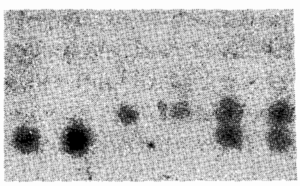
whether from local stocks (*S. niloticus* B, Ein Hamifrats Israel) or from different countries in Africa (Uganda, Ghana, Kenya), all possess a unique esterase band, electrophoretically distinct (Rm 74.3%) from that of *S. aureus.* All F_1 *S. niloticus* x *S. aureus* hybrids were found to possess both SE bands (Plate 5). Thus, the SE test was found very useful in controlling broodstocks. It is noteworthy that the same gels, after being stained for SE can undergo an additional staining for proteins (using Coomasie blue) or alternatively can serve for both LDH (upper part of the gel) and SE (lower part of the gel) tests.

(+)



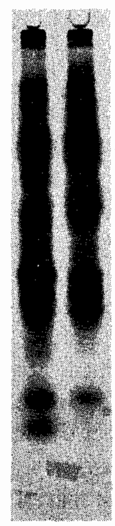
—E_2
—E_1

SA SN HB

(−)

Plate 5. Electropherogram showing serum esterase patterns (E_1, E_2) of *Sarotherodon aureus* (SA), *S. niloticus* (SN) and their hybrids (HB). 6% polyacrylamide gel.

m f



—0

T + A

MSP

(+)

Plate 6. Electropherogram of *Sarotherodon aureus* serum in 7% polyacrylamide gel showing the male sex protein band (MSP) and the overlapping of transferrins (T) by the albumin band (A); m, male; f, female.

Male Sex-Protein (MSP)

Male-specific bands were found in 7% polyacrylamide gel electropherograms of *S. aureus*, one band (Plate 6); *S. niloticus*, 2 bands and *S. galilaeus*, 2 bands (Avtalion et al. 1975, 1976). The position of these bands in the electropherogram was found to be species-specific. This subject is now under study in our laboratory and some preliminary results have been obtained. This protein was purified using preparative electrophoresis and its molecular weight as determined by sodium dodecyl sulfate (SDS) electrophoresis is 40,100 Δ. Anti-MSP antibody raised in rabbits gave a single precipitin line when tested against MSP. However, this antibody was also reactive against female serum (Avtalion et al., in prep.). This result suggests that another serum protein might exhibit cross antigenicity with MSP, or that MSP exists in another form in females. At any rate, the antigenic determinants seem to be present in higher quantities in mature than in immature males. The *S. aureus* MSP was found to display cross antigenicity with *S. galilaeus* MSP. Some males were found to possess especially high quantities of this antigen, and we wonder whether these MSP-rich males are more capable than other males with less MSP, in their ability to give rise to a higher percentage of male offspring. This would be in agreement with our autosomal theory on sex determination in *Sarotherodon* (Hammerman and Avtalion 1979) which is summarized below.

Sex Determination

The autosomal theory suggests that the sex determination is by female and male gene products, which interact quantitatively (Avtalion and Hammerman 1978; Hammerman and Avtalion 1979). The crossing of males, which produce more male-sex regulating factors (SRF) with females, which produce less female-SRF, would provide a high percentage of male hybrids and *vice versa.* This balance theory is called "autosomal" because it is based on the assumption that the regulatory genes are located on autosomes (A,a) as well as on gonosomes (X, Y, W). This theory explains in a highly satisfactory manner the unusual sex ratios obtained by Chen (1969) who performed a comprehensive study in which hybrids of *S. mossambicus* and *S. hornorum* were extensively crossed between themselves, and were backcrossed with parents for up to four generations. This theory also explains most of the sex-ratio results obtained by Jalabert et al. (1971). It is noteworthy that a four-chromosome theory was originally suggested by Bellamy (1936) (XX-XY and WZ-ZZ) and modified by Gordon (1946, 1947) (3 sex chromosome theory, X, Y, Z) on the basis of their results on platyfish. This theory was reviewed by different authors (Kosswig and Oktay 1955; Anders and Anders 1963; and Kallman 1965) and was applied to *Sarotherodon* species by Hickling (1960), Chen (1969) and Jalabert et al. (1971) in order to explain the sex-ratio results they obtained in intercrossing these species. Since some of these sex-ratio results could not be explained on the basis of this theory, they all came to the conclusion that an autosomal influence on the sex determination process must be taken into account.

Assuming that autosomes indeed exert an influence on sex determination, the simplest system of sex-influencing chromosomes would consist of three gonosomes (X, W, Y) appearing as a complement of two, in any one of the possible combinations (XX, XY, WX, WW, WY or YY) and a combination of a pair of autosomes (AA, Aa or aa), all involved in primary sex determination. Within each pure species the pair of autosomes would be identical AA or aa. Thus, the complete set of chromosomes influencing sex determination in the pure species was suggested to be AAXX ♀ and AAXY ♂ in *S. niloticus* and *S. mossambicus* (homogametic female and heterogametic male), and aaWY ♀ and aaYY ♂ in *S. aureus* and *S. hornorum* (heterogametic female and homogametic male). The number of genotypes resulting from the combination of autosomes and gonosomes is 18. The sex of all the genotypes was determined on the basis of analysis of the sex ratio results obtained in Chen's crosses (Chen 1969).

The theoretical sex ratios which could be predicted for a cross between any male-female pair are presented in Table 1, where different theoretical sex ratios (♀:♂) of 0:1, 1:3, 3:5, 1:1, 9:7, 5:3, 3:1 and 1:0 can be observed. The sex ratios 3:1, 3:5 and 1:0 have not as yet been observed experimentally.

Table 1. Predicted sex-ratios (female:male) following crosses between males and females with different complements of autosomes (Aa) and gonosomes (WXY) influencing sex determination, AAYY = supermale; framed crosses generate all males (after Avtalion and Hammerman 1978).

		Males							
		AAYY	AaYY	AAWY	AAXY	aaYY	AaWY	AAWW	AaXY
Females	AAWX	0:1	$\boxed{0:1}$	1:3	1:1	$\boxed{0:1}$	3:5	1:1	1:1
	aaWY	0:1	1:3	1:3	1:3	1:1	1:1	1:1	1:1
	AaWW	0:1	1:3	1:3	1:1	1:1	1:1	1:1	5:3
	aaXY	0:1	1:3	1:3	1:3	1:1	1:1	1:1	1:1
	AAXX	0:1	$\boxed{0:1}$	1:1	1:1	$\boxed{0:1}$	1:1	1:0	1:1
	AaWX	0:1	1:3	3:5	1:1	1:1	9:7	3:1	5:3
	aaWW	0:1	1:1	1:1	1:1	1:0	3:1	1:0	3:1
	AaXX	0:1	1:3	1:1	1:1	1:1	5:3	1:0	5:3
	aaWX	0:1	1:1	1:1	1:1	1:0	3:1	1:0	3:1
	aaXX	0:1	1:1	1:1	1:1	1:0	3:1	1:0	3:1

AAYY = supermale; framed crosses generate all males.

