

Fish Population Genetics and Management of Captive Breeding Populations

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The aim of genetic improvement is not to change individual fish, but rather the fish stock. Hence, the '*Mendelian Genetics*' extended at the level of population is the "*Population Genetics*". It is thus most essential to understand the meaning of a stock or population.

Definition of population

In general, a population refers to a group of individuals of a species assembled/living at a place at a time. *Statistically*, a population is referred to a group or collection of individual/items having the similar properties. *Biologically*, a population refers to a group of organisms/individuals of a species functioning together as a unit at a given place and time. *Genetically*, in population genetics, a population is defined as a group of interbreeding individuals. As a result of interbreeding there is gene exchange among the individuals of a population and hence they contribute to the gene pool of the offspring generation. The gene exchange is thus the main and important factor to define population. The population for a population geneticist means the "*Mendelian Population*" which is defined as a group of *interbreeding individuals developed over both space and time* sharing a common pool of genes, from which meaningful samples can be drawn and within which the characteristics under study follow the Mendelian rules of inheritance. The *gene pool* is taken as the sum total of genes in a population. In other words, the gene pool includes collectively all the genetic information distributed among all the individuals of a population.

Size of Population: The number of individuals constituting a population decides the size of the population. Therefore an individual is the unit of population. The number of individuals in a population should be large enough so that the sampling variation is as small as to be negligible. Thus, a population should not be affected by the sampling variation. Such a population which is not affected by the sampling variation is known as large population and consists the number of individuals in hundreds or even in thousands rather than in tens.

The total number of individuals forming the population is important. The differential reproductive success of different individuals molds the genetic structure of a population in coming time. The counting of the number of individuals in a population is done for three purposes: to assure the existence of population, to determine the gene frequencies, and to estimate the role of chance factor played in the transmission of genes.

Genetic structure of a population

The organization of the genes into genotypes is the most essential part of population genetics. The genotypes are not transmitted to the offspring as such but they are broken during meiotic cell division as a requirement of genetic transmission from one generation to the next. Thus genotypes of the parents are broken into gametic pool and each offspring has its newly formed genotype different from its either parent. Therefore, the array of genotypes in a

population is re-determined in each generation. For example, the heterozygous parent (Aa) may not have any heterozygous offspring. The gametes produced by a heterozygous parent (Aa) contain either A or a allele which may unite with any allele of opposite sex and thus parental heterozygosity is not transmitted directly to the offspring. The relative genotypic frequencies in a population are determined by some biological forces *viz.* breeding behavior, genetic factor (mutation) and environmental factors (migration, selection, sampling process in small population) which act on individuals by affecting their survival and reproduction. Thus the genotype frequencies from one generation to the next are under the control of these forces.

Among the breeding behavior, the simplest and important one is the random breeding or random fertilization which follows no principle (criteria) for breeding of individuals of opposite sex and individual of one sex has equal chance to breed with any individual of the opposite sex. The main feature and consequence of random breeding in a large population is that the relative gene frequencies and genotype frequencies remain constant from generation to generation and thus there is no change in genetic structure of large population under random breeding. This is called as genetic equilibrium. The genetic equilibrium is disturbed if the breeding is non-random and if any of the genetic and environmental force is in action. Any force is capable to change the genetic equilibrium from one generation to the next. There are a number of situation and environmental factors (migration, selection and sampling) to disturb the genetic equilibrium.

Most of the captive populations are not ideal to maintain the genetic equilibrium in view of the man's activities and the role of nature. The ideal population is in which no disturbing force comes in action to upset the genetic equilibrium and the random breeding results in a genotypic distribution consistent with the frequencies of genes. However, the fish breeder is interested to change the existing genetic structure of the population in a desired direction to exploit the existing genetic variability to make the animals more productive and more useful. Therefore, breeders are not interested to maintain the existing genetic structure of the breeding population and they make their efforts to achieve high performance of their animals. This is achieved in a number of ways.

