

FULL-SIBS–individuals having both parents in common.

GAMETE–a mature egg or sperm cell.

GAMETOGENESIS–the formation of eggs and sperm (gametes).

GENE–a segment of DNA that occupies a specific position (locus) on a chromosome, is heritable and has one or more specific effects upon the phenotype of an organism.

GENE TRANSFER–the process of inserting genes into the DNA of a recipient cell by artificial means.

GENERAL COMBINING ABILITY–a measure of the average value of a particular line in the production of hybrids; determined by crossing a line with a large number of other lines.

GENETIC CORRELATION–correlation between the phenotypic values for two traits (e.g., growth rate and age at maturity) due to genes that affect both traits.

GENETIC DISTANCE–a statistical measure of the genetic similarity or difference between two populations.

GENETIC DIVERSITY–all of the genetic variation in an individual, population, or species.

GENETIC DRIFT–random changes in allelic frequencies due to natural sampling errors that occur in each generation; the rate of genetic drift increases as effective population size decreases.

GENETIC MARKER–a phenotypic characteristic (e.g., allozyme, chromosome band, or pigmentation) that can be used to infer the genotype of an organism.

GENOTYPE–the set of alleles at one or more loci in an organism; the entire set of genes carried by an individual.

GENOTYPE-ENVIRONMENT INTERACTION–the effect of interaction between genes and the environment on the phenotype of an individual or mean phenotype of a population.

GENOTYPIC FREQUENCY–the proportion of individuals in a population with a particular genotype.

GENOTYPIC VALUE–the mean phenotypic value of individuals in a population that have a particular genotype.

GYNOGENESIS–the production of offspring having all maternal inheritance (all chromosomes and genes obtained from the mother).

HALF-SIBS–individuals having one parent in common and the other parent different.

HAPLOID–a cell or organism with a single set of homologous chromosomes.

HAPLOTYPE–a description of the alleles at two or more loci on the same chromosome.

HARDY-WEINBERG EQUILIBRIUM–the relationship between allelic and genotypic frequencies in an idealized population after a single generation of random mating.

HERITABILITY–the fraction of the total phenotypic variance in a population that is due to the additive effects of genes; used to predict the response to artificial selection.

HERMAPHRODITE–an organism that is both male and female.

HETEROCHROMATIN–sections of condensed chromosomes that are readily observable when stained and examined under a light microscope; heterochromatin can be used to identify particular chromosomes or as a genetic marker.

HETEROGAMETIC–the condition of having two different sex chromosomes.

HETEROSIS–see hybrid vigor.

HETEROZYGOTE ADVANTAGE–superior phenotypic value due to heterozygosity.

HETEROZYGOTE–an organism or cell with two different alleles at a particular locus.

HOMOGAMETIC–the condition of having two copies of the same sex chromosome.

HOMOLOGOUS CHROMOSOMES–chromosomes that carry the same genes.

HOMOZYGOTE–an organism or cell with two copies of the same allele at a particular locus.

HORMONE–a chemical that controls and coordinates the condition of cells and tissues in organisms.

HYBRID VIGOR–increased phenotypic value of a hybrid strain relative to the parental strains used to produce the hybrids; hybrid vigor is usually attributed to heterozygosity at many loci.

HYBRIDIZATION–interbreeding between different species, races, lines, or varieties.

IDEALIZED POPULATION–an infinitely large population that has a balanced sex ratio, random mating, non-overlapping generations, no migration, no mutation, no variability in reproductive success and no artificial selection; a population to which the Hardy-Weinberg law applies exactly.

INBREEDING–the mating of related individuals, or self-fertilization.

INBREEDING COEFFICIENT (*F*)–a measure of the amount of inbreeding and genetic drift that a population has experienced; also called an F-statistic.

INBREEDING DEPRESSION–a reduction in fitness or vigor due to inbreeding and increased homozygosity.

INCOMPLETE DOMINANCE–partial dominance by one allele so that both alleles at a locus are expressed phenotypically in a heterozygote but to different degrees.

INDEPENDENT ASSORTMENT–random distribution of alleles or chromosomes (into gametes) during gametogenesis.

INDEPENDENT CULLING–a selection program designed to improve several traits simultaneously; individuals are selected for breeding only if they meet independent criteria for all of the traits under consideration.

INDIRECT SELECTION–artificial selection applied to one character in order to improve some other, genetically correlated character.

INDIVIDUAL SELECTION–selection of individuals, rather than family groups, for breeding in an artificial selection program.

INTENSITY OF SELECTION–a standardized measure of the intensity of selection in an artificial selection program; intensity is equal to the selection differential divided by the standard deviation of the trait in the population from which the breeders were obtained.

