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Use and exchange of genetic resources of Nile tilapia (*Oreochromis niloticus*)

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Abstract

The worldwide use of Nile tilapia (*Oreochromis niloticus* Linnaeus, 1758) in aquaculture represents a somewhat unique scenario. The natural distributions and global genetic resources of tilapias are in Africa, yet the main centers of utilization for aquaculture are primarily in Asia. Within a few decades, Nile tilapia graduated from being an 'orphan commodity' (i.e. of interest to only resource-poor fish farmers) to a globally traded commodity. Most aquaculture production of Nile tilapia in Asia and elsewhere has relied on a narrow genetic base. The natural genetic resources have not yet been fully documented and tapped for use in aquaculture, and many natural populations are under severe threat of irreversible change or loss. Although genetic improvement is now well underway, an important question is how the wealth of Nile tilapia wild genetic resources shall be used for the benefit of a wide range of users, at present outside Africa. This review focuses on documenting the status of Nile tilapia genetic resources (including the potential threats), providing a case for their conservation and for the judicious utilization of genetic diversity for the benefit of all stakeholders; and on analysis of the lessons learnt from a major Nile tilapia genetic improvement initiative, the genetic improvement of farmed tilapia (GIFT) project. Information about other genetic improvement efforts by means of hybridization, sex reversal and YY male technology is also presented.

Key words: genetic improvement of farmed tilapia project, genetic resources, Nile tilapia, *Oreochromis niloticus*.

Introduction

Management of aquatic genetic resources should ideally involve a continuum of activities: documentation of genetic resources and the variety of ecosystems in which they are functional components, including the status of potential threats to these resources; characterization to determine the genetic structure or distinctness and conservation value of the resource; evaluation to estimate either direct or indirect economic potential; and utilization in sustainable genetic improvement schemes, with due regard to the emerging codes of practices of access to and benefit sharing of the genetic resources. The underlying theme of these activities is conservation and judicious utilization of genetic diversity for the benefit of all stakeholders.

Unlike the other aquatic genetic resources for discussion in this series, tilapias represent a somewhat special scenario.

- Natural distributions of tilapia genetic resources are restricted to Africa and the Levant, whereas the main areas of utilization, primarily for aquaculture, are outside Africa. Many natural populations of tilapia in Africa are under severe threat of irreversible change or loss as a result of factors such as habitat disturbance, overfishing, continued neglect and irresponsible fish transfers.
- Tilapia farming worldwide is in a dynamic state of expansion to satisfy both domestic and international markets. After carps, tilapias are now the world's second most popular group of farmed fish. Global production of farmed tilapia, cultured in at least 85 countries, exceeded 2.5 million t in 2007 (FAO 2009).

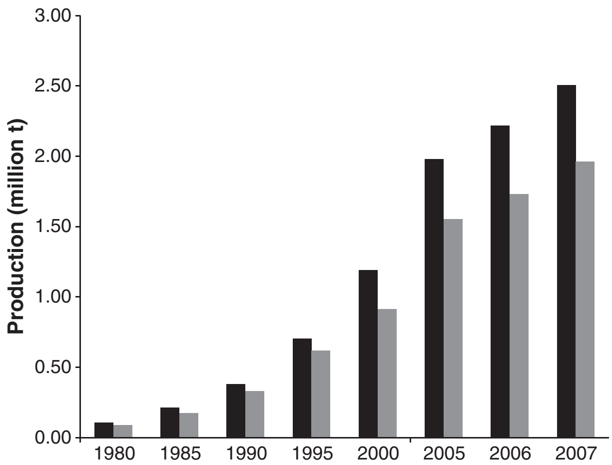

Figure 1 Total contribution of Asia towards global tilapia production from 1980 to 2007. Source: FAO (2009). ■, Global; ■, Asia.

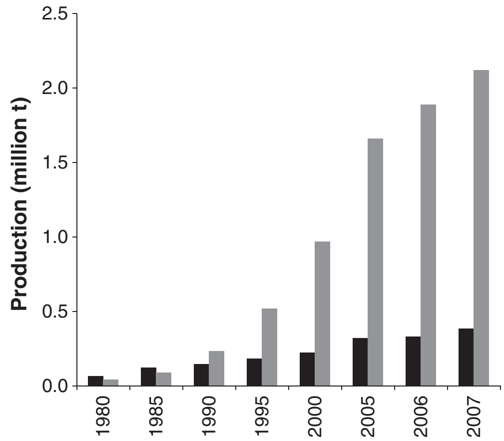

Figure 2 Total contribution of Nile tilapia (*Oreochromis niloticus*) to total global tilapia production from 1980 to 2007. Source: FAO (2009). ■, Other tilapia species; ■, Nile tilapia.

Most of the production comes from Asia, accounting for up to 80% of the global production (Fig. 1). The dramatic annual increase in tilapia production from the top countries can be seen in Table 1. For example, tilapia production in China (including Taiwan) has increased from 44 832 t in 1980 to over 1.2 million t in 2007. The Philippines, which hitherto was one of the largest producers of tilapia, has registered a steady increase in production to approximately 240 000 t in 2007. There have been some major changes in food habits with the introduction of tilapia in some countries. In the Philippines, for example, there appears to be a major shift in preferred consumption of tilapias over the traditional milkfish.

- Although several tilapia species are cultured, the most widely preferred (in over 50 countries) is the Nile tilapia, *Oreochromis niloticus* Linnaeus, 1758, which has accounted for more than 80% of global production in recent years (Fig. 2). The actual percentage of global Nile tilapia production is estimated to be approximately 50–60% because from China, the largest tilapia producer, all production is reported to be Nile tilapia, whereas in reality an important strain used in culture is the hybrid between Nile tilapia and blue tilapia (FAO 2009).
- Within a few decades, tilapias have graduated from an 'orphan commodity' (i.e. of interest to only small-scale, resource-poor fish farmers in developing countries with no substantial commercial investments) up until the early 1970s to a globally traded prime white fish commodity by the late 1990s. As in the case of the poultry industry, the relatively simple 'backyard'-type tilapia farming coexists with relatively sophisticated medium and large-scale corporate farms. An extensive profile of the tilapia industry covering the dynamics of diverse tilapia farming practices in Asia, trends in production, prices and international trade has been presented by Dey and Eknath (1997).

Table 1 Tilapia production (t) in the top countries from 1980 to 2007

Country	1980	1985	1990	1995	2000	2005	2007
China (including Taiwan)	44 832	76 542	159 313	361 346	598 109	928 163	1 210 167
Egypt	9000	22 346	24 916	21 969	157 425	217 019	265 862
Philippines	13 214	42 640	76 142	81 954	92 575	163 004	241 183
Indonesia	14 901	29 302	53 768	74 125	85 179	189 570	248 305
Thailand	8419	16 542	22 895	76 383	82 581	203 911	190 258
Brazil	nr	nr	nr	12 014	32 459	67 851	95 091
Honduras	6	35	120	172	927	28 376	28 356
Colombia	93	300	2040	16 057	22 870	27 953	27 960
Malaysia	366	314	1145	8866	18 471	28 635	32 258
Global	107 459	211 594	379 184	703 712	1 190 016	1 980 450	2 505 465

Source: FAO–Fisheries and Aquaculture Information and Statistics Service (2009).
nr, not recorded.