Acknowledgments

This work was supported in part by a grant from the National Commission for Research and Development, Israel, and the GKSS & Geesthaght-Tesperhude, Germany. Thanks to Mr. J. Muravich for the excellent photographic work.

Discussion

LOVSHIN: I have an observation on your terms for degrees of maleness: males and supermales. With all-male hybrids in Brazil, we have observed that some fish sit on a nest just like females would and are courted by other males. We thought that we actually had some females and would get spawning, but we never did. There are obviously various degrees of maleness and femaleness, even in the all-male hybrid.

AVTALION: Yes. We have not of course studied this for all the crosses given in our autosomal theory because this would take a lot of time, but I agree that there is a balance between maleness and femaleness.

LOVSHIN: Regarding your theory of sex determination by sex chromosomes and autosomes, can you determine the genotype within a species by electrophoresis?

AVTALION: Not directly by this method. It is better done indirectly by performing crosses and analysis of the sex ratios of the progeny as I have indicated in my paper. Unfortunately, I do not have the facilities for this. Why don't you try out these crosses in America?

JALABERT: Does the quantity of male sex protein in the serum vary with time for a given male?

AVTALION: Yes, it can rise or decrease.

JALABERT: This could be related to sexual activity. Do you see any correlation between the levels of male sex protein and the intensity of sexual activity?

AVTALION: This is going to be tested by Mr. Mires and myself next year.

JALABERT: I think that this is very important.

ROBERTS: Our studies over the last two or three years on electrophoresis of muscle proteins are in agreement with Dr. Avtalion's. We have looked at possibly a wider range of natural populations and compared them with so called pure populations being used for culture. Many of these latter strains are in fact hybrids and we feel that this explains why many people in the past have not been able to repeat Chen and Prowse's work as they have not been using pure lines. We have not been able to make observations on male sex protein but we have found that in any hatchery situation where there is a limited number of females or a limited amount of nest-building area, certain males dominate the rest and adopt the courting habit. If the dominant male is removed from such a family, a new male becomes dominant to replace him. I also wonder about a correlation between male sex protein and dominance.

Tilapia Hybridization

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Tilapia hybrids have demonstrated impressive growout potential using a wide variety of commercial and agricultural by-products as diets. The opportunity of stocking all-male tilapias without prior manual sex separation has tantalized fish culturists for many years. However, all-male tilapia hybrid culture has yet to be accomplished on a large commercial scale. Problems of maintaining pure genetic strains of broodstock and technical problems of producing commercial numbers of all-male tilapia hybrids have limited expansion. Research is needed to determine systems for mass producing all-male tilapia hybrid fingerlings.

When the technology for producing all-male tilapia hybrids on a commercial scale becomes available, culture will likely be limited to governments and wealthy farmers with money to build properly designed hatchery facilities and to hire trained biologists to manage the hatchery.

Introduction

Biologists working with tilapias have been experimenting for many years with methods to reduce or eliminate uncontrolled spawning in growout ponds. One method found to reduce tilapia reproduction is by hybridizing two species of tilapias resulting in offspring that are either all-male or contain a high percentage of males. This paper will attempt to determine the state of hybrid tilapia culture in the world today and to present the major strengths, limitations, and needs of this culture system. Unless otherwise noted, the female parent will appear first in all hybrid crosses.

Hickling (1960) was the first to report the possibility of producing all-male hybrids. He was attempting to produce a sterile hybrid with superior growth potential when he crossed *Sarotherodon mossambicus* with *Sarotherodon hornorum* (this fish was originally classified as *T. mossambica* (Zanzibar strain). To Hickling's surprise and satisfaction, crossing the female *S. mossambicus* with the male *S. hornorum* produced all-male hybrids. The hybrids were not "mules" or sterile but were fertile and capable of reproducing. These results stimulated other scientists to hybridize tilapias in the hope that with a homogametic female (XX) and heterogametic male (XY) and in *S. macrochir* with a heterogametic female (WZ) and homogametic male (ZZ) did not explain the results obtained in some crosses. Jalabert et al. (1971) hypothesized that autosomes were influencing sex determination in some hybrid crosses. Avtalion and Hammerman (1978) theorized that a pair of autosomes compliments the sex-determining chromosomes. Using the sex ratios obtained in Chen's crosses with *S. mossambicus* and *S. hornorum*, they were able to postulate the relative influence of the different chromosomes and the sex of all the genotypes. The sex of each genotype as well as the resulting theoretical sex ratios for all possible hybrid crosses were predicted. It remains to be seen if the autosomal theory of Avtalion and Hammerman holds true when the actual crosses are performed.

Commercial production of all-male hybrids has been difficult to maintain over a long period of time due to contamination of pure broodstock lines resulting in the appearance of varying proportions of females. At this time, there is no way to determine the genotype of tilapia broodstock routinely on a commercial scale. This problem has been especially troublesome in Israel with *S. niloticus* x *S. aureus* hybrids.

Avtalion et al. (1975) suggested electrophoretic comparisons of the blood proteins of broodstock to select pure genetic strains that will produce a high percentage of male offspring. However, this method has not been sufficiently developed to permit determination of the genotype and cannot be claimed as a complete method for ensuring all-male broods at this time.

Hulata et al. (in press) have proposed a system for determining genetically pure strains of *S. aureus* and *S. niloticus* so that all-male hybrids can be consistently produced. The system involves a series of aquarium spawnings of female *S. niloticus* and male *S. aureus* and their reciprocal cross. Those females and males of each species producing the correct male to female hybrid offspring ratios, 100% males for the *S. niloticus* x *S. aureus* cross and 3 to 1 males to females in the *S. aureus* x *S. niloticus* cross, will be mated with the selected individual of the opposite sex of the same species. The pure *S. aureus* male and *S. niloticus* female offspring from the selected matings will then be hybridized. This process will be continued until all-male offspring are consistently produced. The pure line broodstock of *S. aureus* and *S. niloticus* will then be isolated so that contamination will not occur again.

Fingerling Production: Installations and Systems

1. Artificial Environments

The maintenance of pure genetic lines to produce consistently all-male tilapia hybrids is difficult. Control of tilapia spawning and fry raising is often best accomplished in artificial environments: aquaria, concrete tanks, plastic pools, etc. Rothbard and Pruginin (1975) described a technique for induced spawning of *S. niloticus* and *S. aureus* to produce hybrids between the two species. The authors used aquaria that were 200 cm long, 50 cm wide, and 40 cm high in which one male *S. aureus* and 7 to 10 female *S. niloticus* were stocked. Immature fish were used and allowed to mature in the aquaria to form spawning families, which greatly reduced male aggression on the females. Spawning either took place naturally in the aquaria or the eggs were stripped from ripe females and fertilized with milt taken from the male. The eggs were incubated artificially and the young fry were raised in aquaria, concrete tanks, cages or ponds. Maintaining the water temperature between 25 and 29°C and daily artificial illumination of 12 hours permitted year-round spawning.

