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How Issues of Genetic Diversity Affect Management of African Inland Fisheries

The Example of the Lake Victoria Region Fishery

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The management of African inland fisheries, like the management of any other natural resource, increasingly requires knowledge and understanding of how genetic diversity affects the biological functioning and evolution of the constituent populations. Of most concern will be the loss of genetic diversity in natural populations, an issue that will be at the fore in repair and maintenance of any fisheries resources. The loss of genetic diversity is attributed to population subdivision, reduced or lack of gene flow, inbreeding, genetic drift, and genetic swamping of marginalized populations and species. This chapter seeks to explain how issues of genetic diversity have shaped the inland fisheries of Africa and can be used effectively to manage, conserve, and restore fish populations. Several factors have had a severe impact on both the aquatic species diversity and overall genetic diversity within Africa's inland fisheries. Before the twentieth century, the evolution and distribution of inland fisheries of Africa were driven by natural climatic changes and changes in water resources brought about by earth movements (see Livingstone, chapter 1). Since the turn of the twentieth century, most of the changes in Africa's inland fisheries have come about as a result of the direct influence of humans trying to harness fisheries products. These changes have often resulted in reduced population sizes and local or even widespread extirpation of populations (see Welcomme, chapter 8). This chapter describes how such changes in population structure affect the genetic diversity and evolution of the fisheries species. Examples are provided from throughout Africa, with particular emphasis on the Lake Victoria region, where a combination of factors—including dramatic limnological changes in the lake waters, elevated fishing pressure, and subsequent introduction of alien species—has resulted in drastic changes in the fish fauna. An understanding of how management decisions and actions may affect the evolution and genetic diversity of natural populations should form the basis of the management strategies to be adopted either to increase production or to ensure the conservation of aquatic biodiversity.

Why Issues of Aquatic Genetic Biodiversity Are Important in Fisheries Resources Management

The threat of loss of genetic diversity predicates that managers continuously monitor the genetic diversity and assess the extent of its loss. Knowledge of the rate of loss of genetic diversity is required to determine the population sizes necessary to maintain genetically viable population units. A genetically viable population is one with a level of genetic variation at which natural evolutionary changes can take place without detrimental effect on the continued existence of that population. Normally, a large and continuous population with freely interbreeding individuals allows for natural evolution without negative impacts on the population. Any factor that leads to breaking up of an originally continuous and uniform population into smaller units will reduce the genetic variation within the resulting subpopulations. This principle leads to the issue of determining the size of a genetically viable population and the portion of that population responsible for its continued existence.

Because a population at any time has individuals that do not take part in breeding, such as juveniles and reproductively spent individuals, only a portion of the population contributes to its propagation. This portion of the population is technically known as the effective population size and is considered as that size of the population that actually contributes to the gene pool and continued existence of that population (Wright 1931, Kimura and Crow 1963). Knowing the effective population size allows for estimation of the time when loss of genetic diversity is likely to threaten the continued existence of a population (Wright 1938). Many studies agree that the key measurement needed for successful conservation is the effective population size (Soule 1980, Shaffer 1987, Nunney and Elam 1994). There is contention, however, about the approach for estimating the effective population size (Lande and Barrowclough 1987, Gregorius 1991, Nunney and Elam 1994, Sugg and Chesser 1994).

Before the effective population size can be estimated, the actual population size has to be known. However, measuring the population size has always been notoriously difficult for most aquatic life, including fish. One of the major hurdles is in defining a population. Population limits based on geographical demarcations sometimes erroneously represent the actual populations. Most fish populations do not exist as single continuous panmictic units. Instead, they exist as several subdivided units that are geographically disjunct and have a limited degree of migration between units, forming what is known as a metapopulation. However, since the structure of the genetic variation is dependent on the reproductive interaction within populations and on isolation among populations, population structure, for purposes of demarcating populations, is equivalent to the genetic structure of a species. Individuals of a population are genetically more similar to one another than to any other individuals of the same species. The evolutionary units are demarcated by breaks within the level of genetic relatedness among individuals in a particular geographical location, known technically as the genetic structure.