- The major sources of references and bibliographies have been discussed in Eknath (1995). In addition, International Symposia on Tilapias in Aquaculture (ISTA) are held regularly to provide a forum for the exchange of information and documentation on experiences in almost all disciplines from biology to socioeconomy to policy research and analysis. Although the amount of published information on tilapia is vast, it appears that there is a general lack of interdisciplinary approaches to match development efforts and the needs and circumstances of producers and consumers (Pullin & MacLean 1992). Pullin (1996) has described in detail the perceived constraints to future expansion of tilapia aquaculture.

Most quantitative genetics research into tilapias has, until the mid 1980s, focused on interspecific hybridization and monosex male fry production. Only a few studies have focused on the effects of inbreeding, on evaluation of stocks or strains, and on crossbreeding within a species. Tilapia species differ markedly from one another in many traits of evolutionary importance, which also reflect on their suitability for aquaculture. Intraspecific variation among stocks/strains has been seriously evaluated only in *O. niloticus*. The differences found suggest that choosing an appropriate strain for a given set of conditions can improve performance. No advantage of intraspecific crossbreds between stocks of the same species was observed, but producing them may be a method for preventing inbreeding depression in the future.

The occurrence of interspecific or intergeneric hybrids involves the disruption of mating barriers that keep species and genera in reproductive isolation. Geographical, ecological and behavioural isolation mechanisms, mainly within the genus *Oreochromis*, have been observed in several African lakes. Disrupting these isolation mechanisms appears to be relatively easy in tilapias, and this may explain the frequent occurrence of tilapia hybrids.

The objective of this paper is to review the published information available on Nile tilapia genetic resources along the lines of documentation, characterization, evaluation, utilization and conservation.

The genetic improvement of farmed tilapia (GIFT) project implemented by the International Center for Living Aquatic Resources Management (ICLARM) (now the WorldFish Center) from 1988 to 1997 is presented here as a case study to demonstrate how stepwise progression from documentation of genetic resources through their evaluation to utilization in breeding programmes can generate rapid benefits to both farmers and consumers. The focus is on the experiences gained and the lessons learned from this multicountry, multisite and multidisciplinary project. The GIFT project highlights several core issues in deriving policies for the management and sharing of aquatic genetic resources. Discussion of the GIFT Project is based on the first author's association with the GIFT Project throughout the tenure of the project. The information presented in this regard is largely based on the following key documents: Asian Development Bank (ADB) (2005); Dey and Eknath (1997); Eknath (1992, 1995); Eknath and Acosta (1998); Eknath *et al.* (1998); Pullin (1988); Greer and Harvey (2004); and many important references therein.

Documentation of Nile tilapia genetic resources

Natural distribution and transfers in Africa

An authoritative account on the ecological diversity of Nile tilapia is provided by Trewavas (1983), and this is also the fundamental source of information on the mechanisms of evolution and for understanding the biodiversity of tilapiine fishes of the genera *Sarotherodon*, *Oreochromis* and *Danakilia*. The original natural distribution of the genetic resources of Nile tilapia extended from 8°N to 32°N, covering the River Nile and its tributaries and lake systems in the north, the watersheds of the lakes of Tanganyika in the south (Trewavas (1983, p. 140)), and the sub-Sahelian watersheds of West Africa, including the basins of rivers Niger, Volta, Gambia and Senegal. Its existence in the Yarkon River (Israel) mentioned by Trewavas (1983), however, is thought to be dubious (Hulata 1988). Introductions of tilapia species outside their known original natural distributions for varying purposes and reasons were reviewed by Philippart and Ruwet (1982). The records of and reasons for introductions/transfers include stocking of natural lakes in which the species concerned did not occur (e.g. Nile tilapia into many lakes in Uganda and Rwanda), to fill an ecological niche (e.g. Lake Victoria and Lake Kyoga), to develop new fisheries (e.g. reservoirs of southern Tunisian Oasis), and for the development of aquaculture. A number of inadvertent transfers have also occurred, mostly owing to confusion between sympatric species.

The impacts of such deliberate introductions (within and outside Africa) indicate the following two general trends: (i) introductions into water bodies offering a vacant ecological niche or those not containing any tilapias have been successful (examples in this category include the introduction of Nile tilapia in Uganda (Koki Lakes) and in Madagascar and augmentation of local reservoir fisheries resources in Indonesia, Sri Lanka and Mexico); and (ii) introductions into water bodies already containing indigenous tilapias have had negative consequences on aquatic biology and on the fisheries. An important example here is the case of Lake Victoria (see Lowe-McConnell 1982). Nile tilapia stocks inadvertently introduced along with other tilapia species to boost fisheries in Lake Victoria and those that entered the lake from aquaculture trials in areas that drain into the lake have displaced almost completely or hybridized with the endemic *Oreochromis esculentus* (Graham, 1928). A similar example comes from Lake Itasy, Madagascar, where *Oreochromis macrochir* (Boulenger, 1912) (introduced in 1958) prospered for several years before disappearing and being replaced by Nile tilapia (introduced in 1961–1962). Hybridization of the two species has produced slow-growing and sometimes deformed individuals (Philippart & Ruwet 1982).

According to Trewavas (1983) *Oreochromis aureus* (Steindachner, 1864) and *O. niloticus* have a common natural distribution in 'the Nile delta, the coastal rivers of Israel, the Chad basin, the middle Niger and the Sénégal River' [according to Goren (1974) the natural distribution of *O. aureus* included the Jordan river system and several coastal rivers, whereas *O. niloticus* was found in only one coastal river (Yarkon) completely separated from the Jordan system (see also Pullin 1988). The chances of natural interbreeding of these two species in Israel have been very low]. Despite this common natural distribution they do not interbreed in nature (e.g. Payne and Collinson 1983). Commercial and experimental interspecific hybridization is usually carried out by stocking females of one species (e.g. *O. niloticus*) together with males of another (e.g. *O. aureus*). The relative ease of obtaining interspecific hybrids with this technique suggests that the mating block in nature is probably a behavioural and not a physiological isolation mechanism. Differences between strains of *O. niloticus* in responsiveness to mating with heterospecific males, noted in hybridization experiments in tanks and ponds (Hulata *et al.* 1985), support this conclusion. Interspecific hybridization may also result from 'sneaking' males, dashing up to a spawning pair and discharging sperm between them. Hulata *et al.* (1981) reported cases where batches of eggs of *O. niloticus* were fertilized by males of both *O. niloticus* and *Oreochromis urolepis hornorum* (Trewavas, 1966) stocked together in tanks. This could have happened if one male sneaked into the territory of another male during the mating process, as described above, or if the female moved from one territory to another and had part of the eggs fertilized in one spawning nest and the others fertilized in the second spawning nest. Fessehaye *et al.* (2006) reported similar phenomenon in intraspecific mating of Nile tilapia.

