

Genetic quality of cultured tilapia stocks in Africa

R. E. BRUMMETT¹

African aquaculture is poised for rapid expansion. Local and international markets for the Oreochromiine tilapia species in particular have been growing in the face of dramatic declines in marine and inland capture fisheries, growth of human populations in developing countries and increases in wealth and health consciousness. One of the key constraints holding back growth of the sector is the poor quality of the fish stocks available for culture.

Quality of Current Stocks

African aquaculture has for many years been dominated by small-scale producers who purchase few inputs, relying almost exclusively on family labor and composts or manures that can be found on the farm. The species most commonly produced is Nile tilapia (*Oreochromis niloticus*), fingerlings of which are usually obtained from friends or neighbors. The typical practice is to sell or eat all fish of a certain minimum size, leaving smaller individuals to be either sold as fingerlings to other farmers or restocked to continue growing. In the case of tilapia, only some of these small fish are actually fingerlings, many being small, sexually mature adults. Such selection for small adults amounts to inadvertent selection for slow growth and/or early sexual maturation (Doyle 1983) and can lead to declines of up to 20 percent in growth rate within six generations, or less than three years (Silliman 1975).

Even in hatcheries, the situation is little better. Small-scale fingerling production in Africa is typically based on earthen ponds between 50 and 500 m², with or without some kind of hatchery building (Figure 1). Into these ponds are stocked various numbers and sex ratios of male and female tilapia of mixed sizes and genetic backgrounds. New broodfish are expensive, difficult and sometimes illegal to acquire, so individuals seeking them often resort to obtaining minimal numbers, thus building low genetic diversity into their production systems from the outset (Eknath 1991). Often the effective number of broodfish that contribute to each subsequent generation (N_e) is far less than the 100-150 pairs needed to maintain healthy genetic variability (Smitherman and Tave 1987). Even when the numbers are sufficient, simply stocking 100 males and 100 females into a brood pond will not solve the problem. Inasmuch as male tilapia are highly territorial and competitive for mates, only about 30 percent of males (the most aggressive; not necessarily the fastest growing) dominate the fertilization of the females (Fessehaye *et al.* 2006). Without some method of ensuring that all males are represented, N_e will still be too low.



Fig. 1. A typical small-scale tilapia hatchery in Cameroon, comprised of 23 small ponds of 10-150 m² selling an average of 5,000 tilapia per month based on feral *O. niloticus* broodfish captured from the Sanaga River.

Declines in growth performance are often associated with such loss of genetic diversity (Table 1). Typically, genetic variability of fish held in small-scale African hatcheries is 40-70 percent less than for wild populations (Table 1). These levels of loss are associated with growth rate declines on the order of 12-40 percent compared to wild stocks. In addition, response to selective breeding (see below) can be reduced by up to a third by even moderate reduction of genetic variation (Bentsen and Olesen 2002). Heritability (h^2) for growth in tilapia is naturally low to moderate, averaging less than 20 percent and can easily be swamped by low N_e (ICLARM/UNDP 1998). Even with the relatively low fish production in Africa, a 20 percent decline in growth rate represents lost production on the order of 80,000 t, with associated lost profits on the order of US\$200 million per year to Africa's fish farmers (FAO 2000).

Large farms are not immune to the problems of deteriorating genetic quality. Largely out of ignorance, rather than lack of capital, larger-scale fish farms have both inbreeding and outcrossing problems. Not only are most large hatcheries based on the same type of open pond spawning system used by small-scale hatcheries, they also tend to import stocks and species from other farms and countries. The Baobab Fish Farm Kenya, for example, until recently (they are

now no longer operating) grew a hybrid strain of *O. niloticus*, *O. spilurus* and *O. mossambicus*. Kafue Fish Farm in Zambia maintains stocks of *O. niloticus*, *O. andersonii*, *O. aureus* and gets wild *O. mortimeri* and *O. macrochir* from the Kafue River. All of these easily cross with each other and perform less well than the original *O. andersonii* stock.²