Genetic structure is assessed using the distribution of alleles (alternative forms of genes) and variance in the allele frequencies within and between populations. Studies of genetic structure reveal breaks in genetic diversity typical of noninterbreeding populations and therefore evolutionarily dissimilar units. Populations that are geographically proximate and that genetically interact through gene flow will be more similar than populations that are geographically isolated or that have barriers to gene flow. Combined with understanding of gene flow patterns, distinction among populations is normally helped by a wide knowledge of the biology of the fishes and the ecology of the system.

Also important in marking and monitoring populations of wild fisheries is the ability to identify unique polymorphisms within populations and among the multitude of species that may be found in any particular system, features that are typical of most inland fisheries in Africa. Population-specific polymorphisms act as natural tags and as indicators of changes in the genetic structure of the population. Unique polymorphisms tend to be rare and are easily lost by processes such as genetic drift, especially after reduction in population size or population subdivision or both (Fuerst and Maruyma 1986). The disappearance of rare forms within a population is normally an indicator of natural selection against such forms or of the evolutionary demise of the population as a whole. In most cases though, unique or rare polymorphisms may not be easily discernible and may be lost without the knowledge of the managers. Fortunately, molecular techniques have been developed that can reliably identify such unique polymorphisms (Avise 1994). This ability to genetically differentiate strains and to assess unique polymorphisms is an important development for fisheries management because it ensures meaningful use of the limited funds and human resources allotted to monitoring genetic biodiversity.

How Do Genetic Diversity Issues Affect the Ecological Functioning and Evolution of the Inland Fisheries?

To understand the role of genetic variability in the functioning of African inland fisheries, one must understand the forces that shaped the evolution of these systems before the human alterations. Glacial and interglacial periods associated with arid and wet periods, respectively, characterized African climate since the Pleistocene (see Livingstone, chapter 1). This cycle resulted in cycles of major spread and retreat of aquatic habitats that greatly restructured fish fauna populations in the associated waters (Leveque 1997; Kaufman, chapter 12). Major lakes, such as those in Central Africa, receded, while backflow of rivers after earth movements created lakes in eastern Africa. Such events created habitats and allowed species that were originally riverine to evolve into lacustrine species, forming new species as the subdivided populations filled the new open niches. Those that could not survive in the changed conditions went extinct. Africa's volatile climate played a significant role in restructuring populations of cichlid species and drove cycles of radiation and extinctions in the African Great Lakes (Kaufman et al. 1997; chapter 12).

Before the twentieth century, the evolution of Africa's inland fisheries was influenced by climatic changes and earth or tectonic movements. In the twentieth century, changes were mostly human induced (Fryer 1972, Kaufman 1992, Carvalho and Hauser 1995). During the twentieth century, most of the fisheries turned from artisan to commercial; water bodies and waterways were drastically altered for development; and natural water bodies were planted with nonindigenous species to augment the wild fisheries or to create a favored sports fishery (see Welcomme, chapter 8). The changes of the twentieth century, in some cases, such as the case of Lake Victoria, were more dramatic and resulted in unprecedented losses of species and marginalization of the originally dominant species (Barel et al. 1985, Trewavas et al. 1985). As the environmental change accelerates even further into the twenty-first century, human-induced factors will conspire to reduce genetic variation and overall biodiversity. Although consideration of the list of factors affecting fish populations suggests that managers should first focus directly on inbreeding and population size, it makes more sense to first consider how human pressures and management decisions lead to loss of genetic diversity through population subdivision and reduction in size.