The **first** is the selection of the better production animals and to eliminate the low productive and inferior ones. This is called the artificial selection. **Secondly**, the selected animals are bred following certain criteria rather than allowing random breeding. Thus breeding is non-random (assortative). **Thirdly**, the breeders keep their captive population in relatively small size. This results in small population size which upsets the genetic equilibrium in two ways. One is that inbreeding is inevitable in small population size which changes the genotype frequencies of next generation. The other effect of small population size is that the possibility of expected genotypic frequencies is low due to lesser number of animals according to the probability because higher number of events makes the expectation more close to reality. Thus smaller number of animals in the herd results in the occurrence of errors in sampling due to chance events. This leads to differentiation of gene frequencies in local populations resulting from sampling. The **fourth activity** of fish breeders is the trade breeding under which the animals

are sold or transferred to another breeder and thus migration of animals occurs which further increases the possibility of gene flow (migration) from one corner to other corner of the country or the world.

It is thus obvious that most of the conditions for genetic equilibrium are not fulfilled. The fish population size maintained under captive conditions in India is small, the breedings are not random but selective breeding is practiced and the animals are migrated for a number of reasons. Therefore, the genetic equilibrium is not observed in hatchery and farm conditions in all practical situations and the change in genetic structure of populations is likely to occur. The change can be brought to favourable direction and magnitude after having the knowledge and being aware of the genetic effects. Therefore, it is most essential for a breeder to know the process of change in genetic structure of populations under the influence of various forces. These forces capable to change the genetic structure of a population can be classified in several ways as under-

Natural Vs. artificial factors: Both nature and manmade interventions disturb the existing genetic equilibrium and contribute to changes in the genetic structure of the population. The factors which are under the control of nature to upset the genetic equilibrium are the mutation (change in genetic structure of a gene) and the natural selection. The natural selection operates through differential fertility and viability. The manmade activities include artificial selection by way of selective breeding and preferential breeding (non-random breeding), migration of animals through purchase or transfer, and to keep small population size leading to inbreeding and sampling error (random drift).

Factors involved at individual and population level: The first is the change at gene level (mutation) whereby the genetic structure of gene is changed and produces a new gene. The second is the change at population level by gene flow (migration), selection, small population size, and by a change in breeding system from random breeding to preferential breeding (non-random breeding).

The second category of forces brings a change in gene frequencies between generations and consequently result a change in genotype frequencies. These forces include gene mutation, gene flow (migration), selection, small population size and disassortative breeding. The genetic changes brought by the forces of second category are permanent even after switching to random breeding. This is because these forces involve the change in gene frequencies.

Amount and direction of change: On this basis all the forces are divided into two groups. The first group is of the deterministic or systematic forces which are also called as the vectorial process. The second category is the stochastic process or random or dispersive forces. Among the systematic forces are the mutation, migration and selection which tend to change the gene frequencies predictable both in amount and direction. The dispersive process arises in small population. The change brought by dispersive process is predictable only in amount but not in direction.

Importance of recording the data

If the purpose of selection is to improve a production trait, the first step is to measure or record this trait on all animals in the population, and then estimate the average and standard deviation. Selection is then practised by selecting those animals, which have highest breeding values. A fishhatchery or farm is a dynamic and complicated enterprise having the objective of increasing the productivity and profit. In order to achieve the objective of increasing the productivity and changes, activities and requirements for which the fish breeder has to keep the records and get useful information for taking right decisions about selection of genetically superior animals on the basis of their breeding values.

The data or records are essential in a hatchery or farm for the following purposes:

- To know the pedigree and history of each brooder pertaining to the production, reproduction and health performance.
- This helps to compare the between farm or between hatchery performance of brooders
- The breeding value for different economic traits can be estimated which help in culling and selection of animals for breeding purposes which in turn bring the genetic improvement of future generations.
- Based on the production performance the feeding requirement can be estimated.
- This also helps in research and development planning.
- To know the health status by keeping records of the daily treatment of animals.

Selection and its Response

Selection is applied to change the fish population for making genetic improvement in performance. The selection is a process of giving preference to certain individuals in a population to reproduce than other individuals which are denied the opportunity to produce next generation. Therefore, selection is the choice of individuals to produce the next generation. In genetic terms, the selection is a process of differential reproduction and survival of genotypes which may be natural or artificial or both.