However, some hybrid crosses are very difficult to perform in aquaria because of male aggression, resulting in the death of the female. Lee (1979) eliminated female mortality in 100-l aquaria, stocked with 1 male and 3 females, by surgically removing the premaxilla of the male fish. The male fish continued his aggressive behavior but he was unable to damage the female without his premaxilla. This technique increased the number of successful aquarium spawnings. Lee also increased the frequency of spawning in female *S. niloticus* and *S. aureus* without decreasing egg production by removing the eggs from the mouths of the females and incubating them artificially. Spawning intervals of females from which eggs where removed were every 13 to 18 days as opposed to every 30 to 60 days for females that mouthbrooded eggs and young.

Lee produced tilapia hybrids by stocking 3 males and 9 females in 3-m diameter plastic pools of 3,500-l with or without a bottom substrate. Hulata et al. (1980) produced a number of tilapia hybrid crosses in 700-l plastic tanks stocked with 1 male and 5 to 10 females using the system described by Rothbard and Pruginin (1975). The *S. niloticus* x *S. hornorum* cross could not be successfully completed in these plastic tanks. However, when 3 males and 10 females were stocked in 4 m^2 concrete tanks, all-male offspring were obtained. I have also been unable to produce the *S. niloticus* x *S. hornorum* hybrid cross in 80-l aquaria or 1000-l cement-asbestos tanks. However, Lee (1979) produced the *S. niloticus* x *S. hornorum* hybrid in 100-l aquaria stocking one male and three females.

The use of artificial systems to produce tilapia hybrids permits control of the environment allowing year-round spawning in temperate climates. Taking the eggs from an incubating female increases the spawning frequency and thus, the number of hybrids that can be produced in a given period of time. Survival of eggs to fry is higher because of controlled conditions and better care. Finally, genetic control is much greater because of the reduced chance of contaminating pure genetic lines. However, some hybrid crosses are difficult to carry out in small, confined environments. There is no conclusive proof that an aquaria or tank-based hatchery will be able to produce commercial numbers of tilapia hybrids economically.

2. NATURAL ENVIRONMENTS

Tilapia hybrids have traditionally been produced in earthen ponds where the environment cannot be controlled and genetic lines are more difficult to maintain. Lovshin et al. (1977) and Lovshin and Da Silva (1975) describe several systems by which earthen ponds can be manipulated to produce and remove hybrid fingerlings and fry.

Lovshin (1980) describes a series of experiments performed in Brazil to determine the best method for producing all-male tilapia hybrid fingerlings by crossing *S. niloticus* x *S. hornorum*. One hundred and forty-two crosses were made over a 6-year period in 350-m^2 earthern ponds. A fingerling production system for use in Brazil was developed from these experiments and is detailed below (Figure 1). Plates 1-3 (see p. 308) illustrate some of the facilities and species in use in Brazil.

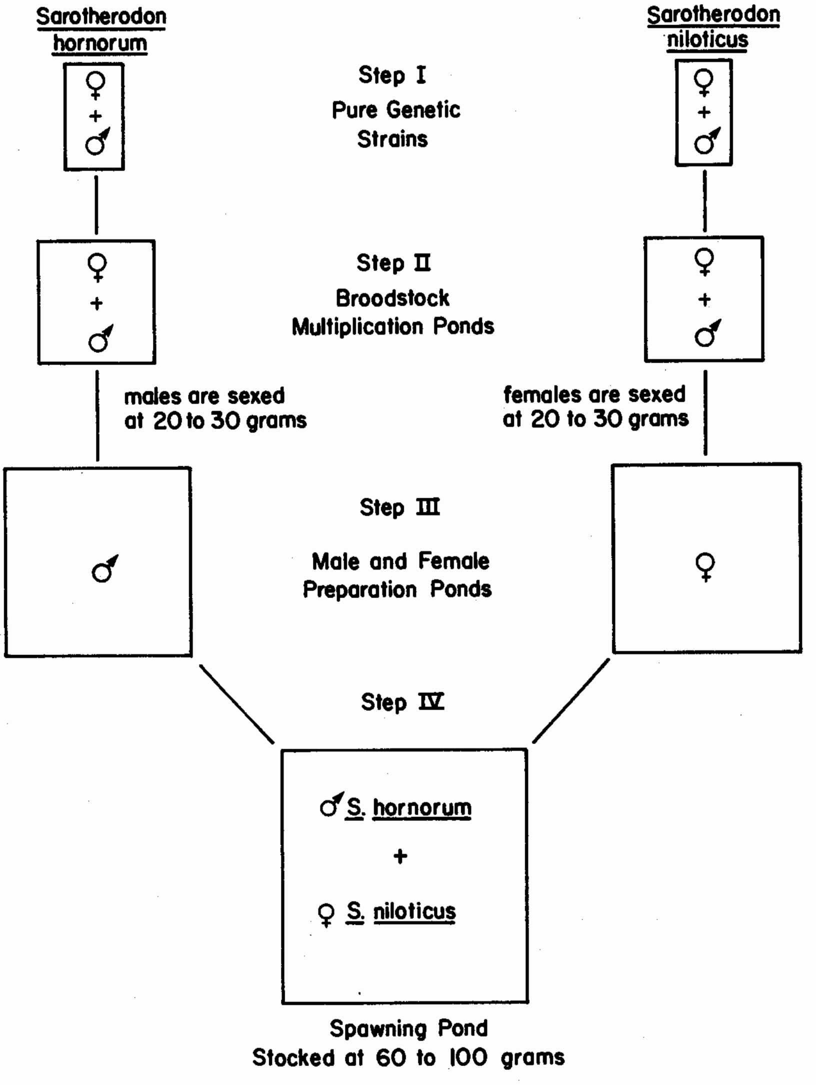

Figure 1. System used for producing all-male tilapia hybrids, *S. niloticus* x *S. hornorum* in Northeast Brazil (after Lovshin 1980).

Pure genetic strains that are known to give 100% male hybrid offspring should be carefully isolated from other tilapia species and hybrids so that contamination does not occur. This point cannot be overstressed, as a major drawback to producing tilapia hybrids is the failure to preserve pure genetic lines over long periods of time. If possible, pure strains should be held in tanks or small ponds isolated from the rest of the hatchery ponds and supplied with water free of natural tilapia populations. Well water would be the ideal water source but surface water can be used if care is taken. In Pentecoste, Brazil, pure stocks of *S. niloticus* and *S. hornorum* have been held for 7 years in 36-m^2 concrete tanks with earthen bottoms supplied with irrigation water. Water entering the tanks passes through several screen filters and a gravel filter before entering the tanks. The tanks are covered with nets to eliminate the entrance of predatory birds and animals. Thus, if at any time contamination of broodstocks is observed, the broodstock production ponds can be drained and restocked with pure strains taken from the concrete tanks.