Among the elements that reduce genetic diversity through population subdivision and reduction in size are the following. (1) Inbreeding and random genetic drift are results of restricted distribution and small population size. (2) Introduction of alien species leads to direct competition or predation and indirect effects caused by alterations in the environment. (3) Biological and physical factors can hinder genetic exchange between populations of species, potentially leading to the subdivision of large continuous populations into small disjunct units. (4) Introgressive hybridization of species is likely to lead to genetic swamping of the marginalized species or to evolutionarily disruptive interactions between species, or to both. (5) Augmentation of one or a few species to the detriment of the rest of the species will result in monotypic fisheries.

Such factors indirectly result in changes in the genetic composition of populations by subdividing originally wide populations into disjunct smaller units, which lead to increased inbreeding and genetic drift (Frankel and Soule 1981). Inbreeding results directly in loss of genetic diversity through homogenization by the breeding of closely related individuals. With inbreeding, there is the danger of exposing deleterious recessive alleles and losing vital rare alleles, both of which may result in species fitness decline. The chances of inbreeding increase with the reduction in population size. Similarly, genetic drift leads to loss of genetic diversity by chance alone, and as in the case of inbreeding, the smaller the size of the population the more pronounced the impact. Human influences that alter watercourses and habitats partition natural populations into smaller, disjunct subpopulations. Genetic drift and inbreeding in the resultant small disjunct or isolated units can ultimately lead to total loss of the affected species (Fuerst and Maruyama 1986, Hartl and Clark 1989).

In the Lake Victoria region, excessive fishing pressure and the introduction of closely related tilapiine species have resulted in ecological and genetic marginalization and ecological displacement of the native tilapiine species of lakes Victoria and Kyoga (Mwanja 2000). The original two most commercial fish species of the two lakes have been relegated to isolated populations that are genetically less diverse than the introduced nonindigenous congeners (Mwanja 1996). Similarly, *Garra johnstonii*, which was once a common feature in the Victoria Nile rapids and added to the beauty of Owen and Budhagali Falls with their famous leaps

(Greenwood 1966), has not been seen since the completion of the Owen Falls hydropower dam. Whether the disappearance of *G. johnstonii* is due to simple loss of habitat or to a combination of ecological and genetic effects is unknown. However, subdivision of a single continuous population into several smaller units leads inevitably to increased inbreeding and genetic drift that may ultimately result in extinction of such subpopulations.

Because a continuous large population is likely to contain similar genetic forms throughout its range, subdivision will most likely lead to a loss of low-frequency variants from all locations and will lead to localized differentiation of the subpopulations. This is what happened to *Labeo victorianus* in lakes Kyoga and Victoria. Until the 1960s, *L. victorianus* was the main commercial riverine fishery in the Lake Victoria region. The species is currently extant only as disjunct, locally differentiated, smaller populations and has a greatly diminished commercial value (Mwanja 2000).

The removal of geographical barriers between aquatic systems that were naturally unconnected allows accelerated gene flow among independent populations. Such gene flow results in a disruption of evolutionarily and geographically coadapted and locally adapted gene pools (Futuyma 1986). Coadaptation is viewed as individuals of a population that have evolved an internally well-balanced gene pool with respect to reproductive fitness. Opening up such populations to hybridization by conspecifics disrupts the genetic balance and results in lower fitness due to genetic aberrations (Dobzhansky and Pavlovsky 1953). Local adaptation results from populations evolving, over a long time, a gene pool that best suits the habitat conditions (Dobzhansky 1955).

On the other hand, erecting barriers in the way of natural flow of water typically has the effect of blocking gene flow between populations and subdividing originally continuous populations into independent population units. This process has the genetic effect of taking away the source for new variation that naturally would take place through exchange of alleles between adjacent populations. The quest for economic development and the pressures of an ever-increasing human population in Africa have made inland water systems very susceptible to disruption and abuse by human activities that affect natural evolutionary processes. There is urgent need to incorporate into any developmental design those factors that promote and allow for the natural process of evolution of the fisheries to ensure continued survival of these resources. For example, even if dams were to be erected or watercourses changed, channels to allow natural flow and movement of fishes could permit continued connection between the subdivided populations.