Genetic Improvement Strategies

While difficult, proper management of captive tilapia genetic resources is not impossible. In those few cases where the genetic diversity of hatchery stocks has been systematically managed either through the use of large effective breeding numbers, rotational mating or controlled outcrossing, growth rates equal or exceed those of natural populations (Pauly *et al.* 1988). In addition, organized selective breeding can, if properly conducted, lead to increases in growth rate of 16-70 percent per generation (Jarimopas 1990, Rognon and Guyomard 1996, Vreven *et al.* 1998).

That improvements in genetic quality can increase production is unarguable. To be profitable at all, crop agriculture relies heavily on improved varieties. However, how these improvements are made can have a large impact on the rate of progress and who benefits and how. There are two general approaches to improving the genetic quality of fish raised in aquaculture:

1. Import an exotic species or improved variety developed elsewhere (centralized approach).
2. Locally develop a new species or variety (decentralized approach).

Agricultural research and development has long relied on the option of domesticating or breeding a new variety in a central location and then subsequently disseminating seed or broodstock. This approach requires the international and often intercontinental transfer of genetic material thus risking both negative environmental impacts and the possibility of genotype by environment (G X E) interaction, which renders improved genotypes less competitive in culture systems that differ from those under which they were bred.

The major advantage of the centralized approach is that complicated technologies can be more easily managed in larger, more sophisticated facilities. Breeding progress is faster. For example, the Genetically Improved Farmed Tilapia (GIFT) strain of *O. niloticus* developed by ICLARM, the Asian Development Bank and the United Nations Development Program in the Philippines and Malaysia grows 20-70 percent faster than most captive *O. niloticus* strains (ADB 2005). However, in Thailand and China, GIFT exhibit signs of G X E interaction and are not substantially superior to locally adapted and bred strains under certain conditions. GIFT was produced in four years while the strains in Thailand and China were slowly selected over 30 and 20 years, respectively (ICLARM 1998).

Decentralized genetic improvement normally takes longer than the centralized approach. Decentralization requires more people to be involved and is consequently less efficient in terms of capital use. It also tends to be more difficult to implement within the short-term projects preferred by government. On the other hand, one of the key constraints to improved ge-

Table 1. Documented erosion of genetic variability and growth performance among African hatchery tilapia populations.

- Introgression *O. macrochir* into *O. niloticus* reduced growth 20% (Micha *et al.* 1996)
- Backcrossing 3 generations of red hybrids lowers reproduction⁴
- Well-managed stock 12% better than small hatcheries (Morissens *et al.* 1996)
- Genetic variability down 50% in small hatchery stock (Morissens *et al.* 1996)
- Wild fish 43% more genetic variability than small hatcheries (Pouyard and Agnese 1996)
- 50% loss of genetic variability in small hatchery stocks (Agustin *et al.* 1997)
- Wild populations better than African hatchery stocks (Eknath *et al.* 1993)
- 70% loss of genetic variability among hatchery stocks (Ambali *et al.* 1999)
- 50% less growth in hatchery Vs Lake Victoria stocks⁵
- 40% decline in growth of stocks held on small-scale farms (Brummett *et al.* 2006)

netic management of African aquaculture species is the lack of high quality human resources and hatchery infrastructure. Without the capacity to undertake proper management and breeding, the potential gains inherent in a new strain will be quickly lost. The on-the-job training opportunities created by decentralized genetic improvement projects is an excellent means of creating both new strains for culture and the capacity to manage them at the same time.

For indigenous or feral (alien species already established in the wild) species, there are ready reserves of broodstock well-adapted to local environmental and climatic conditions. If those populations are large enough (over 1,000 randomly breeding individuals) they will usually be more genetically diverse than captive populations. If new wild or feral broodfish were regularly outcrossed into hatchery populations to maintain genetic diversity at natural levels, the performance of most captive tilapia populations, even those with low N_e , could be enhanced.