The selection, without creating any new gene, changes the genetic structure of the population by changing the frequency of genes and genotypes. The frequency of desired genes is increased in the population through selection at the expenses of the frequency of undesirable or less desirable genes. This is the genetic effect of selection. The selection is more efficient for dominant genes at low frequency but it is relatively easy to select for a recessive gene.

The characters are controlled by genes. Therefore, with the increase or change in the frequency of desirable genes, the phenotypic mean of the character of offspring generation is also increased or changed. The change in performance of offspring generation due to artificial selection is known as **response to selection or genetic change or genetic gain**. Now the point of discussion here is that how the performance of the offspring generation of selected parent is changed.

Intensity of selection

The intensity of selection denoted by “ i ” is the mean deviation of the selected animals in units of σ_p of the trait *i.e.* it is the number of σ_p of the trait by which the mean of the selected group is above the population mean before selection. The intensity is expressed as:

$$i = s / \sigma_p$$

Factors affecting the response to selection

The change in performance due to artificial selection known as response to selection depends on the following factors:

- 1 Additive genetic variability in the trait (σ_A)
- 2 Intensity of selection (i)
- 3 Accuracy of selection (r_{ap})
- 4 Population size

Additive genetic variability in the trait (σ_A)

The selection acts on additive genetic variability. The variation in breeding values (BV) of the individuals within the population is the raw material to act for artificial selection. The selection will not be effective to bring change if there are no genetic differences among animals. Therefore if $V_A = 0$, the $R = 0$. The magnitude of R increases with the increase in differences in B.V. between animals. However, the genetic variability of a trait (B.V.) within a population is determined by the population and the characters and hence it is beyond the control of breeder. It is therefore better to exploit other factors like intensity and accuracy of selection.

Intensity of selection (i)

The intensity of selection depends on the proportion (p) of the population selected. When p is small, the selection is said to be more intense or rigorous. But when p is large (increase in proportion selected) then there is decrease in intensity of selection. The R will be more when p will be small. This is a straight forward way to improve the rate of genetic progress. If all fishes are selected, the S will be zero and no change in offspring mean will occur. The change occurs if some of the best fishes are selected. Therefore, the proportion of fishes selected should be less.

Accuracy of selection (r_{ap})

The selection is effective only when the animals with highest B.V. are selected. The true B.V. of fishes is not known. This requires one or more sources of information to know the estimate of B.V. of fish. The information to estimate the true B.V. of a fish may be collected on the performance of the fish itself and or of its any close relative. The estimate of true B.V. so estimated should be as much accurate as it can be to make the selection more accurate. The accuracy of selection is taken as the correlation between the true B.V. of a fish and the source of information (Selection criteria) which is denoted as r_{ap} where A is the true B.V. and P is the selection criteria. The selection criteria may be a single record of average of repeated records of the fishes itself or on any relative *viz.* dam or average performance of a group of relatives like full sibs, half sibs or offspring groups.

The r_{ap} is equal to square root of heritability ($r_{ap}=h$). Thus if h^2 estimate is higher, then r_{ap} will also be higher. The h^2 is an indication of the reliability of phenotypic value as a guide to the breeding value (B.V.) because the h^2 shows the correspondence between B.V. and phenotypic value. In other words, the h^2 shows the extent to which the B.V. constitutes the phenotypic value. Thus is directly correlated to h^2 as $r_{ap}=h$ which is a measure of the accuracy of selection. It is, therefore, that for maximum accuracy of selection, the r_{ap} must be as high as possible to make the selection accurate. Thus selection will be more accurate when the h^2 of the trait is high.

The accuracy of selection can be increased by the following methods:

1. *Minimize the environmental variance:* It can be minimized by providing uniform environment, by use of multiple records to estimate h^2 , by adjusting the data for environmental effects, by accurate measurement of data, and by analyzing the data based on contemporary group mean.
2. *Combined Selection:* When two or more criteria of selection are used to estimate an individuals' true breeding value (BV) it is called as the combined selection. This means to supplement the individuals' performance belonging records with those of its relatives. This gives more accurate estimate of B.V of the individual. The family selection may be used to support individual selection when h^2 of a trait is low. It is better to select an individual with better record belonging to a superior family compared to an individual with similar performance belonging to a mediocre or inferior family. The half sib family selection is better than FS family selection.