Use of alien species to boost fisheries production or to modify local fisheries into sport fisheries has also transformed fisheries in Africa (Carvalho and Hauser 1995; Kaufman, chapter 12). In addition to ecological displacement through competition, aggression, and predation, exotic forms can directly affect the genetic diversity of native forms through hybridization. When the exotic forms are closely related to and hybridize with the native species, the resultant genetic interaction may lead to introgression that may "swamp out" one of the species involved (Soltz and Naiman 1978, Allendorf and Leary 1986). Introgressive hybridization occurs when hybrids of two distinct taxa (species) are reproductively viable with each other or with either or both of the parental species. The species that is more ecologically labile (an attribute normally used in choosing the species for introduction) swamps out the marginalized species through hybridization and repeated back-crossing. Such hybridization also leads to breakdown of coadapted gene pools of native species, often resulting in reduced fitness through a process technically referred to as outbreeding depression (Allendorf and Leary 1986). The effects of introductions are not immediate, and the establishment of the alien species, in most cases, takes place long after the act of introduction and the collapse of the already marginalized native species (Leveque 1997).

Mechanisms that would naturally guard against genetic interaction between closely related species tend to break down with increased disturbance of the environment (see Seehausen et al., chapter 13). Disturbed environments tend to have a high incidence of hybrids and normally form hybrid zones in the systems (Anderson 1949, Hubbs 1955, Rieseberg 1991, Mwanja 2000); increasingly, most inland waters of Africa have become unnaturally altered and therefore disturbed (Shumway 1999).

Of course, resources will be needed to address genetic biodiversity issues. Unfortunately, as in crop and animal husbandry, only a handful of commercially important species receive most of the available resources and only a minor portion is put to protection of the species considered to be of no economic importance. The disparity in resources makes the management of the wild species even tougher. Yet, by definition, traditional agriculture strain-improvement practices result in the loss of genetic diversity of the species involved and in increased monoculture. Similarly, efforts to boost fisheries have concentrated on a few dominant and versatile species, leading to the monotypic dominance of ecosystems by the few highyielding species or strains to the detriment of the majority of the species. In lakes Victoria and Kyoga, the once-multispecies fisheries were transformed into a Nile tilapia and a Nile perch fishery in less than 20 years. The effect on the genetic diversity of the original commercial fish species is exemplified by the two native tilapiines, which now form highly genetically subdivided units with reduced within-population genetic variation (Mwanja 1996, 2000).

The ecological landscape all over Africa has greatly changed, and many aquatic systems are under enormous human pressure (Shumway 1999). In addition to concern about excessive resource exploitation, there is a growing concern about the environment- and human-induced changes in the quality of the inland waters. Together with high fishing pressure, these changes in water quality have resulted in detrimental changes to the inland fishery, both in catch composition and in catch per unit effort. Competing demands on fresh waters and wetlands, such as agriculture's need for water, have only worsened the situation (see Day, chapter 3). An increasing number of fish species, both commercially important and commercially unimportant, are listed as endangered or threatened (IUCN 1990). Worse still is the possibility that an equivalent or far greater number of fish species in Africa have lately become extinct.

Unfortunately, many of the changes in African aquatic habitats and their associated fisheries took place before systematic studies could lead to an understanding of the affected systems. Certainly, there are many great works by early scientists, but more work will be needed before it will be possible to adequately conserve and develop the aquatic biodiversity in Africa's inland waters. Much more change may be happening in these systems than is suspected. One of the challenges in the development of African science in the twenty-first century will be to gain more insight into genetic diversity issues as indicators of the impact of human actions and natural occurrences on the functioning of the inland fisheries.