Pure-line *S. niloticus* and *S. hornorum* fingerlings or adults are stocked into individual earthen spawning ponds to produce the number of broodstock needed to obtain commercial numbers of hybrid fingerlings. When pure *S. niloticus* and *S. hornorum* fingerlings reach 20 to 30 g and are still immature, they are sexed and the female *S. niloticus* and male *S. hornorum* are stocked into broodstock preparation ponds isolated from the opposite sex. If pond facilities are limited, fish can be stocked into cages to mature. Immature female *S. niloticus* and male *S. hornorum* should reach sexual maturity in 2 to 3 months: 60 to 100 g when stocked at 2 to 3/m^2 and fed 5% of their body weight daily. These fish should not be overstocked and should be well cared for so that numerous, healthy gametes are produced.

Mature male *S. hornorum* and female *S. niloticus* with swollen genital papillae are placed in the hybridization pond at the ratio of one male to one female, stocking one female/7 m^2 of pond surface area. The water depth of the spawning ponds should be less than 1 m. The broodstock are fed agricultural by-products (bran and oilseed cake) at 5% of their body weight daily during the hybridization period. After 2.5 months, the spawning ponds are drained and the hybrid fingerlings transferred to a nursery pond where they are stocked at up to 10/m^2 and fed agricultural by-products to attain further growth. Lovshin and Da Silva (1975) recommended that spawning ponds be drained after 3 months to avoid backcrossing with the female *S. niloticus*, but now a 2.5 month spawning period is recommended as mature hybrids have been found before 3 months. When transferring hybrid fingerlings to nursery ponds, a number (25 to 50) of large, sexable fingerlings should be checked to determine whether all-male hybrids have been produced.

Upon draining a hybrid spawning pond female hybrids are sometimes found or an extremely large number of small fry, 1-2 cm in length, that are too small to sex at harvest but contain a high percentage of females when sexed at a later date. The presence of female hybrids is almost always the result of backcrossing between a mature all-male hybrid and female *S. niloticus*: human error. After a 2.5 month spawning period, the pond has to be completely dried to eliminate any small hybrids that may remain. If the spawning pond cannot be dried, the pond should be carefully poisoned.

Every little puddle is a potential hiding place and small fry and fingerlings can live for weeks in a footprint filled with water. Partial pond filling before poisoning facilitates the elimination of fish in many small holes. Screens filtering pond water supplies should be checked daily and repaired when needed. Predatory birds should also be controlled.

Broodstock "families" that have produced sufficient numbers of hybrid fingerlings are immediately transferred to a freshly prepared spawning pond where a new 2.5 month cycle is begun. Broodstock "families" that have not given adequate fingerling numbers are eliminated and new broodstock are used. Broodstock "families" that produce low numbers of hybrid fingerlings in the first spawning cycle will usually produce poorly on subsequent spawning cycles.

Preliminary studies, (Lovshin 1980) have shown that broodstock used for more than one spawning season should be replaced because of declining fingerling production after 3 to 4 hybridization cycles or when the broodstocks are 14 to 17 months old: assuming they were stocked when sexually mature at 5 to 6 months old. The average number of hybrid fingerlings produced in a 350-m^2 pond when 50 female *S. niloticus* are stocked with 50 male *S. hornorum* is approximately 2,700 in 2.5 months.

Berrios-Hernandez (1979) demonstrated that cannibalism by fingerlings on newly hatched fry greatly reduced fingerling production of *S. aureus* in 7-m^2 plastic pools. Partial harvesting of the fry at weekly intervals increased fingerling production 35 times compared with total fingerling harvest after a 4 month spawning period. Initial studies done in Pentecoste, Brazil have not been able to demonstrate an increase in hybrid fingerling production with partial harvesting at 10 day intervals. While cannibalism by fingerlings is an important factor in fry survival in confined environments, it is not known what influence cannibalism has in a larger spawning pond environment. When hybrid spawning ponds are drained, an attempt should be made to grade and stock hybrid fingerlings and fry separately to minimize cannibalism in nursery ponds.

Pretto-Malca (1979) describes a system, similar to that used in Brazil, to produce *S. niloticus* x *S. hornorum* hybrids in Panama. The principal difference is that the all-male hybrid fry are partially harvested at 5 day intervals with a fine mesh seine and transferred to concrete tanks for further growth. The hybrid fry and small fingerlings are graded by size for stocking into separate tanks to reduce cannibalism. The fry are fed zooplankton in the concrete tanks.

Mires (1977) and Morissens (1977) outlined the procedure used in Israel to produce hybrid fingerlings of female *S. niloticus* and male *S. aureus* (Figure 2). The hybrid fingerling production system used in Israel is more complicated and time-consuming than the hybrid fingerling system used in Brazil and Panama because of the temperate climate, lack of genetic purity of the broodstock, and the need to hand-sex the less than 100 percent male hybrid fingerlings. Pure genetic strains of *S. niloticus* and *S. aureus* are selected electrophoretically and the broodstock placed in aquaria to spawn. The pure *S. niloticus* and *S. aureus* fry produced are either raised in the laboratory until reaching 50 g or raised in the laboratory up to 2 to 3 g when they are transferred to earthen ponds for growth to 50 g. After reaching