INTERPHASE–the stage of the cell cycle between cell divisions.

ISOZYMES–enzymes that promote the same chemical reaction but are the products of alleles at different loci.

LINKED GENES–alleles at two loci that tend to be inherited as a single unit because the loci are located near one another on the same chromosome; genes that do not assort independently.

LOCUS–the location of a particular gene on a chromosome.

MALE FACTOR–a gene not found on a sex chromosome that promotes masculine characteristics.

MASS SELECTION–a form of artificial selection in which only individuals with phenotypic values greater or less than some threshold level are used for breeding.

MATERNAL EFFECTS–non-genetic influences of a mother on the phenotypes of her young.

MEIOSIS–a sequence of cell divisions that lead to reduction in the number of chromosomes prior to the production of eggs and sperm.

MENDEL'S PRINCIPLES–1) each gamete contains only one allele from every pair in the parent organism (the principle of segregation) and 2) alleles at different loci assort independently during gametogenesis (the principle of independent assortment).

MENDELIAN TRAIT–a trait that is controlled by genes that segregate and assort independently during gametogenesis.

MERISTIC TRAIT–a trait that displays discrete rather than continuous variation (e.g., number of ribs and number of scales along the lateral line).

MESSENGER RNA (mRNA)–ribonucleic acid that is used to communicate genetic information obtained from DNA inside the cell nucleus to the sites of protein synthesis in the cytoplasm of the cell.

METAPHASE–the second stage in the division of a cell nucleus during mitosis or meiosis when condensed chromosomes line up midway between opposite ends of the cell.

MID-PARENT MEAN–the average of the phenotypic value of both parents.

MIGRATION–the movement of individuals from one population to another.

MITOCHONDRIA–organelles in the cytoplasm of cells that contain DNA and function in energy metabolism.

MITOCHONDRIAL DNA (mtDNA)–DNA found in mitochondria.

MITOSIS–division of nuclei during cell divisions that do not lead to the production of gametes; chromosome number is not reduced during mitotic divisions.

MOLECULAR GENETICS–the study of genetics at the level of molecules (e.g., structure of DNA, the genetic code, replication of DNA).

MONOMORPHIC–a locus that has just one allele in a population; a locus that is always homozygous for the same allele.

MONOPLOID–an organism or cell having a single haploid set of chromosomes.

mRNA–see messenger RNA.

mtDNA–see mitochondrial DNA.

MULTIPLE TRAIT SELECTION–artificial selection on the basis of two or more phenotypic traits.

MUTAGEN–an environmental agent (e.g., radiation or chemicals) that is capable of inducing mutations.

MUTATION–a change in the DNA or chromosomes of a cell or organism.

NATURAL SELECTION–the selection of successful breeders by natural environments on the basis of phenotypic traits related to fitness.

NON-ADDITIVE COMPONENT–the portion of the total phenotypic variance for a trait in a population that is due to non-additive effects of genes (i.e., dominance effects and epistatic effects).

NUCLEAR DNA–DNA in chromosomes within the nucleus of a cell.

NUCLEOTIDE–a unit of the DNA molecule containing a phosphate, a sugar, and a base.

NUCLEUS–an organelle that contains chromosomes in the cells of fish and other higher plants and animals.

ONE GENE - ONE PROTEIN CONCEPT–a definition of a structural gene as the DNA that codes for a single protein.

ORGANELLE–a specialized part of a cell with particular functions.

OUTCROSSING–matings between individuals from one line and entirely unrelated individuals.

OVERDOMINANCE–the condition that exists when heterozygotes have greater phenotypic value than homozygotes.

PENETRANCE–the frequency with which a genotype is expressed phenotypically in different individuals.

PHENOTYPE–the detectable properties (i.e., one or more traits) of an individual that are produced by the genotype and the environment.

PHENOTYPIC VALUE–a measurement of some trait (e.g., weight, number of dorsal fin rays) obtained from an organism.

PLASMID–a small bacterial chromosome useful for transferring genes from one organism to another in the laboratory.

PLEIOTROPY–the condition in which a single gene affects more than one phenotypic characteristic.

POLYGENIC–traits that are determined by genes at many loci.

POLYMORPHIC–a gene or qualitative trait that exists in two or more forms in a population.

POLYPLOID–a cell or organism possessing three or more haploid sets of chromosomes.

POPULATION–a group of organisms that freely interbreed.

POPULATION BOTTLENECK–a temporary decline in population size that dramatically reduces mean effective population size over many generations; population bottlenecks increase the mean rates of inbreeding, genetic drift, and loss of genetic diversity in a population.

