Genetic impacts of some fish species introductions in African freshwaters

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Introduction

Africa is a continent that has suffered relatively few fish species' introductions (WELCOMME, 1988). However, certain cases are famous such as the Nile perch *Lates niloticus* introduced to Lake Victoria in the 1950's. The consecutive disappearance of several hundred native haplochromine species brought to light the problems that species introductions may cause. The elimination of native species is with no doubt, the most spectacular and the most important long-term impact. It is also an impact that is sometimes difficult to evaluate separately from other manmade effects such as the environmental modifications brought about by man. Although there is a large body of literature on the introduction of exotic species, there is much less works which evaluate the genetic consequences of these introductions.

Genetic impacts can be defined not only as changes to the gene pool of native species but also as changes suffered by the introduced species themselves. We can consider that there are two types of genetic effects. On one hand, the alterations to the gene pool of a species can be direct by hybridization between a native species and an introduced species, or by crossing between a native population and an introduced population of the same species, or even between two introduced species or populations. On the other hand, the genetic effects can also be indirect; in this case, they result from a serious decrease in the effective size of the population (native or not) which is to say, a decrease in the number of individuals participating in the establishment of the next generation. Such decreases, if they are important enough can cause an increase in genetic drift and in the consanguinity of the population. This loss of variability naturally threatens the adaptive value of these populations. The works of FERGUSSON and DRAHUSHCHAK (1990) showed that in rainbow trout, *Oncorhynchus mykiss*, those individuals which were the most heterozygous had a resistance to disease greater than that of less heterozygous individuals.

Another indirect genetic effect more difficult to show is the displacement of the selective forces acting upon the population. We can assume that this modification of the selective forces leads to a modification of the gene pool of the population.

Hybridizations

As soon as the reproductive isolation of two species or populations is maintained by only geographic or ecological barriers, any of man's actions which may affect these barriers will have hybridizations and or introgressions as a consequence.

These hybridizations can have an effect on the adaptive value of the individuals produced. If in certain cases we can expect an increase in this adaptive value, heterosis or hybrid vigor, in most cases there are genetic incompatibilities between the two parental species and a decrease in the adaptive value of hybrid individuals results.

In the case of hybrid vigor, if in the first generation (F1) each individual have a complete copy of the parental genome, the following generations, because of recombinations during meiosis will have different combinations of the parental genomes which will

have as a consequence a decrease in the adaptive value below that of both parents almost every time.
In certain cases, hybridizations can give rise to new populations with different potentials. ARTHINGTON (1991) and MATHER and ARTHINGTON (1991), showed that the tilapia population from North East Australia results from a hybridization between several species including *O. mossambicus*, *O. hornorum* and *O. niloticus*. These same authors showed that the hybridization between two strains of carp *Cyprinus carpio* also in Australia gave birth to a new strain that spread very quickly and has posed some ecological problems.

Generally speaking however, hybridization like introgression often results into a decrease in the fecundity of the hybrids. This decreased fecundity can go as far as total sterility in the first generation's hybrids.

Bottlenecks

Bottlenecks are serious decreases in the effective size of a population, acting both on the number of alleles (loss of rare alleles) and on the allelic frequencies (heterozygosity). However, the heterozygosity rates are less affected in the beginning and much more sensitive in the growth phase of the population. NEI *et al.* (1975) showed that the more slowly the population grew after the introduction, the better chance it had for an important loss in heterozygosity.

The time necessary, in generations, for one allele to be lost and the other to remain (with two alleles at the same locus), is of course a function of the respective frequencies of each allele but also of the effective size of the populations.

The loss in heterozygosity over time expressed in generations is a function of the effective size. It appears that for an effective size of 500, the loss is low after 500 generations. On the contrary, with an effective size of 10, heterozygosity drops very rapidly.

Lastly, the number of alleles which will be transmitted to the following generation is a function of their respective frequencies and the effective size of the populations. For a locus with 4 equally frequent alleles (25%), an effective size less than 10 conserves the four alleles. On the contrary, when we have one very frequent allele and the other three are rare, more than 100 individuals are required to have a high chance of preserving the four alleles.