The reason being that family selection is more effective when the environmental variations common to all the members of a family are as small as possible. This means that environmental similarities among family members should be low. The common environmental variance is less among half sibs than among full sibs. Thus, the environmental correlation among F.S. is more than among H.S. Secondly, the F.S. family selection reduces the genetic variability in the population and also results in a certain amount of inbreeding. The selected parents based on F.S. family averages are more closely related. Thirdly, the effective selection intensity is also reduced for a given testing facility for F.S. family selection.

3. *Selection based on future performance:* The selection should be based on the future performance (most probable producing ability or the expected producing ability) of the animal with more number of records.

Size of the population

The effect of population size on response to selection can be viewed in terms of inbreeding and genetic drift. The inbreeding is unavoidable in a population of small size. But inbreeding is less when the animals of both sexes are equal which is not possible in fish breeding for the reason that fewer individuals of either sex may be required according to species under selection. This needs to estimate the effective population size (N_e). The N_e is the number of

individuals that would give rise to the same rate of inbreeding, if they breed in the manner of an idealized population, in which the rate of inbreeding is $\Delta F = 1/2N$.

Criteria of selection

The performance records of ancestors and collateral relatives of the individual are also used as selection criteria to estimate the breeding value of an individual for the trait under selection.

Selection based on pedigree

The pedigree is a list or record of ancestors in the past few generations of the individual. The ancestors are the parents, grand parents, great grand parents etc. The pedigree having information on the economic characters of the ancestors is useful in selection of an individual. The B.V. of an individual is estimated on the basis of the performance of the ancestors. The selection criteria based on ancestors performance is called as the pedigree selection.

Basis of pedigree selection

An individual receives genes from his ancestors. The percentage of ancestral genes is halved in each generation. This decides the genetic relationship between an individual and his ancestor(s). This relationship is reduced to half in each generation. It is thus important to consider more recent ancestors (parents) rather than distant ancestors (great grandparents) for pedigree selection. This inclusion of more remote ancestors results only in marginal gain in accuracy of selection due to the halving process and sampling nature of inheritance. The pedigree selection adds very little to the accuracy of estimating the B.V. of an individual if the information on individual are available. The significance of pedigree is decreased when information are available either on the individual or its family members (sibs and offspring).

Guides to pedigree selection

The following factors determine that how much attention is to be given to pedigree selection.

- The degree of genetic relationship of the individual with its ancestor – more closely related ancestors should be given more emphasis.
- Heritability of the character - the pedigree selection is more accurate for traits of high heritability.
- Environmental correlations among the individuals used in the prediction.
- Information available on ancestors.

Practical difficulties to use pedigree selection

- The ancestors' records are always not available.
- The pedigree records are destroyed with passage of time.
- Most of the characters have low heritability.

Merits of pedigree selection

- It is less costly as only compilation of pedigree is required.
- Allows selection at younger age and provides first-hand information.

- It is helpful in multistage selection.
- It is useful for sex limited traits and traits expressed in later life or after death of animal.
- It is helpful when two individuals have similar performance but one belongs to a better pedigree.

Demerits of pedigree selection

- There is a disadvantage of using pedigree selection that all animals of similar pedigree are culled out in spite of the fact that an individual may be of good merit and free from recessive allele causing defect.
- Some pedigree gets undue emphasis and favoured irrespective of the true merit of the individual. Better environment is provided to the offspring of favoured pedigree.
- It introduces non-random biases because pedigree records are for different environmental conditions.
- Pedigree selection provides no basis of selection among individuals which are descendants of the same ancestor.