POPULATION FITNESS–see fitness.

PROGENY SELECTION–the selection of breeders in an artificial selection program on the basis of the mean phenotypic value of their progeny.

PROPHASE–the first stage of mitotic or meiotic cell divisions during which chromosomes condense and become visible by light microscopy.

PROTEIN–a molecule composed of a chain of amino-acids.

QUALITATIVE TRAIT–a phenotypic trait that is described qualitatively rather than by measurement (e.g., eye color).

QUANTITATIVE TRAIT–a phenotypic trait that is described by a measurement (e.g., weight at maturity) and usually controlled by genes at many loci.

RECESSIVE–an allele or trait that is expressed only in homozygotes.

RECIPROCAL CROSS–mating males of one strain to females of another and vice-versa.

RECOGNITION SITE–a specific sequence of nucleotides in DNA that are recognized and cut by a restriction endonuclease.

RECOMBINATION–exchange of alleles between homologous chromosomes due to crossing over during meiosis.

REGULATORY GENE–a gene whose function is to control the rate at which other genes are transcribed.

REPLICATION–duplication of a DNA molecule.

RESPONSE TO SELECTION (*R*)–change in the mean phenotypic value of a population due to artificial selection.

RESTRICTION ENDONUCLEASE–an enzyme that cuts DNA at specific sequences of base pairs called recognition sites.

RNA–ribonucleic acid; present in several forms in a cell and involved in the production of proteins.

ROTATIONAL LINE CROSSING–a breeding program involving three or more lines that minimizes inbreeding and loss of genetic diversity.

SECONDARY CHARACTER–the trait used to select breeders in an indirect selection program.

SEGREGATION–the separation of homologous chromosomes or alleles during the production of gametes.

SELECTION–the natural or artificial process by which breeders are chosen from a population on the basis of fitness or phenotypic value.

SELECTION DIFFERENTIAL (*S*)–the difference between the mean phenotypic value of selected breeders and the mean phenotypic value of the population.

SELECTIVE NEUTRALITY–the hypothesis that the genotype at a locus does not affect the fitness of an organism.

SEMIDOMINANCE–the condition of an allele that is incompletely dominant; see incomplete dominance.

SEX CHROMOSOME–a chromosome that is involved in sex determination.

SEX REVERSAL–the process of switching sex.

SIB SELECTION–the selection of breeders in an artificial selection program based on the phenotypic value of their sibs.

SOMATIC CELL–a cell in the body of an organism that is not a gamete.

SPECIFIC COMBINING ABILITY–the difference between the mean phenotypic value of hybrids and the sum of the general combining abilities of the two parental lines used to produce the hybrids; the specific combining ability may be positive or negative and is a measure of the value of a hybrid line relative to what would be expected on the basis of the general combining abilities of the parental lines.

STATISTICAL POWER–the ability of a statistical test to discriminate between alternate statistical hypotheses.

STOCK–a population of organisms which, sharing a common environment and participating in a common gene pool, is sufficiently discrete to be considered a self-perpetuating, manageable system (Larkin 1970).

STRUCTURAL GENE–a gene that codes for a protein.

SUPERIOR SEX GENE–a gene that is a primary determinant of sex and is found on a sex chromosome.

SYSTEMATIC PROCESSES–processes that change allelic frequencies of a population in some predictable, nonrandom fashion (i.e., mutation, migration, and selection).

TANDEM SELECTION–an artificial selection program designed to improve several traits; breeders are selected on the basis of one trait in the first generation, another trait in the second generation and so on.

TELOPHASE–the fourth and final stage in the division of a cell nucleus during mitosis or meiosis when the chromosomes group together at opposite ends of a cell just before the nucleus divides.

TETRAPLOID–a cell or organism with four haploid sets of chromosomes.

TETRASOMIC–an otherwise diploid organism or cell that has four copies of one or more chromosomes or genes.

TRAIT–any detectable, phenotypic property of an organism.

TRANSCRIPTION–the process of forming messenger RNA from DNA.

TRANSFER VECTOR–a segment of DNA which facilitates insertion of new genes into the genome of a recipient cell.

TRANSLATION–the process of protein synthesis in ribosomes using mRNA as a template.

TRIPLET CODE–a sequence of three nucleotides that code for one amino-acid in a protein.

TRIPLOID–a cell or organism having three haploid sets of chromosomes.

TRISOMIC–an otherwise diploid cell or organism that has an extra copy of a chromosome or gene.

WITHIN FAMILY SELECTION–selection of the best individuals within a family for breeding.

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