Most managers of Africa's inland fisheries unfortunately lack knowledge of issues pertaining to genetic diversity. Most managers are focused on fish production and on the ecological functioning of the fisheries, not on genetic issues. Although there is hardly any information on the genetics of wild populations, it is generally assumed that levels of genetic variation were at least at current levels, and possibly higher in many species. For example, the best estimates of protein polymorphism suggest that the fishes of Lake Victoria are slightly less variable than the average freshwater fish species (Sage et al. 1984). Studies using nucleic acid markers provide data baselines with which to compare future studies and follow changes with the evolution of the fisheries. Such information is very important because the most likely scenario involves loss of genetic variation for many species.

Management Options

A *natural evolutionary process* implies the ability of species and communities to adjust naturally to the rigors of the environment without human interference; it allows populations the "evolutionary flexibility" (genetic variation) to adapt to changing conditions. A natural evolutionary process is considered more effective than any attempt to assess and manage all the extant genetic diversity of a species. A number of management options to preserve the evolutionary process of the most vulnerable species are available, but these options require commitment from the managers and fishermen for such measures to succeed. One option is to reduce fishing pressure on marginalized species. This option would be in direct conflict with the survival and economic goals of fishing communities and has always failed. Another option includes use of selective cropping gears that would target only the dominant species. Yet another option is the traditional approach of "keeping clear of the breeding grounds," or instituting closed seasons during the peak of breeding activity for key species. This requires identifying the breeding grounds, and, given the variation among species characteristic of African and other tropical waters, breeding grounds may be too extensive to close off.

An option considered very enforceable is to prohibit fishing on some water bodies, especially on the minor lakes that contain remnant populations of species at risk and on streams used by a main fish species in a system for breeding. Normally, the minor lakes are not that economically productive, and their small size allows for effective monitoring. Creating such preserves would offer a natural refuge for species facing overexploitation by humans.

Creation of connections between water systems isolated by human activities, equivalent to corridors between habitat patches for game animals, is another management option. This option would ensure continued genetic exchange and interaction between originally uniform, but currently subdivided, units. The other option would be selective augmentation of the restricted native forms through hatchery cultures and aquaculture. This option may be the only means available to maintain several endangered species still extant in the wild. Selective augmentation has the effect of boosting the population of the restricted species and, if genetically monitored, increasing the genetic diversity of the endangered species. Restoration uses captive brood stocks of marginalized populations and those extinct from the wild. Restoration is difficult but, if well planned and executed, has the effect of revitalizing the ecology and adding to the species diversity. Efforts to do exactly this have been suggested for haplochromine fishes from the Lake Victoria region (Kaufman and Ochumba 1993, Mwanja 1996).

Repair of disrupted aquatic ecosystems in the Lake Victoria region and Africa's inland fisheries in general will require information about genetic diversity. Most African conservation efforts have focused on rescuing species near extinction. A better approach would involve routine monitoring of changes in population structure, emphasizing habitat heterogeneity and integrity of populations based on genetic analysis. Of course, such a route would be costly and in direct conflict with economic efforts of struggling nations. This strategy is better because evolution occurs not at the species, but at the population, level. Thus, any efforts to stem the loss of inheritable variation among individuals of species can work only with extensive knowledge of populations within a species. Genetic diversity is a quality of populations and is the raw material for the evolution of species. Genetic diversity offers a species the evolutionary flexibility to adapt to the changing environment. The loss of genetic diversity has been a challenge to past efforts and will continue to be the main challenge, especially where resources to take on such a challenge are limited.

The large number of species in African fisheries makes consideration of the conservation of their genetic diversity an enormous challenge; it is nearly impossible when the decision is to conserve the status quo of the extant genetic diversity. Thus, efforts should be directed toward preserving natural evolutionary processes, especially of key ecological species. Preserving the evolutionary process rather than the status quo is not an easy task. Among the major challenges to this approach are obtaining knowledge about the ecological and biological working of the aquatic ecosystems needed to preserve the natural evolution of African fisheries. Yet, several aquatic systems are becoming increasingly disrupted and appear to be heading toward genetic or biotic collapse.

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