Selection based on collateral relatives

The selection criteria to estimate the B.V. of an individual may be the information (Performance records) of its collateral relatives. An individual's collateral relatives are those which are not related with the individual on direct genes donor-recipient basis but receive common genes from their common ancestor(s) e.g. full sibs, half sibs, cousins, etc. The collateral relatives should be more closely related to the individual and these are full sibs and half sibs. The more closely related collaterals to the individual are likely to have more common genes possessed by the individual and can provide more accurate information about the individual. The more closely collaterals can be grouped as full sib families and half sib families. The family mean of these collateral relatives then form the basis to select the superior individual. The procedure to estimate the B.V. of an individual on the basis of family mean is called the family selection or sib selection depending upon the inclusion or exclusion of individual's own record in estimating the family mean. The selection criteria is called as family selection when the individual's own record is included to estimate the family mean but the selection criteria is called as the sib selection when the individual's own recorded is not included in estimating the family mean.

Sib Selection

It is the selection of an individual based on its sibs performance. The sibs may be full sibs or maternal half sibs or paternal half sibs. Thus sib selection is of two types viz. Full sib selection and half sib selection. The sib selection is practiced for the following traits for which the measurements on the individual are not available or recorded –

- Slaughter traits
- Sex limited traits

- Threshold traits like disease resistance
- Traits with low heritability in species with high reproductive rate so as many sibs are measured in short time
- The full sib (F.S) selection is more accurate than half sib (H.S.) selection. However, the H.S. selection is favoured for the following reasons:
 - Half sibs are easily available in more numbers than F.S.
 - The rate of inbreeding is more for F.S. selection than H.S. selection. The inbreeding counter balances the effect of selection.
 - The F.S. correlation is more likely to be increased by c-effects (common environment shared by F.S.). The intra class correlation (t) is rh^2 for H.S. and rh^2+c^2 for F.S. where c^2 is the added contribution of maternal or common environmental effects. This reduces the accuracy of F.S. selection.

Family Selection

The selection criteria are known as family selection when based on the performance of the sibs plus the individual's own record. The family selection like the sib selection is of two types of sibs viz Full sib family selection and Half sib family selection. The family selection is also taken in another way viz. as a unit of selection. Based on the family mean the whole of the family is selected or rejected as a unit of selection.

Common environment (c-effects)

The environmental effects which are different for different families but same for all members of one and the same family are known as common environmental effects denoted as c-effects. The family members share common environment during pre and post natal stage. The c-effects thus create resemblance within family members over and above the resemblance due to having common genes and this contributes to the variance between families. This increases the intra class correlation (t) among family members. The c-effects are more for F.S. than for H.S. To some extent the half sibs also share common environment viz. all the offspring of a sire being born almost at the same time and being reared together are likely to be subjected to similar environmental conditions like climatic conditions, feeding regime and management practices etc.

When environmental similarities (c-effects) are present among family members, the intra class correlation among the phenotypic values of family members (t) is increased equal to the amount of c-effects as $(t+c^2)$ where C^2 is the portion of the total variation caused by differences in c-effects among families. This makes the denominator larger and hence the regression is decreased. Thus the c-effects decrease the accuracy of sib and family average.

Advantages of family selection

- The family selection can improve the characters of low heritability in species with high reproductive rates so as to get many sibs in a short time.
- The family selection does not allow the generation interval to increase

- Family selection is a support to individual selection because it is better to select an individual from a superior family.

Limitations of family selection

The family selection to be effective requires large family size and more number of families to avoid inbreeding as well as to increase the intensity of selection. In view of this it can be inferred that –

- Family selection is costly of space particularly when the breeding space and testing facilities are limited. The limited facilities reduce the intensity of selection.
- The family selection as a unit of selection results in inbreeding and thus limits the genetic diversity. This is because only few families represent the next generation.
- The F.S. family selection can only be applied in species with high reproductive rates to get large family size.

Within family selection

It is the selection criteria when individuals are selected on the basis of their performance expressed as deviation from their mean. The individuals that exceed their family mean by the greatest amount are selected. Thus it is opposite to family selection because family mean is given no weight. This selection criteria is preferred when c-effects are important i.e. when a large component of environmental variance is common to all members of a family. A large component of environmental variance common to members of a family arises when the different families differ in the environment to which they are exposed. Thus the families differ largely due to differences in environment and hence whole family get good or poor environment. The selection within family eliminates the environmental differences among families.