It should be reiterated that the relatively low-cost option of maintaining genetic variation through outcrossing to local wild populations exists, most typically, only for indigenous species, making a strong argument against the importation of aliens as a simple solution to poor performance in culture. Even if the alien species in question outgrow local species at the time of introduction, without careful genetic management they will deteriorate with the resulting need to repeatedly import new broodfish.

Risks of Using Improved Lines in Africa

As part of the domestication process that has produced all of the strains used in modern animal husbandry and as the result of relatively new initiatives to selectively breed tilapia,



Fig. 2. *Oreochromis andersonii*, a fast-growing and docile tilapia native to the upper Zambezi is being threatened by rampant introduction of *O. niloticus* for aquaculture.

a number of tilapia populations housed on fish farms outside Africa have been improved, sometimes considerably so, as compared to the wild African stocks from which they were derived. For example, GIFT, which have been maintained in captivity in Asia by professional geneticists and selectively bred since the late 1980s, has a growth rate at least 60 percent, and even 100 percent in some cases better than most cultured stocks, and now reaches over 800 g in 10 months under good conditions. Despite a certain loss in genetic diversity as a result of the selection process, rates of gain in performance per generation remain in excess of 10 percent.

There are currently insufficient data available on tilapia ecology and/or genetic diversity to permit fully informed decision-making with regard to the potential negative impacts on wild African tilapia stocks of bringing back or developing new improved strains. However, in general, the debate over the use of genetically modified fishes, either naturally through selective breeding or through the use of transgenic techniques, has become global and includes a large number of case studies from, especially, Europe and North America. Whether or not those data are sufficient to adequately assess the risks involved in the use of selected tilapia strains for aquaculture is debatable.

Genetic Introgression. That cultured populations of indigenous species, such as caged Atlantic salmon in Europe, will escape and breed with wild fish is undeniable. Huge negative affects of the accidental escape of cultured salmon and/or the purposeful introduction of hatchery stocks on wild salmon runs have been repeatedly documented (Utter and Epifanio 2002, McGinnity *et al.* 2003). The main cause of those declines has been through the process of genetic introgression; that is, the migration of genes from the captive population into the wild population through interbreeding. Mixing the genomes of captive fish that are specifically adapted to a hatchery environment with those that are specifically adapted to a particular river, or by increasing the relative percentage of genes from one subset of a wild popu-

lation into a river or lake, the overall degree of adaptation or fitness of the wild population could be reduced (Ryman 1991). The magnitude of this problem is proportional to:

1. The degree and importance of the adaptation of the wild population to the waterbody in question. In cases where only a narrow range of genotypes can survive in a particular waterbody, the genetic base (variability) of the fish population narrows, rendering the wild population vulnerable to environmental changes, one of which is the presence of large numbers of fish of other genotypes.
2. The relative sizes of the captive and wild populations. In cases where relatively small (<10,000 individuals) wild fish populations that are highly adapted to a particular river or lake are inundated by hundreds of thousands of stocked or escaped fish, such as is the case for many wild runs of Atlantic salmon, the consequences of the reduction in fitness can be catastrophic and may ultimately result in the extinction of the wild genome, even in cases where the total number of fish in the waterbody has actually increased (McGinnity *et al.* 2003).
3. The degree of difference between the genomes of the wild and captive populations. The more distant the relationship between the introduced and wild genomes, the greater could be the reduction in fitness.
4. The goals of having captive and wild populations in the same stream. If preservation of the indigenous genome is considered of primary importance, the increased number of fish in a particular waterbody as a result of stocking or escapes may be of less interest than the relative fitness of the population.