The behavioural sequences in intraspecific and interspecific mating of the opposite sexes were studied in *O. niloticus* and *O. macrochir* (Falter & Dufayt 1991). These species differ both in their sexual colouration and in their behaviour during courtship, that is, their agonistic acts outside the nest. Spawning in observation tanks occurred in the two intraspecific combinations as well as between *O. macrochir* females and *O. niloticus* males. Spawning did not take place in the reciprocal interspecific combination (*O. niloticus* females $\times$ *O. macrochir* males). To investigate whether the mating barrier resulted from the colour or the behaviour of the male, *O. niloticus* females were confronted with F_1 males. These males show a sexual colouration very similar to *O. macrochir* and an aggressive behaviour similar to that of *O. niloticus*. Spawning occurred repeatedly, indicating that aggressiveness is probably a more powerful component in behavioural isolation mechanisms than sexual colouration.

Lowe-McConnell (1982) has recorded a number of instances where the same species introduced into different water bodies often respond in an unpredictable manner, depending on the prevailing environmental characteristics: fish from large lakes grow to and mature at larger sizes than those from lagoons and ponds; in larger lakes there is no significant sexual dimorphism in growth and maturation size, but in small water bodies males are larger than females; although fish from large lakes are relatively free of parasites, fish from shallow waters are often heavily parasitized and are usually dwarfed populations. Fishing pressure has also brought about significant changes in the biology of fish. For example, in Lake George, Uganda, fishing pressure reduced the size at maturation of Nile tilapia over an 11-year period (Lowe-McConnell 1982). Early in the history of the fishery, 50% of the females were mature at 27.5 cm, by 1960 this had fallen to 24.5 cm and in 1972 it was only 20 cm.

Tilapia introductions into Asia are likely to have occurred in the late 1940s, when *Oreochromis mossambicus* (Peters, 1852) was spread widely across many Asian countries for the purposes of increasing food fish supplies. Populations of this species established in many natural and quasi-natural waters rather quickly, and indeed are thought to have been responsible for the establishment of inland fisheries in countries such as Sri Lanka (Fernando & Indrasena 1969; De Silva 1985, 1988). The second phase of tilapia introductions, prompted by the relative unsuitability of certain traits of *O. mossambicus* for aquaculture, such as a tendency to stunt when grown in ponds, was that of *O. niloticus* when it was hailed as the 'aquatic chicken' and was associated with the strategy to kick start small-scale aquaculture development in Asia (Smith & Pullin 1984). Although many tilapia species have been introduced into Asia and South America over the years, *O. niloticus* remains the most dominant species in aquaculture in these regions.

The introduction of tilapias has raised many concerns over its impact on biodiversity. A recent analysis of the subject (De Silva *et al.* 2004) concluded that explicit scientific evidence is lacking to demonstrate that any of the tilapia introductions into the Asia–Pacific region have actually impacted biodiversity. These authors went on to demonstrate that tilapias tend to get established in waters that have been deteriorated as a result of anthropogenic activities and/or in modified water bodies, such as reservoirs, irrigation systems or rice paddies, where they tend to fill a vacant niche.

Taxonomy and plasticity of life-history traits

The taxonomy of tilapias, particularly at the level of assigning a given population to a new species, subspecies or strain, has been a matter of passionate debate (Pullin 1988). This situation is not surprising because water bodies become isolated and the populations therein change through natural selection, mutation and genetic drift. Indiscriminate fish transfers, interbreeding between wild and cultured fish populations and deliberate interspecific and intraspecific hybridization programmes, further complicate the taxonomy. For natural populations, the nomenclature proposed by Trewavas (1983) is widely followed. Thys van den Audenaerde (1988, p. 9) has cautioned that 'the conventional system of nomenclature is inadequate for an aquaculture situation in which interbreeding can occur'. However, so far no adequate alternative system has been proposed.

There are seven recognized subspecies of Nile tilapia (Trewavas 1983), *O. n. niloticus* (Linnaeus, 1758) inhabiting the River Nile system; *O. n. eduardianus* (Boulenger, 1912) and *O. n. cancellatus* (Nichols, 1923) (commonly found in East African lakes and Ethiopian lakes, respectively); *O. n. vulcani* (Trewavas, 1933) (common in the crater lakes of Lake Turkana); *O. n. filoa* (Trewavas, 1983) (from hot alkaline springs in the Awash system); *O. n. baringoensis* (Trewavas, 1983) (Lake Barigo, Kenya); and *O. n. sugutae* (Trewavas, 1983) (Suguta River and the surrounding areas). The number of subspecies not only suggests that Nile tilapia is an 'evolving supra-species' (Prunet & Bornancin 1989), but is also testament to its inherently high diversity, and one way that this is expressed is in its extraordinary physiological tolerances.

Extensive literature on the varied range of physical and chemical parameters preferred by Nile tilapia have been reviewed by Balarin and Hatton (1979) and Philippart and Ruwet (1982). Nile tilapia is capable of surviving in habitats where the salinity reaches as high as 30 g L^{-1} (Bitter Lakes and Lake Qarun, Egypt), the pH ranges from 8 to 11 (Sudanese ponds) and where dissolved oxygen levels are as low as 0.1 p.p.m. However, reproduction occurs only in lower salinities (Prunet & Bornancin 1989). Colonization in these varied types of water bodies have brought about, over a period of many generations, a variety of responses in terms of growth, maturation and morphological characteristics, eventually leading to subspeciation (Lowe-McConnell 1982).

The plasticity of growth and maturation of Nile tilapia, of primary interest to aquaculture, within its natural distribution has been reviewed by Lowe-McConnell (1982) and Pullin (1988). In Lake Albert, which is connected to the River Nile, *O. n. eduardianus* grows to a very large size, but populations trapped in lagoons consist of very small fish. The latter also mature at a small size and exhibit sexual dimorphism in growth and size attained. One important conclusion that can be drawn from these observations in the plasticity of life-history traits is that the natural distribution of a given population may not be a reliable guide to the environmental tolerance of that population or to its growth or maturation performance outside its natural distribution. Clearly, systematic research on the relative importance of genetics and environmental factors and their interactions is warranted.