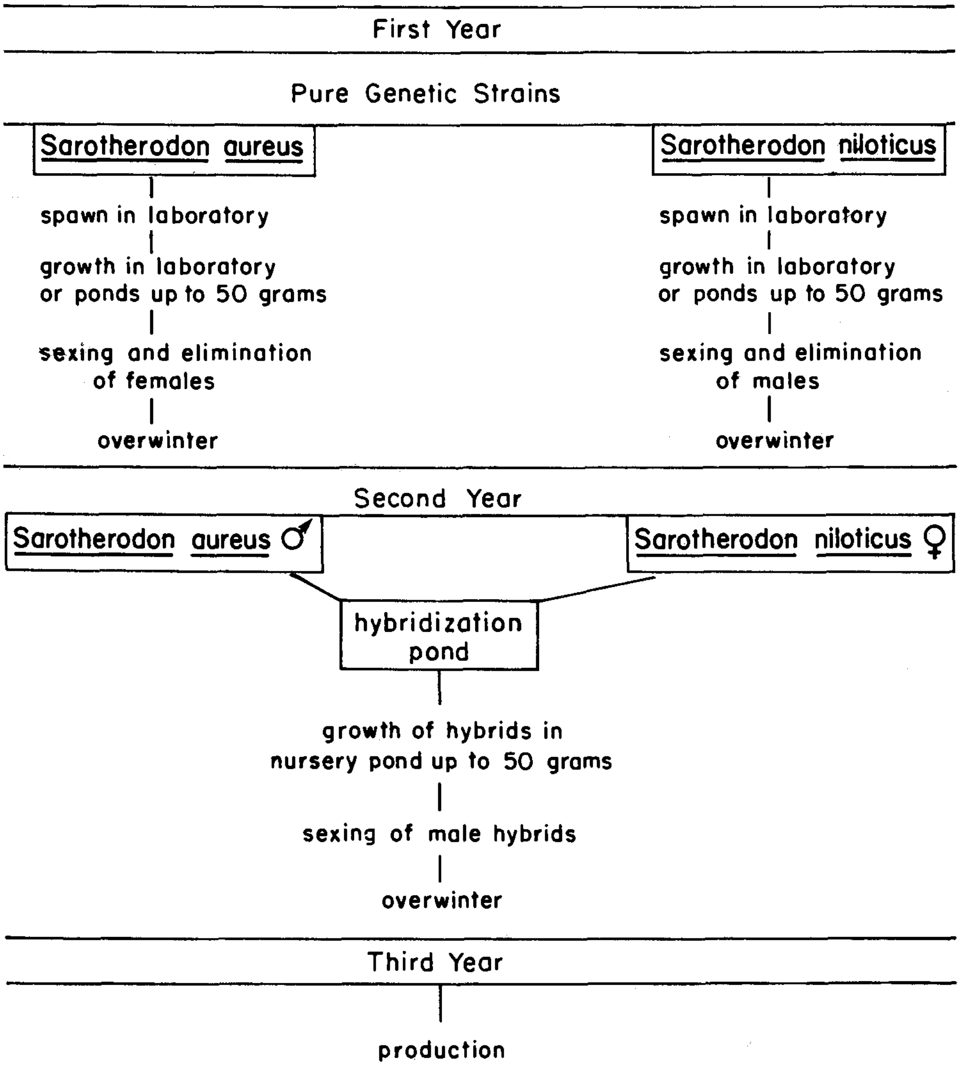

Figure 2. System used for producing tilapia hybrids, *Sarotherodon niloticus* x *S. aureus* in Israel (after Morissens 1977).

50 g, the fish are sexed and only the female *S. niloticus* and male *S. aureus* are kept. Often the female *S. niloticus* and male *S. aureus* are tagged so that they can be identified from wild, unselected tilapia. Selected female *S. niloticus* and male *S. aureus* broodstock are overwintered in deep earthen ponds, small ponds or concrete tanks covered with polyethylene sheets or supplied with heated water. In the spring the selected broodstock are stocked into earthern ponds of approximately 1 ha with a water depth of about 50 cm. The stocking density is 150 to 200 *S. aureus* males with 500 *S. niloticus* females/ha. Mires (pers. comm.) reports that the fish farming kibbutz where he works has doubled hybrid fingerling production by increasing the number of females stocked to 1,000/ha and altering the ratio of females to males to 1:1.

The first harvest of hybrid fingerlings is 1.0 to 1.5 months after stocking the broodstock and is continued at approximately 3 week intervals. The hybrid fingerlings, 1 to 2 g, are harvested with a seine in the feeding areas where the fingerlings concentrate. No mention is made of the length of time the tilapia adults are left in the spawning pond before removal to prevent backcrossing. The small hybrid fingerlings are transferred to nursery ponds and stocked at 30,000/ha. The nursery ponds also serve as growout ponds for carp *(Cyprinus carpio)* adults and fingerlings.

The hybrids are grown until they reach a sexable size of 50 to 100 g. In most cases the percentage of males is not high enough to permit direct stocking into growout ponds so the hybrid fingerlings have to be sexed to eliminate the females. Hybrid males must be overwintered for stocking the following summer in growout ponds. Tal and Ziv (1978) state that the production cost of 50 g hybrid fingerlings in Israel is very expensive: as much as 35% of the market price of the tilapia.

Pruginin (1967) describes a system used in Uganda to produce 100% male hybrids by crossing *S. niloticus* x *S. hornorum*. The need to regularly drain hybrid spawning ponds was a handicap in many areas of Uganda. Also, the handling of small fingerlings during transfer to nursery ponds caused 25 to 30% mortality. To reduce the need for regular draining and transfer of small hybrids to nursery ponds, a pen spawning system was tested. In a 0.2 ha earthen pond, pens measuring 8.8 x 6.0 m were placed in shallow water. The pens were made of welded steel fencing with a 2.5 to 3.5 cm mesh. Each pen was stocked with 8 female *S. niloticus* and 6 male *S. hornorum*. The small hybrid fry were able to pass through the mesh into the spawning pond where they would grow to 30 g before removal. The larger hybrid fingerlings were unable to reenter the spawning pens at maturity so the chances of backcrossing were reduced.

Lovshin and Da Silva (1975) divided a 350-m^2 spawning pond in the shallow end with a fence to form a 100-m^2 enclosure to facilitate the removal of broodstock after the spawning period. The mesh of the fence permitted the hybrid fingerlings to pass out of the spawning area containing the parents. This allowed easy removal of the adults when the spawning pond was lowered. This system worked fine in most cases, but, for each 3.5 month fingerling production period (consisting of 2.5 months of spawning and 1 month of additional growing time) 1 month of spawning time was lost while the fry were growing.

Lovshin and Da Silva (1975) describe a spawning-nursery pond designed to continually produce all-male tilapia hybrids and eliminate the need to handle hybrid fry. Figure 3 shows a modified design that is being built in Brazilian government hatcheries to produce tilapia hybrids. Mature adults are stocked in the 400-m^2 upper spawning pond. When the spawning period has terminated, the dam boards dividing the spawning and nursery units are removed and the water from the spawning pond drains by gravity into the nursery pond carrying hybrid fingerlings and fry. The broodstock are retained in the spawning pond by a screen. Large fingerlings descending from the spawning to nursery pond can be collected with net graders and stocked immediately. Small fingerlings and fry needing more growth before handling pass into the nursery pond. The spawning pond can then be pre-