In the case of small, highly adapted, with relatively narrow genetic diversity Atlantic salmon runs, the risk of introducing large numbers of less well adapted hatchery fish has been shown to reduce whole lifetime population fitness, at least in the short term (McGinnity *et al.* 2003). On the other hand, long-term and large-scale releases of marine fish fingerlings in an effort to enhance relatively large and genetically diverse species such as cod, redfish and red sea bream have generally failed to produce any noticeable change in productivity (Utter and Epifanio 2002).

Incidences of ecological disruption resulting from, or in conjunction with, the introduction of Oreochromiines have been widely if not thoroughly documented (Lever 1996, Canonico *et al.* 2005). The introduction of any strain of *O. niloticus* to places where it currently is not should, therefore, be undertaken with the utmost caution. Inasmuch as most captive populations eventually find their way into the wild, the transfer and culture of *O. niloticus* into new watersheds would be wisely avoided (Figure 2).

However, the principal debate between wildlife conservationists and fish farmers with regard to the importation of domesticated tilapia species to Africa revolves around the danger of genetic introgression with wild populations that probably contain genetic diversity of important adaptive significance that is lacking in captive stocks. Nevertheless, there are substantial and important differences between Atlantic salmon (for which the majority of documented cases of genetic erosion have been published) and tilapia (Table 2).

Table 2. Comparison of key biological and ecological traits of salmon and tilapia.

Salmon
<ul style="list-style-type: none"> • Top carnivores • Relative few in number • Generally narrow genetic bases • Complex life history strategies; highly adapted to specific river systems • Reproduce once and die
Tilapia
<ul style="list-style-type: none"> • Forage species feeding low on the food chain • Large population sizes, even in small waterbodies • Probably broad genetic bases, • High levels of phenotypic plasticity; not specifically adapted to local habitats • Reproduce at least three times per year

While it must be stressed that there is no compelling empirical evidence arguing either for or against the possibility of negative impacts resulting from the introgression of captive tilapia strains into indigenous populations, the substantial differences between tilapia and salmon, upon which most of the concerns over genetic erosion are based, imply that the risks of introducing improved tilapia specifically for aquaculture might be significantly less than feared.

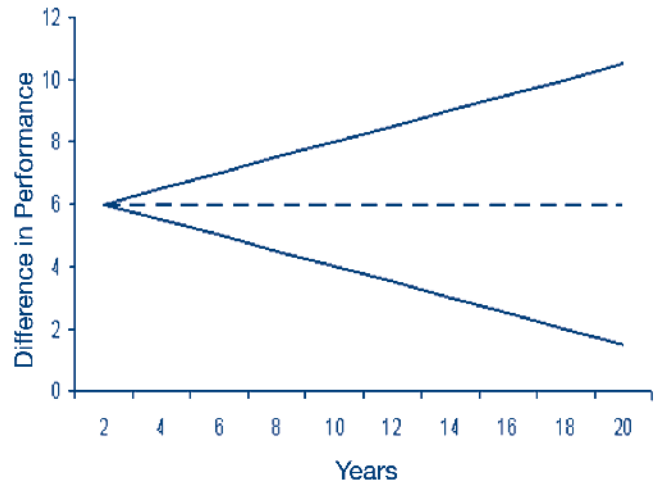


Fig. 3. Theoretical trajectories of hatchery populations under various management regimes, relative to a hypothetical panmictic wild population from which they were derived.

Referring to the list of conditionalities presented above:

1. Tilapia are generalists, often exhibiting high degrees of phenotypic plasticity, but not normally genotypically adapted to specific water bodies.
2. Wild tilapia populations are generally huge, in excess of millions of individuals, while escapes from aquaculture are minimized (relative to intentional stocking programs, (Continued on page 70))

Høgskolen i Bodø

JOB OPPORTUNITIES

in Norway - Bodø University College

Professors in:

- Fish Nutrition
- Marine Ecology

Bodø University College (BUC) invites applications for two positions at the Full Professor level in the areas of fish nutrition and marine ecology. Both positions are new and a part of a strategic development of research and education in aquaculture at the Faculty of Biosciences and Aquaculture (FBA).