Global transfer of Nile tilapia for aquaculture

Nearly all 'domesticated' aquaculture stocks supporting the expanding tilapia culture have been derived from very small founder populations and are probably suffering from genetic bottleneck effects and possibly also introgression of genes from other species (details in Pullin 1988; Pullin & Capili 1988; Dey & Eknath 1997). For example, early transfers into francophone Africa (principally Bouake, Côte d'Ivoire) were all derived from a small isolated population inhabiting a waterhole in Burkina Faso. From Bouake, transfers have been made to many other destinations (Pullin 1988). A shipment to Brazil in 1971 contained only 60 individuals of unknown parentage and founder population. Auburn University subsequently received a foundation population of approximately 100 fry from Brazil. Likewise, the 'Ghana strain' of Nile tilapia used in Israel was established from some 50 individuals of unknown parentage and founder population, and transfers have further been made to various destinations. A founder stock collected from the wild in Egypt in 1962 was transferred to Japan and the descendents used for transfer to Thailand in 1965, and from there to the Philippines in 1972. This 'strain' is still used by tilapia farmers in Thailand and the Philippines. After nearly 26 years (or approximately 50 generations) under 'domestication' in an aquaculture environment, the performance of the Thailand strain in the Philippines, across a wide range of environments, is inferior to, or similar to, that of new founder stock of wild fish from Egypt collected in 1988 (Eknath *et al.* 1993). Genetic deterioration of introduced stocks is widespread owing to generations of poor broodstock management resulting in inbreeding and introgression of genes from other less desirable feral tilapia species. Furthermore, a number of hybrids of different attributes have also been produced. This situation is, however, slowly changing mainly as a result of the GIFT project implemented by ICLARM.

Characterization of Nile tilapia genetic resources

Genetic variation of aquaculture stocks of Nile tilapia has been studied extensively. Intraspecific variation among cultured stocks/strains has been evaluated repeatedly in *O. niloticus*. Khater (1985), Khater and Smitherman (1988), Jayaprakas *et al.* (1988) and Tave *et al.* (1990) compared three strains of *O. niloticus* held at Auburn University, Egypt, Ghana and the Ivory Coast. They found differences among strains in growth rate, cold tolerance and isozymic variability (the Egypt strain was the best) and fecundity (the Ghana strain was the best). The differences found suggest that choosing an appropriate strain for a given set of conditions can improve performance. Hulata *et al.* (1985) found differences in hybrid fry production between females of the Ghana (better) and Ivory Coast strains of *O. niloticus*, when hybridized with either *O. aureus* or *O. urolepis hornorum* males. Hulata *et al.* (1988, 1993) evaluated *O. niloticus* × *O. aureus* hybrids, progeny of different geographical isolates, under varying management conditions. Differences in growth rate were also found between the Chitralada strain (better) and the Ghana strain of *O. niloticus* (Uraiwan & Phanitchai 1986). In the early phase of the GIFT project, Eknath *et al.* (1993) evaluated four strains of *O. niloticus* recently collected from the wild with four established Asian farmed strains of that species under 11 farm environments in the Philippines. Highly significant differences were found among the growth performances of the eight strains and among the mean performances over strains in the different environments. However, the importance of the strain × test environment (G × E) interaction over the investigated range of test environments was low. To study the magnitude of heterosis to choose between pure breeding and crossbreeding strategies for the breeding programme, a complete diallel cross among those strains was carried out and the 64 possible different pure strains and reciprocal crossbreds evaluated in eight test environments (Eknath *et al.* 1993). This preliminary report indicates that the additive, reciprocal and heterotic effects were estimated and that the overall heterosis for growth rate and survival was very low ($\sim$0.02).

Unfortunately, our knowledge about the genetic structure of natural populations within their native range is inadequate. However, studies carried out in recent years may be considered as the foundations of our current knowledge. Rognon *et al.* (1996), Agnese *et al.* (1997) and Rognon and Guyomard (1997, 2003) investigated the genetic differentiation among natural populations of Nile tilapia. Variable allozyme loci showed that these populations can be clustered into three groups: (i) West African populations; (ii) Ethiopian Rift Valley populations; and (iii) Nile drainage and Kenyan Rift Valley populations. Within the Nilo-Sudanian region, the level of variation observed in *O. niloticus* was rather low. Mitochondrial DNA (mtDNA) variation allows strict discrimination between eastern and western African populations, although Nile populations show affinities both with West African populations and with specimens from Lakes Tana and Turkana. Nyingi and Agnese (2007) found mtDNA alien haplotypes, but not nuclear genes, in *O. n. baringoensis*, suggesting introgressive hybridization with *O. leucostictus*. Hassanien and Gilbey (2005) assessed the genetic diversity of Nile tilapia from five Egyptian populations using microsatellite markers and found differences between the delta lakes, river and upstream populations. Most of the geographical variation observed in the Nile tilapia populations analysed was present in the cultured stocks. In contrast to fish-farmed stocks analysed in other countries, stocks from the Ivory Coast and Niger displayed neither evidence of loss of genetic diversity nor any trace of introgression with other cultured tilapia species, indicating that these stocks have been properly managed.

To identify the distinctness at various levels (e.g. population, subspecies, species) of both natural and aquaculture populations, a variety of techniques have been applied successfully. For a list of important studies and experiences see Eknath (1995). The emerging DNA genotyping and sequencing methods (e.g. Liu & Cordes 2004; Hallerman 2006) have the greatest potential advantage by far, including data standardization, identification of genetic lineages, estimation of inbreeding rates in aquaculture stocks, monitoring fish transfers and securing breeders' rights. Lee and Kocher (1996) identified the first set of microsatellite markers for Nile tilapia. These and more markers developed subsequently have been used to create genetic maps of Nile tilapia (Kocher *et al.* 1998; Lee *et al.* 2005). Despite some progress (e.g. Rutten *et al.* 2004; Shirak *et al.* 2009), the potential of using DNA markers for species and stock characterization, however, has yet to be realized for tilapias.

Evaluation of Nile tilapia genetic resources

Evaluation of tilapia genetic resources has been restricted to date to assessing their aquaculture potential, in particular their growth performance in a range of aquaculture environments (Wohlfarth & Hulata 1983; Pullin 1988; Eknath *et al.* 1993). Nile tilapia stocks have been screened for important traits, such as growth, tolerance to cold temperature and a range of salinities, and production of all-male hybrids. The limited number of studies conducted on estimating genetic parameters indicates considerable genetic variation within strains for important traits such as growth. Where careful experimental designs have been used, a good response to selection has been demonstrated (see the section on the GIFT project below). Systematic evaluation, definition and recording procedures for other traits of economic importance, such as maturity, resistance to disease and parasitic infestations, are becoming available (Acosta & Eknath 1998)

A major problem, however, is that most evaluation programmes have been based on stocks of unknown origin and almost invariably derived from the introduction of small numbers of fish. Such results may have limited relevance to natural tilapia genetic resources. Systematic evaluation of tilapia genetic resources from their natural distribution is lacking.

Utilization of Nile tilapia genetic resources

Nile tilapia is a prime internationally traded commodity. Its importance as a food fish is growing in a number of developing countries, even in countries that for a long period restricted tilapia introductions. The methods used in their production include capture fisheries, aquaculture and also culture-based fisheries.