African examples

If we consider all of the cases of introductions or transfers of species in Africa, there are unfortunately very few studies undertaken from the angle of their genetic impacts.

For example, *O. niloticus* and *O. mossambicus* have been hybridized in Lake Itasy in Madagascar, and in Lake Ihema in Rwanda.

In Lake Itasy, in Madagascar, *O. macrochir* was introduced in 1958 and *O. niloticus* in 1961. In 1965 and 1966 intermediate specimens of these two species were harvested and called tilapia 3/4 (DAGET and MOREAU, 1981). These hybrid individuals possessed notably a pharyngial bone resembling that of *O. niloticus* but having a morphology closer to that of *O. macrochir*. Between 1963 and 1969, the hybrid population in the captures went from 5% to 74%. *O. macrochir* was considered a vanished species in 1971. Finally the *O. niloticus* population became predominant.

Inversely, in Lake Ihema in Rwanda, *O. macrochir* was introduced around the end of the 1960's, after the introduction of *O. niloticus* around the end of the 1940's. Hybrids were observed around the end of the 1970's. From 1983 to 1987, the proportion of *O. niloticus* decreased from 30 to 20%, that of hybrids increased from 10 to 20%, while the population of *O. macrochir* has remained stable at 60% (MICHA *et al.*, 1996).

In both these cases, no genetic studies could be done. Of course it's too late to follow the progression of these hybridizations but it would still be interesting to study the tilapias which form the actual populations of these lakes in order to determine if introgressions have occurred.

The situation is somewhat similar in Lake Victoria, where *O. niloticus* was introduced forty years ago in 1967, WELCOMME notes the existence of hybrids between *O. niloticus* and *O. variabilis*. These hybrids could all be males. Hybridizations with *O. esculentus* were also suspected by other authors. These two native species *O. variabilis* and *O. esculentus* have since disappeared from Lake Victoria and *O. niloticus* is suspected of being at the origin of these disappearances (WELCOMME, 1967; OGUTU-OHWAYO, 1990). Here also, hybridizations between *O. niloticus* and *O. variabilis* or *O. esculentus* were not studied genetically. Today, we are beginning to have a few data on the genetics of these populations. The works of AGNESE and collaborators recently targeted the *O. niloticus* population of Lake Victoria and *O. esculentus* from one of the satellite lakes, Lake Kanyaboli.

Two investigations dealt with the *O. niloticus* population of Lake Victoria: One on its origin and the other on its purity in regard to phenomes passed by hybridization with native tilapias. The genetic analyses showed that this introduced population no doubt had multiple origins, composed in part of individuals from the Nile basin (probably Lake Edward) and in part of individuals from Kenya (probably Lake Turkana). These works also showed that the *O. niloticus* population of the lake, considering its multiple origins, had lost a great deal of its genetic variability. We can assume that the effective sizes of the introduced populations, that is, the number of individuals which effectively contributed to the next generation, was low. WAPLES (1991) showed that the mortality following the release of cultured individuals can be very high. In this case, *O. niloticus* was very likely introduced from cultured stocks. We also have no idea of the speed of expansion of the introduced population which may have been low from the beginning. This speed as shown by NEI *et al.* (1975) can also have played a role in the observed loss of variability.

We also have observations on the genetic variability of the *O. esculentus* population of Lake Kanyaboli. It seems almost certain that this population suffered no introgression of genes from *O. niloticus*. However, its low genetic variability may have been caused by a bottleneck during the colonization of the lake.

These early data lead to the assumption that *O. niloticus* must have taken the place of the two native species by competition rather than by hybridization. This hypothesis is yet to be confirmed.

The last two examples do not concern hybridization but are studies of the introduced populations themselves.