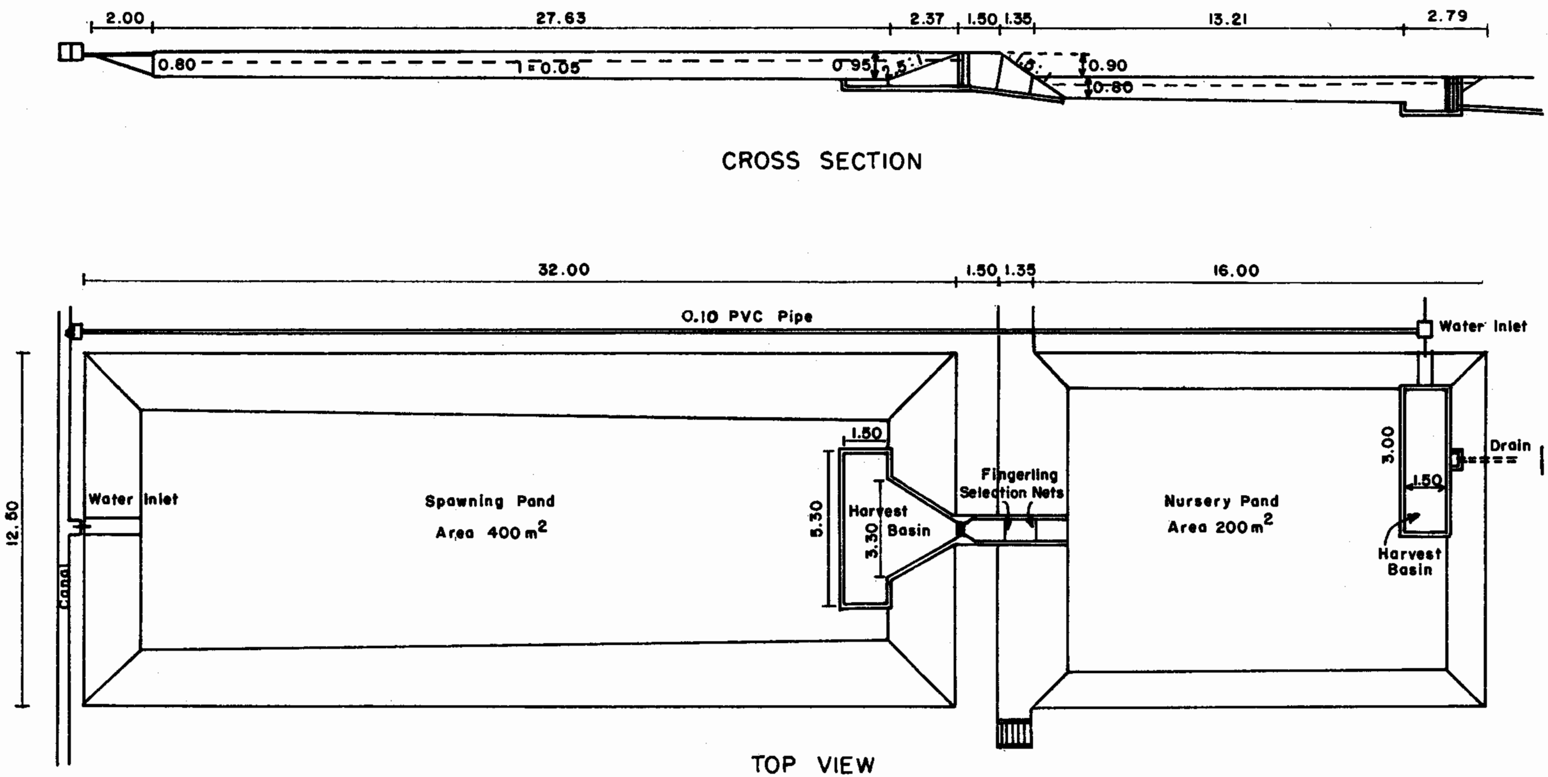

Figure 3. Design of tilapia hybrid spawning-nursery pond used in Northeast Brazil (all measurements in meters).

pared for a new spawning period while the fry are growing in the nursery pond below. These ponds should allow for continual production of tilapia hybrids, increased survival of hybrid fry and fingerlings, reduced amount of labor needed to drain spawning ponds, and conservation of water (as water from the spawning pond can be used to fill the nursery pond). It still remains to be determined if the above advantages will offset the added cost of building these spawning-nursery ponds.

Consistent production of all-male tilapia hybrids in earthen ponds takes more dedication and care than any other tilapia fingerling production system.

Growth

One of the apparent advantages of culturing male hybrids is their increased growth potential. Hickling (1968) notes that male hybrids produced by crossing *S. mossambicus* with *S. hornorum* grew faster than either parent stock. Kuo (1969) compared the growth of hybrids produced by crossing *S. mossambicus* x *S. niloticus*, hybrids of the reciprocal cross, and pure *S. mossambicus* and *S. niloticus* fingerlings in 600-m^2 earthen ponds. The fish were stocked at $1/m^2$, fed a ration of rice bran and peanut cake, and were harvested after 122 days. The daily growth rates of the hybrid of *S. mossambicus* x *S. niloticus*, *S. niloticus* x *S. mossambicus*, pure mixed sex *S. niloticus*, and pure mixed sex *S. mossambicus* were 1.16, 0.85, 0.74, and 0.59 g, respectively. Pruginin (1967) found that the all-male hybrid produced by crossing *S. niloticus* x *S. hornorum* grew 30% faster than mixed sex fingerlings of *S. niloticus* and 40% faster than mixed sex fingerlings of *S. hornorum* over a 126 day growing period. Lovshin et al. (1977) demonstrated that there was no statistical difference in the growth rate between the all-male hybrid of *S. niloticus* x *S. hornorum* and male *S. niloticus* grown separately and in polyculture with supplementary feeding. The all-male hybrid grew an average of 1.6 g/day and male *S. niloticus*, 1.3 g/day. The all-male hybrid demonstrated an 18% growth advantage over the 180-day culture period. Dunseth (1977) compared the growth of the *S. niloticus* x *S. hornorum* all-male hybrid, male *S. niloticus* and male *S. aureus* grown in polyculture with channel catfish, grass carp, and silver carp. No statistical difference was detected between the growth of the 3 male tilapias. However, the tilapia hybrid grew 7% faster (2.8 g/day) than male *S. aureus* (2.6 g/day) and 14% faster than male *S. niloticus* (2.4 g/day) over 160 days.

Pruginin et al. (1975) were unable to demonstrate a difference in growth rate between the hybrids of *S. niloticus* x *S. aureus*, *S. vulcani (S. niloticus)* x *S. aureus* and their parents. Yashouv and Halevy (1967) did not find a significant difference in growth between the *S. niloticus* x *S. aureus* hybrid and pure *S. aureus*.

Hulata (pers. comm.) compared the growth of three tilapia hybrids grown in polyculture with carp. The *S. niloticus* x *S. hornorum* all-male hybrid, *S. mossambicus* x *S. hornorum* all-male hybrid, and the *S. niloticus* x *S. aureus* hybrid (70% males) were stocked into earthen ponds with mirror carp (var. of *Cyprinus carpio*) and cultured for 105 days. The *S. niloticus* x *S. hornorum* hybrid grew the fastest (1.8 g/day) the *S. mossambicus* x *S. hornorum* hybrid at 1.4 g/day and the *S. niloticus* x *S. aureus* hybrid at 1.3 g/day. The results are preliminary as carp mortalities in several ponds may have biased the data. Pruginin (1967) found no significant differences between the growth of all-male hybrids *S. niloticus* x *S. hornorum* and *S. niloticus* x *S. aureus*.