We are seeking persons with a full professor competence and with ambitions to develop and expand our activities both in education and research. We expect the candidates to be internationally profiled with an extensive network and a high scientific production.

The Fish Nutrition position:
BUC will be flexible in relation to area of expertise, but prioritized areas are: nutrient requirement and metabolism, interaction between nutrition and product quality, and interaction between feed composition and environmental impacts. For further information, please contact:
terje.solberg@hibo.no, phone +47 75 51 73 58, or ole.torrissen@hibo.no, phone +47 90 83 95 56.

The Marine Ecology position:
BUC will be flexible in relation to area of expertise, but the prioritized area is marine aquaculture ecology. For further information, please contact:
magne.haakstad@hibo.no, phone +47 75 51 73 63.

For both positions we can offer a remuneration package or a qualification fellowship for researchers, who are not fully qualified, but has an especially interesting academic record.

Bodø and BUC
Bodø is the capital of Nordland county, a 90 min. flight from the Norwegian capital Oslo. BUC has approximately 500 staff and 5000 students. FBA is situated at the main campus, and has a marine laboratory at the seaside; a large and modern facility for experimental marine biology located within walking distance from the main campus.

Salary
Yearly salary is approx USD \$ 112.450. For special reasons higher salary can be given.

Application deadline: August 4th 2008.

For application details, full announcement, and online job application see: www.hibo.no/english and choose "vacant positions"

www.hibo.no/english

GENETIC QUALITY OF TILAPIA

(Continued from page 49)

for example) by farmers trying to protect their investments.

3. In terms of growth performance, hatchery populations of tilapia are 40-60 percent different from wild populations, at least in terms of growth rate.
4. Food security and economic growth in impoverished communities are key concerns. In addition to the ethical issues involved, failure to address food security needs probably increases the threats to biodiversity posed by overfishing and the bushmeat trade.

Only number three gives substantial cause for concern. If, for example, there are serious threats to a tilapia population of particular significance for local capture fisheries or of special value as a locally adapted race, the rather large difference between captive and wild fishes could represent a real danger. On the other hand, the dangers associated with these genetic differences are proportional to the absolute value of the difference, not whether the difference is positive or negative.

At present, hatchery populations across Africa differ substantially, mostly negatively, from wild populations. From Figure 3, it can be seen that the difference between the threat of introducing an improved strain (GIFT in this example) is not measurable in terms of risk, but in time (8-10 years in this case). That is, if an African hatchery either begins breeding its own improved line, or if the current negative situation continues, whatever the absolute danger to wild populations may be, it will be eventually realized regardless of whether or not GIFT are imported. It is mostly just a matter of time.

There are two additional realities that should not be ignored when making decisions about conservation³ of indigenous tilapia biodiversity in Africa:

1. *O. niloticus* has been repeatedly introduced into thousands of water bodies throughout the African continent since at least the 1940s. Many of those introductions have resulted in the establishment of feral populations.
2. Commercial fish farmers, who are facing increasing competition in both local and international markets from foreign producers using improved strains of tilapia, have in the past made illegal introductions and, confronted with the demise of their businesses, may well resort to such tactics in future.

Regardless of whether existing improved breeds are imported, local hatcheries breed their own local strains or nothing is done at all, risks to the environment and the livelihoods of local people are unavoidable. However, prior to introducing or developing improved lines of tilapia for aquaculture, a careful cost/benefit analysis and risk assessment following the recommendations of the Nairobi Declaration on the Conservation of Aquatic Biodiversity and Use of Genetically Improved and Alien Species for Aquaculture in Africa and similar policy instruments (available on-line at: http://www.worldfishcenter.org/cms/list_article.aspx?catID=39&ddlID=109) made within the prevailing ecological and socio-economic contexts should be conducted.