The Bouaké strain of *Oreochromis niloticus* was released in a great many countries, but first and foremost in all the waterways of Côte d'Ivoire. ROGNON (1993) studied the genetic variability of this strain at its site of origin, the Idessa aquacultural station in Bouaké (Côte d'Ivoire) and certain feral populations from two large rivers in Côte d'Ivoire: that from Lake Buyo on the Sassandra River and that from Lake Kossou on the Bandama River. In both cases, voluntary seeding with large numbers of fingerlings (to increase fishing activities) was carried out (the exact numbers are not known). ROGNON's study (1993) was based on the observation of thirty enzymatic loci. The Bouaké strain is characterized by a heterozygosity rate of 7.1% and a polymorphism P99% rate of 26.7% (P95%=23.3). The Buyo and Kossou populations possess comparable values to those of the strain they are issued from 8.7 and 5.8% respectively for the H values, 23.3 and 26.7 respectively for the P99% values (23.3 and 16.7 for P95%).

We can therefore state that, concerning the allozymes, there was no notable loss of genetic variability during the transfer and adaptation phases of this strain to the natural environment.

Another fairly well documented case concerns *Limnothrissa miodon*. This Clupeidae originates in Lake Tanganyika. In the hope of increasing fish culture production in Lake Kivu, 57,400 clupeidae (in part *Limnothrissa miodon* but also some *Stolothrissa tanganicae*) were introduced from Lake Tanganyika in 1959. Only *Limnothrissa miodon* succeeded in establishing itself in Lake Kivu. HAUSER *et al.* (1995) recently published a study in which they compare the transplanted population to the original population.

They performed a morphologic study, but also genetics with allozymes and DNAmt. They saw no statistically significant changes in the allozymic diversity: no differences between samples from Lake Tanganyika and those from Lake Kivu for heterozygosity levels, for the number of mean alleles, or for the percentage of polymorphous loci. Ninety-eight percent of the genetic variation can be attributed to sample variation and 0.26% to the differentiation between lakes. For the mtDNA analysis, they amplified a fragment of 2.5 Kb from the ND 5/6 region. They found 85 different haplotypes in 363 analyzed fish. The nucleotidic diversity like the number of haplotypes were significantly lower in samples from Lake Kivu which indicates a decrease in the genetic diversity of the mtDNA in the population of introduced fish.

This decrease in mtDNA variability following the phenomenon of introduction may, as we have already seen, come from a low effective size of the founding population and from the time required by this population to achieve a sufficient effective size (NEI *et al.*, 1975). In this case, it is highly likely that *Limnothrissa miodon* because of its very high fecundity, took very little time to recover its important effective size. It follows that the loss of mitochondrial variability observed in Lake Kivu is probably due entirely to a low effective size in the founding population. We might be surprised if we considered the large number of fish introduced (57,400). However, these fish represented two different species (*Limnothrissa miodon* and *Stolothrissa tanganicae*) and we do not know the proportion of *Limnothrissa miodon* in this first population. A calculation suggests that of the 57,400 fish introduced, only a maximum of 150 could be at the origin of the current population. Considering that 24 different haplotypes were observed in Lake Kivu, we can assume that at least 24 females were in this founding population (if we exclude the apparition of new haplotypes by mutation).

Of course it is difficult to cite an exact number when speaking of the effective size of this founding population, but it is almost certain that this number can be counted by tens, not hundreds.

Conclusion

It is probably too early, considering the small number of studies performed, to draw general conclusions about the genetic impact of fish introductions in Africa. A large number of populations remains to be analyzed. These studies are often difficult to carry out because the founding populations are from far-away countries, because data on introductions are not always available, because several genetic techniques must be used simultaneously to correctly estimate a situation. Certain phenomena like hybridizations are transitory and it is not always possible to be there when you should be. It is probable that concerning this subject, the use of museum collections can sometimes aid in going backwards in time.

Two of the first results presented (*O. niloticus* from Lake Victoria and *L. miodon* from Lake Kivu) show losses in genetic variability in introduced populations. Evidently, even when introducing several thousand individuals, the founding population may be made up of only tens of individuals.

It is obvious that if it is easy enough to theoretically predict the possible repercussions of introductions and transfers of species, it is much more difficult to predict the evolution of any particular case. The different behaviors of two confrontations between *O. niloticus* and *O. mossambicus* in Lakes Itasy and Ihema is an example.

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