Production

1. MONOCULTURE

Pruginin (1968), working with the all-male hybrid of *S. niloticus* x *S. hornorum* in Uganda, reported yields of 800 kg/ha/year when 1,500 hybrids/ha were stocked. When hybrids were stocked at 8,000/ha the rate of growth up to 50 g did not differ from that of fingerlings stocked at lower rates. After reaching 50 g, hybrid fingerlings previously maintained at high densities were then transferred to growing ponds at a density of 1,000 to 1,500/ha. Under these conditions, the individual weight gain of hybrids was 1.5 to 3.0 g/day to reach 200 to 450 g after 100 to 150 days. It was not stated whether supplementary feeds or fertilizers were used in these trials. Hickling (1962) reported that all-male hybrids produced at Malacca, Malaysia, reached weights of about 550 g in 6 months when stocked at 1,000/ha, giving a total production of 552 kg/ha/6 months from production ponds receiving 1,000 kg/ha of limestone and 22.4 kg of triple superphosphate (TSP)/ha.

Pond experiments in Ivory Coast by Lazard (1973) resulted in the production of 1.396 kg/ha/year of all-male hybrids (*S. niloticus* x *S. hornorum*) using TSP applied at the rate of 13.5 kg/ha every 2 weeks. The fish were stocked at 10,000/ha at an average weight of 2 g and after 180 days reached an average weight of 98 g.

Lovshin et al. (1977) also studied the growth and production of the same all-male hybrid in 355-m^2 earthen ponds in Brazil. Water entering the ponds had a pH of 7.8 to 8.3 and total alkalinity of 140 to 150 mg/l. An early experiment tested three treatments replicated three times each at two levels of stocking, 5,600 and 8,960 fish/ha. The treatments were a control, culture with cattle manure, and culture with supplemental feed (50% castor bean meal and 50% wheat bran) fed at 3% of the fish biomass per day for 6 days/week. Ponds receiving cattle manure were fertilized once a week with 840 kg/ha. Hybrids were stocked at an average weight of 7 g to determine growth during a 253-day period. The average total productions for ponds stocked at 5,600/ha were 300, 804 and 980 kg/ha for the control ponds, manured ponds, and fed ponds, respectively. The corresponding figures for ponds stocked at 8,960/ha were 277, 1,016 and 1,778 kg/ha. The fish grew best in the fed ponds at 8,960/ha: average individual weight, 229 g; feed conversion ratio (FCR), 2.7. The differences in production between the two levels of stocking and between treatments at each level of stocking were significant ($p < 0.05$).

A second experiment was performed using different culture methods (organic fertilizer, inorganic fertilizer and organic fertilizer plus feeding, all ponds stocked with 8,960 fish/ha averaging 21 g over 356 days. Ponds in one treatment received 1,400 kg/ha/week of cattle manure, while ponds in a second treatment were given TSP and ammonium sulfate (AS), each at a rate of 29 kg/ha every 2 weeks. Ponds in the third treatment were fertilized with 1,400 kg/ha/week of cattle manure and also received a ration of 50% castor bean meal and 50% wheat bran fed at 3% of the fish biomass per day, 6 days a week. All treatments were replicated twice. The average total fish productions were: organic fertilizer, 1,341 kg/ha; inorganic fertilizer, 1,856 kg/ha, and organic fertilizer plus supplemental feed, 4,883 kg/ha. The corresponding average final weights of fish were 154 g, 215 g and 565 g. Total production with feeding plus fertilizer exceeded that with inorganic and organic fertilizer by 163% and 264%, respectively. These differences were significant ($p < 0.05$).

Augusto and Melo (cited in Lovshin 1980) tested the effects of AS (20% N), TSP (46% P_2O_5), AS + TSP and no fertilizer (control) on the growth of all-male hybrids *(S. niloticus* x *S. hornorum)* in 355-m^2 ponds for 190 days. The AS and TSP treatments were replicated three times while the AS + TSP treatment and the control were replicated twice. Ponds in the AS and TSP treatments received equal amounts of N and P_2O_5 (280 g per application). Ponds in the AS + TSP treatment received half this amount (140 g per application) so that the total amount of N plus P_2O_5 applied was equivalent to 280 g. Ponds fertilized with AS or TSP received 1.42 kg/pond application (40 kg/ha) and 0.61 kg/pond application (17 kg/ha), respectively. Ponds receiving both fertilizers had 0.76 kg/pond application of AS (20 kg/ha) and 0.31 kg/pond application of TSP (8.7 kg/ha). Ponds were fertilized every 15 days by placing the fertilizer on a platform located 20 cm below the water surface. All fertilized ponds received an initial application of fertilizer 15 days before fish were stocked. Ponds were stocked with fish averaging 20 g at 10,000/ha. The average productions of the control, TSP, AS + TSP and AS treatments were 350, 832, 977 and 1,016 kg/ha, respectively. Fertilizers increased the total production two to three times that of the control. TSP alone was not as effective as AS alone or the combined treatment.

Paiva et al. (cited in Lovshin 1980) tested the growth of the same all-male hybrid fed three types of agricultural by-products found in northeast Brazil. Nine 355-m^2 earthen ponds were stocked with 400 fish (i.e., 11,250/ha), average weight 15 g. Castor bean meal (30% protein), babacu cake (a palm nut with 21% protein), and cottonseed cake (21.5% protein) were fed daily at 3% of the average biomass of fish in each treatment 6 days a week. Feeding rates were recalculated monthly based on seine samples. Treatments were replicated three times in a random block design. The culture period was 238 days. The average total fish productions for castor bean meal, babacu cake, and cottonseed cake were 3,444, 2,605, and 2,264 kg/ha, respectively. These differences were significant ($p < 0.05$). Fish fed castor bean meal were heavier at harvest (323 g) than fish fed babacu (245 g) or cottonseed cake (239 g), but there was no significant difference between fish fed babacu and cottonseed cake. FCR's for castor bean meal, babacu cake, and cottonseed cake were 2.4, 2.6, and 2.7, respectively.

Brazilian biologists (cited in Lovshin 1977) investigated the growth and production of the same all-male hybrid at higher stocking levels over a 367-day culture period in 350-m^2 earthen ponds, with no replication (Table 1). The fish were fed a ration of 50% babacu cake and 50% cottonseed cake at 5% of pond fish biomass/day, 5 days a week. Feeding rates were recalculated each month based on pond seine samples. Each pond was fertilized with a total of 19 kg (540 kg/ha) of both TSP and AS applied at 2-week intervals over the first 7 months of the experiment. Productions were the highest yet obtained in research with hybrid tilapia in Brazil: very impressive considering that only vegetable materials were fed to the fish. Increasing the stocking rates had a positive effect on production without greatly reducing growth. Feed conversion was good up to 6 months, average at 10 months and poor at 12 months. From the tenth month until harvest, FCR's increased sharply because of extremely poor water quality and high standing crops. The maximum feeding rate was 20 kg/pond (564 kg/ha) in the pond stocked at the rate of 31,000 fish/ha.