Notes

¹WorldFish Centre, BP 2008, Yaoundé, Cameroon

²Fergus Flynn, Kafue Fish Farm, Personal Communication, September 2003

³Pullin (2000) promoted the definition of “conservation” as “management and sustainable use” as opposed to “preservation” in which no use is envisaged.

⁴Behrends pers comm, 1985

⁵Gregory pers comm. 2003

References

- ADB (Asian Development Bank). 2005. An impact evaluation of the development of genetically improved farmed tilapia and their dissemination in selected countries. Operations Evaluation Department, Asian Development Bank, Manila, Philippines.
- Agustin, L.Q., P.B. Mather and J.C. Wilson. 1997. Levels and patterns of genetic diversity in *Oreochromis mossambicus*: wild African vs. introduced feral populations in the Australasian/Pacific region. Pages 75-86 In K. Fitzsimmons, editor. Tilapia Aquaculture, Northeast Regional Agricultural Engineering Service, Ithaca, New York, USA.
- Ambali, J.D., R.W. Doyle and D.I. Cook. 1999. Genetic changes in *Oreochromis shiranus* associated with the early stages of national aquaculture development in Malawi. *Aquaculture Research* 3:579-588.
- Bentsen, H.B. and I. Olesen. 2002. Designing aquaculture mass selection programs to avoid high inbreeding rates. *Aquaculture* 204:349-359.
- Brummett, R.E., D. Etaba Angoni and V. Pouomogne. 2004. On-farm and on-station comparison of wild and domesticated Cameroonian populations of *Oreochromis niloticus*. *Aquaculture* 242:157-164.
- Canonico, G.C., A. Arthington, J.K. McCrary and M. Thieme. 2005. The effects of introduced tilapias on native biodiversity. *Aquatic Conservation: Marine & Freshwater Ecosystems* 15:463-483.
- Doyle, R.W. 1983. An approach to the quantitative analysis of domestication selection in aquaculture. *Aquaculture* 3:167-185.
- Eknath, A.E. 1991. Simple broodstock management to control indirect selection and inbreeding: Indian carp example. *NAGA, The WorldFish Quarterly* 14(2):13-14.
- Eknath, A.E., M.M. Tayamen, M.S. Palada-de Vera, J.C. Danting, R.A. Reyes, E.E. Dionisio, J.B. Capili, H.L. Bolivar, T.A. Abella, A.V. Circa, H.B. Bentsen, B. Gjerde, T. Gjedrem and R.S.V. Pullin. 1993. Genetic improvement of farmed tilapias: the growth performance of eight strains of *Oreochromis niloticus* tested in different farm environments. *Aquaculture* 111:171-188.
- FAO. 2000. FISHSTAT Plus electronic database. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Fessehaye, Y., Z. El-Bialy, M.A. Rezk, R. Crooijmans, H. Vovenhuis and H. Komen. 2006. Mating systems and male reproductive success in Nile tilapia (*Oreochromis niloticus*) in breeding hapas: a microsatellite analysis. *Aquaculture* 256:148-158.
- ICLARM (International Centre for Living Aquatic Resources Management). 1998. Dissemination and evaluation of genetically improved tilapia species in Asia. WorldFish Center, Penang, Malaysia.
- ICLARM/UNDP (International Centre for Living Aquatic Resources Management/United Nations Development Programme). 1998. Estimated heritabilities within each environment, and across all environments, during each generation. In *Genetic Improvement*

(Continued on page 72)

GENETIC QUALITY OF TILAPIA

(Continued from page 70)