The potential application of the ability to produce all-male *Oreochromis* broods by interspecific hybridization in controlling reproduction and preventing overcrowding of production ponds was realized a long time ago (Hickling 1960, 1963; Fishelson 1962, 1966). In fact, this was the aim of the first controlled production of tilapia hybrids (Hickling 1960). Hybridization of Nile tilapia has been extensively investigated (Table 2) and at least five hybrids of female Nile tilapia crossed with males of other species are known to produce all-male progeny. The status of all-male hybrid tilapias in aquaculture and the problems associated with mass production of hybrid tilapia fry were reviewed by Lovshin (1982) and Mires (1982), respectively. Lovshin (1982) stated that of the many crosses carried out, only two are being commercially used: *O. niloticus* × *O. aureus* and *O. niloticus* × *O. urolepis hornorum* (which is still cultured in north-east Brazil; Alexandre Wagner, pers. comm., 2008). Tilapia

Table 2 Hybridization of Nile tilapia

Species comments, (female × male) (females:males)‡	Observations in nature†	Deliberate crosses carried out in ponds or tanks	Sex ratio
O. niloticus × *O. aureus*		5, 8, 11, 16, 17, 20-22	Sometimes all-male
O. aureus × *O. niloticus*		8, 17, 20, 22	1:1–1:3
O. niloticus × *O. esculentus*	15		
O. niloticus × *O. leucostictus*		21	Surplus of males
O. leucostictus × *O. niloticus*		13	Surplus of males
O. niloticus × *O. macrochir*	4	1, 9, 12	Sometimes all-male
O. macrochir × *O. niloticus*		1, 9, 12	1:3
O. niloticus × *O. mossambicus*		8, 10, 16, 24	Surplus of males
O. mossambicus × *O. niloticus*		2, 8, 10, 16, 24	∼1:1
O. niloticus × *O. spilurus niger*	15	3, 13, 21	Surplus of males
O. spilurus niger × *O. niloticus*		16	∼1:1
O. niloticus × *O. urolepis hornorum*		11, 14, 20, 21, 25	Sometimes all-male
O. urolepis hornorum × *O. niloticus*		3, 21	1:3
O. niloticus × *O. variabilis*	26, 27	18, 21	All-male
O. niloticus vulcani × *O. aureus*		22	Surplus of males
O. niloticus vulcani × *O. urolepis hornorum*		21	Surplus of males
O. urolepis hornorum × *O. niloticus vulcani*		3	Surplus of males
O. mossambicus × *O. aureus*		2, 7, 8, 17, 19, 23	Sometimes Surplus of males
O. niloticus × *O. jipe*		6	All-male
O. jipe × *O. niloticus*		6	∼1:1

†In observations in nature, species of female and male parent are not known.
‡These comments (i.e. all-male, 1:3) relate to some, but not necessarily all of the results.
Data sources: 1. Bard (1960). 2. Chen (1976). 3. Crapon de Caprona and Fritsch (1984). 4. Daget and Moreau (1981). 5. Fishelson (1962). 6. Gillin (1994). 7. Guerrero and Caguan (1979). 8. Hsiao (1980). 9. Jalabert *et al.* (1971). 10. Kuo (1969). 11. Lee (1979). 12. Lessent (1968). 13. Loiselle (1971). 14. Lovshin and Da Silva (1975). 15. Lowe (1958). 16. Mair *et al.* (1991). 17. Majumdar and McAndrew (1983). 18. McAndrew (1989). 19. Pierce (1980). 20. Pinto (1982). 21. Pruginin (1967). 22. Pruginin *et al.* (1975). 23. Talbot (1982). 24. Van Schoor (1966). 25. Verdegem (1987). 26. Welcomme (1964). 27. Welcomme (1965).

hybridization has been practiced in Israel since the early 1960s owing to a combination of production traits making the all-male *O. niloticus* × *O. aureus* hybrid more suitable for culture than either parental pure species (Pullin 1988; Lahav & Lahav 1990; Wohlfarth *et al.* 1990). This hybrid was also found to be superior to other hybrids (*O. mossambicus* × *O. aureus*, *O. mossambicus* and *O. niloticus* × *O. urolepis hornorum*) when growth rate, body colouration, cold sensitivity and sex ratio are considered together (Wohlfarth *et al.* 1990). Variations in growth rate among *O. niloticus* × *O. aureus* hybrids from different farms in Israel (Hulata *et al.* 1988) have led to further evaluation of various parental stocks for this hybrid (Hulata *et al.* 1993). These studies have indicated significant differences in growth rate among the various *O. niloticus* × *O. aureus* hybrids tested. However, low fry production in this hybrid has led more recently to substituting the use of hybrids with hormonal sex reversal for obtaining all-male populations. To overcome the low fry production an F_2 hybrid was produced from the *O. aureus* × *O. niloticus* hybrid consisting of both females and males. Eventually, a local 'Israeli tilapia stock' was developed by continuous further hybridization and sex-reversing the fry to become practically all male.

Resistance of consumers and health authorities to the consumption of fish treated with hormones may lead to a renewed interest in tilapia hybrids in the future or, more likely, to commercialization of the use of sex-reversed broodstock for producing intraspecific all-male Nile tilapia populations. The latter are another type of genetic resource developed over the past two decades in Nile tilapia, that is, broodstock capable of producing genetically male tilapia (GMT) from what are known as 'YY supermales'. These males were developed in a stock collected in Egypt and established at the University of Swansea, UK (Scott *et al.* 1989; Mair *et al.* 1993, 1997; Beardmore *et al.* 2001; see also http://www.fishgen.com/index.htm) and in the Thai Chitralada strain (Tuan *et al.* 1999). Sustained production of all-male hybrid tilapias may be aided by paying more attention to broodstock purity, involving routine inspection of every brooder and culling all doubtful individuals (Wohlfarth 1994). Interest in culturing all-male hybrids (particularly the relatively cold-tolerant *O. niloticus* × *O. aureus*) has recently gained popularity in several countries (e.g. China and Vietnam).

There is a need to promote inter-regional cooperation between African countries that hold the global wealth of Nile tilapia genetic resources and other non-African countries where Nile tilapia is exotic, but forms an important component of the aquaculture sector. Hitherto, performance of farmed stocks of Nile tilapia in Asia has been close to wild types or worse (Eknath *et al.* 1993). This situation has changed dramatically in recent years because of the realization of the importance of genetics in aquaculture and the development of more sustainable and environmentally compatible enterprises. The dissemination of GIFT and GIFT-derived strains has also played a significant role in enhancing production in Asia and in other countries. As tilapia culture expands there will be a greater need to transfer germplasm from Africa to Asia to develop improved breeds. The relevant issues here are: potential socioeconomic and environmental impacts of international transfer of germplasm and improved breeds, access to germplasm and how to compensate Africa for the use of its natural genetic resources.

The current Food and Agriculture Organization Volta project (TiVO) aims to develop an improved line of *O. niloticus* for the Volta riparian states, Ghana, Côte d'Ivoire, Benin, Mali and Burkina Faso. The first step is to compare the GIFT line with the local Akosombo line developed by the Water Research Institute in Ghana using the GIFT approach. Based on the outcomes of that comparison and a new and more detailed map of the genetic diversity of *O. niloticus* in the basin, a cost/benefit analysis will be undertaken with the participation of fisheries and environmental agencies in all of the countries involved. The main issue (and concern) is whether to use the GIFT as a starting point for a new breeding programme to be based in Ghana or to continue with the existing Akosombo line (R. Brummett, pers. comm., 2009; Bartley *et al.* 2008).