The within family selection economizes the breeding space and minimizes the rate of inbreeding. In within family selection, each family contributes equally to the parents of next generation, when single pair breedings are made and two individuals from each family are selected as replacement of the parents. The within family selection is better than individual selection when the sib correlation (t) is very high and caused largely by environmental effects. The within family selection operates on a large amount of additive variance within families.

Selection and breeding for disease resistance

There are three possible methods to identify and select the individuals for differences in resistance/susceptibility to a certain disease/parasite. These are as under:

- Occurrence of the disease under normal environmental conditions,
- Inoculation of animals with pathogen causing the disease, and
- Use of indicators of resistance.

The first method to identify the resistant animals on the basis of the incidence of the disease is not effective in the sense that under the changed environmental conditions the resistant

become susceptible. The second method of inoculation is not likely to be applied because of the objections to deliberate infection with pathogenic organisms. The third one requires very great efforts and research to find a better indicator of genetic resistance; which do not require deliberate exposure to pathogens.

The efficiency of individual selection and family selection on the basis of the incidence of the disease with two visible classes is discussed. The effectiveness of selection depends on the selection differential which, in turn, depends mainly on the proportion selected. But in case if threshold characters (all or none characters), the selection differential depends on the incidence rather than on the proportion selected. Selecting all the resistant individuals or only a portion of them will give their mean as the mean of the resistant group. Thus, selecting a smaller proportion than the incidence, does not give an added advantage. It is, thus, evident that maximum selection differential is achieved when the proportion selected is equal to the proportion of resistant individuals. The individual selection is less effective when the difference between the two (incidence of resistance and proportion selected) is more. Further, the individual selection is less effective when the proportion of resistant individual is very low, but the family selection is more effective. An individual's phenotype as resistant or susceptible is not precisely known whereas the family is more precisely known for the proportion of affected members of the family. However, the precision depends on the family size and on the incidence of a disease in the family.

Conclusion

Although aquaculture as a biological production system has a long history, systematic and efficient breeding programs to improve economically important traits in the farmed species have rarely been utilized until recently, except for salmonid species. This means that the majority of aquaculture production is based on genetically unimproved stocks. In farm animals the situation is vastly different: practically no terrestrial farm production is based on genetically unimproved and undomesticated populations. This difference between aquaculture and livestock production is in spite of the fact that the basic elements of breeding theory are the same for fish and shellfish as for farm animals. One possible reason for the difference is the complexity of reproductive biology in aquatic species, and special consideration needs to be taken in the design of breeding plans for these species.

In aquaculture, selection programs are not commonly used by the industry and for many species production still rely completely on catching wild broodstock and/or fry. There is no obvious reason for the lack of efficient breeding programs in aquaculture. The economically important traits in fish and shellfish appear to be little different from those in farm animals and plants. Selection response is usually higher in fish and shellfish than in farm animals. One reason for the scarcity of breeding programs in aquaculture species is that the reproductive cycle is often complex, and so is frequently not fully understood, and is therefore not able to be completed or controlled in captivity. This is the case particularly for marine species. A further factor contributing to the scarcity of breeding programs in aquaculture species may be the

deterioration of the stock simply because of a rapid build-up of inbreeding as a result of using few broodstock each generation (and without identification to prevent re-use). This is a problem in all species with high fecundity. Because there has been little interest in developing breeding programs in aquaculture, the information about phenotypic and genetic parameters of economically important traits are quite limited for most of the species farmed. Before a breeding program can be established, breeding goal must be defined; estimates of genetic variance, heritability, phenotypic and genetic correlations among traits must be available. There is therefore a great need to run breeding experiments in order to get reliable estimates of genetic parameters for economically important traits in the most important farmed species.

The applications of molecular techniques in aquaculture are promising, but still somewhat uncertain. While high costs seem to be the only hindrance for widespread application of DNA markers for identification purposes and marker assisted selection, the situation regarding commercial use of genetically modified fish is more complex. Although the potential importance of gene transfer technology is large, a major concern relates to the possible impact, which release or accidental escapes of gene-modified individuals may have on natural ecosystems. Other technologies are also rapidly emerging which are either being used or are likely to be used in the future in the aquaculture species. For example micro-array technology has the potential to contribute very large amounts of information on the genes and pathways of genes, which affect the economic traits in aquaculture species.