- of Farmed Tilapias (GIFT) Final Report, Part 2, Attachment 6. United Nations Development Programme & WorldFish Centre, Penang, Malaysia.
- Jarimopas, P. 1990. Realized response of Thai red tilapia to 5 generations of size-specific selection for growth. Pages 519-522 *In* R. Hirano, R. and I. Hanyu, editors. The Second Asian Fisheries Forum. Asian Fisheries Society, Manila, Philippines.
- Lever, C. 1996. Naturalized fishes of the world. Academic Press, Ltd., London, UK.
- McGinnity, P., P. Prodöhl, A. Ferguson, R. Hynes, N.O. Maoiléidigh, N. Baker, D. Cotter, B. Ohea, D. Cooke, G. Rogan, J. Taggart and T. Cross. 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. Proceedings of the Royal Society of London 270:2443-2449.
- Micha, J.-C., R. Cuvelier, Ch. Tilquin, B. Muraille, M. Bourgois and U. Galter. 1996. Comparative growth of hybrids (F_1 , F_2 & F_3) of *Oreochromis niloticus* and *O. macrochir*. Pages 354-360 *In* R.S.V. Pullin, J. Lazard, M. Legendre, J.B. Amon-Kothias & D. Pauly, editors. The Third International Symposium on Tilapia in Aquaculture. ICLARM Conference Proceedings 41. WorldFish Center, Penang, Malaysia.
- Morissens, P., X. Rognon and I. Dembele. 1996. Comparison of growth performance and electrophoretic characteristics of three strains of *Oreochromis niloticus* present in Côte d'Ivoire. Pages 361-367 *In* R.S.V. Pullin, J. Lazard, M. Legendre, J.B. Amon-Kothias and D. Pauly, editors. The Third International Symposium on Tilapia in Aquaculture. ICLARM Conference Proceedings 41. WorldFish Center, Penang, Malaysia.
- Pauly, D., J. Moreau and M. Prein. 1988. A comparison of overall growth performance of tilapia in open waters and aquaculture. Pages 469-479 *In* R.S.V. Pullin, T. Bhukasawan, K. Tonguthai and J.L. Maclean, editors, The Second International Symposium on Tilapia in Aquaculture. ICLARM Conference Proceedings 15, WorldFish Center, Penang, Malaysia.
- Pouyau, L. and J.F. Agnès. 1996. Genetic differentiation in several stocks of *Sarotherodon melanotheron* and *Tilapia guineensis* from Côte d'Ivoire, Senegal and Gambia. Pages 368-376 *In* R.S.V. Pullin, J. Lazard, M. Legendre, J.B. Amon-Kothias and D. Pauly, editors. The Third International Symposium on Tilapia in Aquaculture. ICLARM Conference Proceedings 41. WorldFish Center, Penang, Malaysia.
- Rognon, X. and R. Guyomard. 1996. Study of genetic variation in farmed populations of some species of the genus *Oreochromis*. Pages 398-406 *In* R.S.V. Pullin, J. Lazard, M. Legendre, J.B. Amon-Kothias and D. Pauly, editors. The Third International Symposium on Tilapia in Aquaculture. ICLARM Conference Proceedings 41. WorldFish Center, Penang, Malaysia.
- Ryman, N. 1991. Conservation genetics considerations in fishery management. *Journal of Fish Biology* 39 (Supplement A):211-224.
- Silliman, R.P. 1975. Selective and unselective exploitation of experimental populations of *Tilapia mossambica*. *Fishery Bulletin* 73:495-507.
- Smitherman, R. Oneal and D. Tave. 1987. Maintenance of genetic quality in cultured tilapia. *Asian Fisheries Science* 1:76-82.
- Utter, F. and J. Epifanio. 2002. Marine aquaculture: genetic potentialities and pitfalls. *Reviews in Fish Biology and Fisheries* 12:59-77.
- Vreven, E.J., B. Adépo-Gourène, J.F. Agnès G.G. and Teugels. 1998. Morphometric and allozyme variation in natural populations and cultured strains of the Nile tilapia, *Oreochromis niloticus niloticus*. Pages 175-182 *In* J.F. Agnès, editor. Genetics and Aquaculture in Africa. ORSTOM Editions, Paris, France.