Concerns over managing and conserving natural tilapia genetic resources in Africa have been discussed in several reports in Abban *et al.* (2004). The invasion potential of Nile tilapia, as was demonstrated in Lake Chicamba, Mozambique (Weyl 2008), should also be taken into consideration. The arguments for and against using improved tilapia strains in African aquaculture are summarized in Brummett and Ponzoni (2009, p. 76): 'The real risks to indigenous biodiversity and ecosystems must be weighed against the potential of aquaculture to generate benefits for Africa, the world's poorest continent. … Improved lines of tilapia for Africa aquaculture could be expected to nearly double current growth rates and render economically viable many smaller farms that are struggling to survive. Whether changes in gene frequencies or allele combinations engendered through introgression of cultured tilapia genomes into wild populations represent a real threat is unknown. …In cases where important or rare tilapia biodiversity may be endangered, every effort should be made to assess the actual risks prior to introducing improved populations for culture. In general, however, based on the existing ecological evidence and the compelling economic needs of Africa, it seems reasonable to recommend to African governments and international agencies supporting aquaculture development taking immediate advantage of existing improved lines and supporting the development of new improved lines of, especially, *O. niloticus*'.

Conservation of Nile tilapia genetic resources

Both *in situ* and *ex situ* conservation have been attempted for tilapias. Pullin (1990) summarized the status and issues involved in conserving tilapias. The best strategy for *in situ* conservation is to maintain the original habitats. The first priority is better documentation of the status of the genetic diversity and greater awareness of its value. Documentation of tilapias and their ecology has been initiated through databases such as FISHBASE (http://www.fishbase.org), which also incorporates a tilapia strain registry. An essential prerequisite for *in situ* conservation is a responsible attitude towards fish transfers and an awareness of potential environmental impacts. This involves commitment on the part of both the host country and the international community. In Africa, however, aquaculture has little economic importance. Therefore, it may be difficult to expect a commitment to the cause of conservation for its own sake. Moreover, large water bodies that contain valuable genetic resources are shared between nations. Several nations in Africa are making efforts to protect streams and lakes that hold important stocks of tilapia. Malawi and Ghana are notable examples of nations who have shown commendable commitment to conservation (Pullin 1996). Malawi is making all possible efforts to conserve the Lake Malawi ecosystem and Ghana has established a nature reserve on an ecologically important section of the Volta catchment. To protect its indigenous populations, Malawi strongly regulates transfers of species and has restrictions on the exportation of certain cichlid taxa for the ornamental fish trade. Malawi specifically bans the introduction of all exotic species to protect the unique fauna of Lake Malawi.

Ex situ management techniques, including living collections or long-term storage of frozen spermatozoa, are readily available for many aquaculture species. ICLARM, under the auspices of the GIFT project, initiated a live fish and sperm bank for the African strains that were collected at the start of the GIFT project. The Nile tilapia germplasm from Africa and from farmed stocks in Asia assembled for the development of GIFT, the synthetic base population and selected generations of the GIFT strain are being maintained by the Philippine Bureau of Fisheries and Aquatic Resources at its field facilities in Munoz, Nueva Ecija, the Philippines. Material from this Nile tilapia gene bank is available on request from the Philippine Bureau of Fisheries and Aquatic Resources for research purposes (Contact: Director, BFAR-NFFTRC, Central Luzon State University Campus, Muñoz, NE, the Philippines).

The main issue as far as *ex situ* collection is concerned is the problem of ensuring adequate representation of the population gene pools. Representative sampling throughout the natural range of distribution of a given resource and the consequent maintenance of large populations will be an onerous and expensive task. It should be noted that sperm banks have some limitations, exploiting them for conservation or genetic improvement requires artificial propagation (e.g. Yeheskel & Avtalion 1988), which is not a standard aquaculture procedure with tilapias, and restoring extinct stocks from preserved sperm further requires the use of androgenesis (Mair 1993; Myers *et al.* 1995), which, although successfully applied to tilapia (Tariq Ezaz *et al.* 2004), is not commonly practiced.

The genetic improvement of farmed tilapia (GIFT) project

The GIFT project was an international research and development project coordinated and executed by ICLARM (now the WorldFish Center) from March 1988 to December 1997 in collaboration with the Norwegian Institute of Aquaculture Research (AKVAFORSK, now NOFIMA Marin) and three national institutions in the Philippines, the Philippine Bureau of Fisheries and Aquatic Resources (BFAR), the Marine Science Institute of the University of the Philippines (UP-MSI) and the Freshwater Aquaculture Center of the Central Luzon State University (FAC-CLSU). The hub of the entire research and development effort throughout the duration of the project was the National Freshwater Fisheries Technology Center of the BFAR (NFFTRC-BFAR). The project, as a whole, was a concerted effort on the part of ICLARM and its partners to build on the successes and experiences of various other initiatives in the region and was funded by the ADB, the United Nations Development Programme and ICLARM through its core funds, and the participating national institutions.

The experiences gained and the lessons learned during the implementation of the GIFT project and thereafter have been the subject of discussion in various contexts: development of research methods, development of national breeding programmes and dissemination of improved breeds, tilapia gene banking, impacts of genetic improvement initiatives and improved breeds on socio-economics (production, incomes, employment and human nutrition) and on the environment and biodiversity, public–private partnerships, institutional networks and collaboration mechanisms for common good. There were also some erroneous interpretations made in certain key publications (e.g. the case study on GIFT conducted by Greer & Harvey 2004), which probably resulted from incomplete information and lack of consultation with the personnel directly involved in the execution of the GIFT project.

The focus of this section is on the main results and outcomes of the GIFT project (Eknath 1992; Eknath & Acosta 1998), with emphasis on aspects relevant to impacts, access and sharing of benefits of the GIFT developed improved breeders and genetic resources assembled and public–private partnerships to ensure sustainability of the GIFT programme.

Development context and challenges addressed by the GIFT project

The GIFT project was established to address three challenges. First, could the application of basic principles of genetics and applied breeding technology, as practiced for centuries in plant and animal production (including salmonids), to the emerging tropical aquaculture sector result in enhanced production efficiency? This challenge was highly relevant within the context of: (i) stagnating fish production from capture fisheries and when aquaculture was increasingly seen as a panacea for the looming gap between the demand for and supply of food fish; and (ii) a glaring lack of conscious application of genetics to tropical aquaculture, even though the tradition of fish farming dates back thousands of years. Consequently, the fish stocks used in aquaculture are generally similar to wild undomesticated stocks and in some situations there is strong evidence for genetic deterioration. In fact, before the GIFT project, it had been widely assumed that genetic intervention would require extensive resources and, therefore, should be considered as an option for the future. The second challenge pertained to the dissemination of improved fish breeds once developed. It was understood from the beginning of the programme that genetic improvement and the development of improved breeds would be only half of the story. The other crucial aspect is their dissemination to reach the targeted beneficiaries effectively, including monitoring of the impact and adoption of improved breeds. Ways and means of catalyzing the development of applied fish breeding programmes in countries that needed them most was the third challenge addressed by the GIFT project. Relevant issues in this context included objective assessment of the needs and opportunities for developing applied fish breeding programmes in each participating country, prioritization of species and farming systems and development of the most viable mechanisms for international cooperation and provision for exchange of research methods and, where necessary, genetic materials. ICLARM had already declared its intention to adopt and apply internationally accepted codes of practices for the responsible transfer of germplasm in relation to the GIFT project (ICLARM 1992).

Nile tilapia was chosen as a prominent test species because of its growing importance in aquaculture, omnivorous dietary habits, which suit low cost aquaculture, and short generation time of approximately 8 months, making it an excellent model species for investigating the application of genetics in aquaculture, from conservation of genetic resources to breeding programmes. The research thrust was to develop methodologies and policy guidelines that could be applied or adapted to a wide range of finfish species in national fish genetic improvement programmes. The steps taken during the development of the project and its execution have been published previously (ICLARM 1992, 1998; Acosta & Eknath 1998; Bentsen *et. al*. 1998; Dey & Eknath 1997; Eknath 1992, 1995; Eknath & Acosta 1998; Eknath *et al.* 1993, 1998, 2007; ADB 2005).

Outcomes of the GIFT project

The genetic gain per generation across five generations of selection for growth performance was approximately 12–17%. The accumulated genetic gain in relation to the base population was 85% (Eknath & Acosta 1998; Eknath *et al.* 1998).

On-farm trials, regional dissemination and ex-ante impact assessment of GIFT

Under the Dissemination of Genetically Improved Nile Tilapia in Asia (DEGITA) project, the production potential of GIFT and existing Nile tilapia strains (referred as 'non-GIFT' strains because of their diversity of origins) were assessed through on-station and on-farm experiments in a range of aquaculture systems in Bangladesh, China, the Philippines, Thailand and Vietnam (ICLARM 1998; Dey 2000; Dey *et al.* 2000). Overall, the results of the farm trials indicated that:

- the percentage change in average weight at harvest and survival due solely to the mean superiority of the GIFT strain over the existing non-GIFT strains was highly significant across different countries;
- the magnitude of the effect of the GIFT strain on growth rate, however, varied among countries, ranging from 18% in China to 66% in Bangladesh; and
- the estimated yield potential of the GIFT strain was more than 50% higher than that of the best existing strains, ranging from approximately 54% higher in Vietnam to approximately 97% higher in Bangladesh.

Access and benefit sharing of GIFT: some early discussions and considerations

It was always the intention of the developers of GIFT and the primary institutions participating in the GIFT project that the GIFT breed be made freely available to tilapia farmers in participating countries and through the International Network for Genetics in Aquaculture (INGA) mechanism to any tilapia-producing country that requests it through the appropriate national authorities. Before the Convention on Biological Diversity entered into force in 1993, ICLARM convened a brain-storming meeting in 1992 on the 'International Concerns in the Use of Aquatic Germplasm' (ICLARM 1992). The objective of this meeting was to develop strategies and priorities in fish breeding research and approaches that will benefit small-scale, resource-poor fish farmers. The group made three recommendations relevant for the discussion here: (i) ICLARM should conduct further collection of wild tilapia genetic resources in Africa and include them in the ongoing breeding programme. It was suggested that codes similar to the then existing FAO Code of Conduct for collection of plant germplasm be followed; (ii) develop some mechanism for compensating the African contribution of tilapia germplasm to the GIFT; and (iii) recognize the traditional knowledge of tilapia genetic resources and suggest that ICLARM develop a database for capturing such information for the common good of all stakeholders.

As far as compensating Africa in the near term for its supply of Nile tilapia germplasm for the development of GIFT is concerned, it has been suggested that benefit sharing be addressed by disseminating and providing support for the application of GIFT methods to new tilapia breeding programmes in Africa that are based on indigenous strains and not by direct transfer of GIFT from Asia to Africa. It has been suggested that the international community as a whole should increase its commitment to the development of aquaculture in Africa.

Impacts of GIFT

The GIFT programme has:

1 demonstrated the enormous gains in economic performance of farmed tilapia that are possible from a systematic selection programme;
2 stimulated the planning and implementation of national tilapia breeding programmes in Bangladesh, China, Fiji Islands, Indonesia, Malaysia, the Philippines, Thailand and Vietnam;
3 initiated bilateral and multilateral research initiatives under the INGA that have begun to include other fish species, particularly carps that account for most of the finfish production in Asia;
4 catalyzed aquaculture genetic research in general and tilapia genetic research in particular, including mapping of the tilapia genome;
5 developed methods (Acosta & Eknath 1998) that are now used extensively in all national tilapia breeding programmes and with suitable modifications applied to other finfish species;
6 provided strains that form a major share in national tilapia seed production and supply in Asia, principally in the Philippines (68%) and in Thailand (46%);
7 been a primary source of material for development of more diverse breeds suitable for farming in the relatively colder climates of China.

A thorough analysis of the GIFT impact on the incomes of tilapia hatchery operators and farmers, impacts on employment and on human nutrition has also been carried out (ADB 2005). The use of GIFT has significantly enhanced tilapia production, generated employment, raised farm incomes from hatcheries and farms, and increased household consumption of tilapia (ADB 2005).

At an institutional level, the development and dissemination of GIFT have catalyzed the development of networks at local, regional and international levels, the implementation of national breeding programmes and the emergence of public–private partnerships, and the development of policies and plans for the expansion of tilapia farming in several countries, for example, the Philippines, Thailand and Vietnam (ADB 2005).

The WorldFish Center estimated that the economic rate of return on the investments made in the development and dissemination of GIFT was more than 70% over the period from 1988 to 2010 (ADB 2005). The net present value of the costs and benefits of the whole project has been estimated to be US$368 million in constant 2001 prices, with an annual discount rate of 7%.

Development and dissemination of GIFT, GIFT-derived and other Nile tilapia do not appear to have caused any significant impacts on existing aquaculture or on the natural environment and biodiversity in the Asia–Pacific region (De Silva *et al.* 2004; ADB 2005)

Lessons learned from GIFT experience

The lessons from the GIFT experience and the recommendations thereof, which have been adequately dealt with in the ADB-sponsored study specifically designed to assess the impact of GIFT (ADB 2005) and in Acosta and Gupta (2009), are outlined in brief.

- Development and dissemination of GIFT have shown that selective breeding is a feasible and cost-effective approach to the genetic improvement of tropical farmed fish.