HOUSEFLY MAGGOT MEAL

(Continued from page 18)

References

- Adesulu, E.A. and A.K. Mustapha. 2000. Use of housefly maggots as a fish meal replacer in tilapia culture: A recent vogue in Nigeria. Pages 138-143 *In* K. Fitzsimmons and J.C. Filho, editors. Proceedings of the Fifth International Symposium on Tilapia Aquaculture 2000. Rio de Janeiro, Brazil.
- Buchholz, H. 1997. Bestimmung von Aminosäuren. Pages 1-6 *In* Verband deutscher landwirtschaftlicher Untersuchungs- und Forschungsanstalten Methodenbuch Band III. VDLUFA-Verlag, Darmstadt, Germany
- Fashina-Bombata, H.A. and O. Balogun. 1997. The effect of partial or total replacement of fish meal with maggot meal in the diet of tilapia (*Oreochromis niloticus*) fry. *Journal of Prospects in Science* 1:178-181.
- Jackson, A.J., B.S. Capper and A.J. Matty. 1982. Evaluation of some plant proteins in complete diets for the tilapia, *Sarotherodon mossambicus*. *Aquaculture* 27:97-109.
- Jauncey, K. and B. Ross. 1982. A Guide to Tilapia Feeds and Feeding. Institute of Aquaculture, University of Stirling, Scotland.
- Santiago, C.B. and R.T. Lovell. 1988. Amino acid requirements for growth of Nile tilapia. *Journal of Nutrition* 118:1540-1546.
- Shiau, S.-Y., J.L. Chuang and C.L. Sun. 1987. Inclusion of soybean meal in tilapia (*Oreochromis niloticus x O. aureus*) diets at two protein levels. *Aquaculture* 65:251-261.
- Shiau, S.-Y. and Y.P. Yu. 1999. Dietary supplementation of chitin and chitosan depresses growth in tilapia, *O. niloticus x O. aureus*. *Aquaculture* 179:439-446.
- Shiau, S.-Y. and C.Y. Peng. 1993. Protein-sparing effect by carbohydrates in diets for tilapia, *Oreochromis niloticus x O. aureus*. *Aquaculture* 117:327-334.
- Siddiqui, A.Q., M.S. Howlander and A.A. Adam. 1988. Effects of dietary protein levels on growth, diet conversion and protein utilization in fry and young Nile tilapia, *Oreochromis niloticus*. *Aquaculture* 70:63-73.
- Spinelli, J., C. Mahnken and M. Steinberg. 1979. Alternate sources of proteins for fish meal in salmonid diets. Pages 131-142 *In* J.E. Halver and K. Tiews, editors. *Finfish Nutrition and Fishfeed Technology*, Vol. II. H. Heenemann GmbH, Berlin, Germany.
- Tacon, A.G.J. 1993. Diet Ingredients for Warmwater Fish: Fish Meal and Other Processed Feedstuffs. FAO Fisheries Circular No. 856, FAO, Rome, Italy.
- Teotia, J.S. and B.F. Miller. 1973. Fly pupae as a dietary ingredient for starting chicks. *Poultry Science* 52:1830-1835.
- Teshima, S. and A. Kanazawa. 1988. Nutritive value of methionine-enriched soy plastein for *Oreochromis niloticus* fry. Pages 393-399. *In* R.S.V. Pullin, T. Bhukasawan, K. Tonguthai and J.L. Maclean, editors. Second International Symposium on Tilapia in Aquaculture. Conference Proceeding No. 15, ICLARM, Manila, Philippines.
- Viola, S., Y. Arielia and G. Zohar. 1988. Animal-protein-free diets for hybrid tilapia (*Oreochromis niloticus x O. aureus*) in intensive culture. *Aquaculture* 75:115-125.
- Viola, S., H. Angeoni and E. Lahva. 1994. Present limits of protein sparing by amino acid supplementation of practical carp and tilapia diets. *Israeli Journal of Aquaculture Bamidgeh* 46:203-211.