- GIFT has shown that systematic assessments of the performance of genetically improved fish under diverse conditions are an essential pre-requisite for their commercial production. Multidisciplinary expertise required for the assessment of economic viability, social acceptability, environmental compatibility and the overall impact of improved farmed fish are generally available in a given National Agricultural Research System (expertise from crop and animal sciences) and should be utilized optimally.
- GIFT experience has shown that substantial and sustained funding was required for at least 10 years to cover the broad spectrum of germplasm collection, application of breeding methods, on-station and on-farm trials, research output consolidation, establishment of networks for national breeding programmes and distribution of improved breeds to hatcheries and fish farmers. Gene banking, biosafety and quarantine arrangements, certification of strains and capacity building are other vital investment areas.
- Multilevel partnerships and networks (INGA and regional networks) were instrumental in the accelerated dissemination of GIFT and GIFT research methods. Public–private partnerships also contributed to the sharing of resources, expertise and information in support of tilapia breeding and farming.
- To date the GIFT has focused on size-at-harvest as the breeding goal. Genetic improvement for other important production traits, such as feed conversion, dress weight and tolerance to biotic and abiotic stresses, should be investigated urgently.
- GIFT and GIFT-derived strains are currently the base material for further genetic improvement of farmed tilapias. However, there is a wealth of other wild and farmed tilapia genetic resources that needs systematic evaluation for use as promising breeding materials. International cooperation is clearly needed for a focused attention to this global need for tilapia genetic resources.

Extending the GIFT experience to a much wider context of the expected contribution of aquaculture to global food fish production, the ADB (2005) study strongly recommended the need for increased investment and dedicated efforts in the application of genetics in aquaculture. This applies not only to Asia, which at present is supplying over 80% of the world's farmed fish, but to all regions, as capture fisheries reach their limits.

Benefits to the original suppliers of Nile tilapia genetic resources

As a direct follow up to the letter and spirit of the recommendations made by the group of experts reviewing the initial outcome of GIFT in 1992, ICLARM began, in 2000, training African scientists in the use of selective breeding techniques and in the development of national breeding programmes suited to their needs, opportunities and priority species (Gupta *et al.* 2000). The founding member countries of INGA in Africa, Asia and the Pacific, through INGA, have also successfully initiated national level breeding programmes for genetic improvement of tilapia (where they are important) and other indigenous fish species.

Issues in continuation of the GIFT programme

This section describes in some detail the circumstances at the end of the GIFT project in 1997 and the roles of various agencies (the primary GIFT project partners, the GIFT Foundation and a private company, GenoMar of Norway) in continuing the 'GIFT legacy'. The focus is on issues pertaining to the access and benefits derived from the use of GIFT germplasm and to clarify some misinterpretations made in key publications, notably by Greer and Harvey (2004), with respect to the link between ICLARM, the GIFT Foundation and GenoMar.

The GIFT Foundation International (GFII)

The three significant resources nurtured and fully developed during the tenure of the project were: the GIFT breed and the associated germplasm assembled and maintained at the NFFTRC-BFAR facilities; the new physical infrastructure and dedicated facilities for breeding research and development at the CLSU campus; and, above all, a team of 20 Philippine researchers trained in quantitative genetics and breeding research. From the beginning of the GIFT project it was understood that the Philippines would at the end of the GIFT project in 1997 absorb all these resources as part of their national tilapia breeding programme and develop it into a regional hub for tilapia genetics research. For a variety of reasons this did not happen. In addition, ICLARM did not commit resources to continue the GIFT programme, despite repeated recommendations by the panel of experts appointed by the UNDP–DGIP, who were performing annual reviews and overseeing the project. The GIFT developers, for security reasons and on advice from the Expert Panel, transferred representative samples from selected families of the latest generation of the GIFT strain to the Vietnam Research Institute of Aquaculture No. 1.

Prior to the termination of the GIFT project in 1997, the partners decided to establish in the Philippines a private non-profit self-sustaining GFII to continue the GIFT programme through partnership with progressive tilapia fish hatcheries (Eknath & Acosta 1998). The founding trustees of this foundation were the heads of GIFT partner institutions, except AKVAFORSK. Commercialization of the GIFT strain was chosen as a strategy to generate the funding required to continue the selective breeding and research on the genetic materials assembled by the GIFT project and to sustain the 'GIFT legacy'. Through a memorandum of agreement between all primary partners of the GIFT project the resources were transferred to the GFII on the condition that the GIFT breed be made available to the partners for research purposes only for a period of 1 year. Only ICLARM exercised its right to receiving representative samples from the families of the latest selected generation of GIFT for eventual transfer to its new facilities in Malaysia in 2000. This 'stock' for ICLARM was maintained by the GIFT Foundation for a nominal maintenance fee.

The NFFTRC-BFAR of the Philippines chose to develop a new synthetic base population by crossing an earlier generation of the GIFT strain in its custody with the non-GIFT FAC-CLSU developed FAST strain and original wild African stocks (Egypt and Kenya) collected by GIFT partners. The result was a GIFT-derived strain that BFAR calls the GET EXCEL strain and this strain is now the basis of the Philippines national tilapia breeding programme.

Ever since it was formally established in January 1998, the GFII has not been able to sustain its operations on its own. By June 1988, when staff had been without salaries for more than 6 months, GFII was forced to look for joint ventures with commercial entities elsewhere. AKVAFORSK approached several fish farming companies in Norway and finally settled on BioSoft (now GenoMar) as a partner for the GIFT Foundation.

The Role of GenoMar

Realizing the potential value of the GFII resources and while negotiating with the GFII trustees for an agreement, GenoMar unconditionally supported the entire operations of the GFII (including payment of salary arrears) for more than 16 months. In 1999, GFII finally drew up an agreement with GenoMar. The basic provisions were as follows: in exchange for a representative sample (similar to the one given to ICLARM by GFII) of the GIFT families from the latest generation of selection, GenoMar would provide GFII with an equity position in GenoMar, assured annual funding to GFII for contracted research to sustain its operations in an optimal manner and sharing of benefits from the collaborative research projects conducted jointly. It is important to note that GFII negotiated to retain its own historical broodstocks and to continue independent research and development. GenoMar only asked for the right of first refusal on the products developed independently by GFII.

GenoMar has been a benevolent partner for GFII, particularly in the early years. Without the assistance of GenoMar the 'GIFT legacy' would have most certainly been lost forever. Unfortunately, this partnership dissolved in 2005 due mainly to administrative problems in GFII and certain other commercial initiatives attempted by GFII without the explicit consent of GenoMar. The future of GFII now remains uncertain. Nevertheless, several parallel breeding programmes based on fish derived from the GIFT project and provided by GFII are ongoing (e.g. by GenoMar, the WorldFish Center and a few other organizations). Ponzoni *et al.* (2005) and Khaw *et al.* (2008) describe the work done in Malaysia with fish derived from the sixth generation of the selection of GIFT. A GIFT-derived new strain, GenoMar Supreme Tilapia (GST), has been further improved by selective breeding and by introducing DNA typing as an identification system, replacing the conventional physical tags (GenoMar 2009).

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