Da Silva and Lovshin (cited in Lovshin 1977) tested the culture of the same all-male hybrid in conjunction with the fattening of pigs in Pentecoste, Brazil. Three ponds of 1,000-m^2 were stocked with 25 g hybrid fingerlings at the rate of 8,000/ha. One pig sty was constructed on the margin of each pond and 7 pigs (70/ha of pond water) averaging 17 kg were placed in each sty. The pigs were not allowed to enter the ponds. The sties were cleaned daily and all waste products washed into the ponds. The pigs were fed a daily ration of 5% of their body weight consisting of 35% manioc, 20% wheat bran, 15% corn, 15% babacu cake, and 20% grass. The ration contained 10% protein. After 189 days, 1,490 kg/ha of fish were harvested averaging 205 g. The pigs averaged 60 kg each. The FCR for the pigs was 7.1 and 5.9 for combined pigs and fish production.

Da Silva et al. (unpublished data) carried out a second experiment to study the performance of the all-male hybrid with a waste loading equivalent of 120 pigs/ha of pond water. Hybrids averaging 29 g were stocked in three 1,000-m^2 ponds at the rate of 10,000/ha and received only the organic wastes washed daily into the ponds from adjacent pig sties. The pigs were fed a daily ration of 5% of their body weight consisting of 24% babacu cake, 45% corn, 5% meat meal, 25% elephant grass, and salt. After 180 days, 2,800 kg/ha of fish were harvested averaging 272 g. FCR for the pigs was 7.6 and 5.5 for combined pig and fish production.

Da Silva et al. (cited in Lovshin 1977) carried out a third experiment with six pigs per sty (60/ha of pond water), fed a daily ration of corn, babacu cake, meat meal, and grass (i.e. 11.6% total protein) at 5% of their body weight. Three 1,000-m^2 ponds were stocked with 10,000 fish/ha averaging 31 g. The fish were fed cottonseed cake at 2% of their body weight/day, 6 days a week. Wastes from the pig sties were washed into the ponds daily. After 193 days, 3,043 kg/ha of fish were harvested averaging 304 g. The FCR for pigs was 6.4 and the FCR for cottonseed cake to fish was 1.7.

Da Silva et al. (cited in Lovshin 1977) stocked three 1,000-m^2 ponds with 25 g hybrid fingerlings at 8,000/ha. The ponds were fertilized with 50 kg/wk (500 kg/ha/wk) of chicken manure taken from a commercial

Table 1. Summary of the results of culture experiments in Brazil in which all-male tilapia hybrids (*Sarotherodon niloticus* ♀ x *S. hornorum* ♂) were stocked at different levels in 350-m^2 earth ponds and grown for 367 days. The figures are from single ponds. Source: various Brazilian biologists cited in Lovshin (1977).

	Stocking level (fish/ha)									
	13,000	15,000	17,000	19,000	21,000	23,000	25,000	27,000	29,000	31,000
Fish stocked/pond	455	525	595	665	735	805	875	945	1,015	1,085
Average initial weight (g)	25	27	26	38	22	22	23	23	25	25
Average final weight (g)	452	466	495	456	492	384	444	416	353	410
Production/pond (kg)	197	245	279	303	354	309[a]	371	375	356	419
Production/ha (kg)	5,629	7,000	7,971	8,657	10,114	8,828	10,599	10,714	10,171	11,971
Survival (%)	96	100	95	100	98	100	96	95	99	94
Feed conversion ratio at 6 months	3.3	2.8	2.7	3.2	2.4	2.8	3.3	3.0	3.0	2.7
Feed conversion ratio at 10 months	4.5	4.6	4.0	4.5	4.4	4.1	3.8	4.2	4.3	3.7
Feed conversion ratio at 12 months	6.0	6.3	6.2	6.2	6.2	6.7	5.9	6.2	6.3	6.2
Ration fed/pond (kg)	1,124	1,465	1,648	1,732	2,093	1,947	2,074	2,168	2,067	2,413

[a]Included are 62 kg of fish that died due to poor water quality 2 days before harvest.

Table 2. Summary of results obtained with the all-male tilapia hybrid (*Sarotherodon niloticus* ♀ x *S. hornorum* ♂) cultured with organic and inorganic fertilizers and rations in the northeast of Brazil.

Stocking rate/ha	Fertilizer	Fish ration	Average stocking wt (g)	Average final wt (g)	Net yield kg/ha	Conversion ratio	Growth g/day	Net yield kg/ha/day	Culture period (days)
5,600	control	—	7	58	288		0.2	1.1	253
5,600	Cow manure 840 kg/ha/wk	—	7	166	264	36	0.6	3.0	253
5,600		50% wheat bran, 50% castor bean meal, 3% body weight/d	7	185	941	2.7	0.7	3.7	253
8,960	— control	—	8	36	179		0.1	0.7	253
8,960	Cow manure 840 kg/ha/wk	—	7	148	927	30	0.6	3.7	253
8,960	—	50% wheat bran, 50% castor bean meal, 3% body weight/d	7	229	1,680	2.7	0.9	6.6	253
8,960	Cow manure 1,400 kg/ha/wk	—	22	154	1,159	50	0.4	3.3	356
8,960	TSP[1]-29 kg/ha/15 d AS[2]-29 kg/ha/15 d	—	22	215	1,660		0.7	4.7	356
8,960	Cow manure, 1,400 kg/ha/wk	50% wheat bran, 50% castor bean meal, 3% body wt/d	20	565	4,760	3.6	1.6	13.4	356
10,000	control	—	20	43	151		0.1	0.8	192
10,000	TSP-17 kg/ha/ 15 d	—	19	101	644		0.4	3.4	192
10,000	AS-40 kg/ha/15 d	—	19	118	829		0.5	4.3	192
10,000	TSP-8.7 kg/ha/15 d	—	20	122	778		0.5	4.0	192
10,000	TSP-56 kg/ha/15 d AS-56 kg/ha/15 d	Rice bran, 3% body wt/d	60	340	1,648	2.8	1.6	14.7	180
11,250	—	Castor bean meal, 3% body wt/d	15	323	3,276	2.4	1.3	13.8	238
11,250	—	Palm nut cake, 3% body wt/d	14	245	2,447	2.6	1.0	10.3	238
11,250	—	Cottonseed cake, 3% body wt/d	15	239	2,095	2.7	0.9	8.8	238
15,000	TSP-540 kg/ha/yr AS-540/kg/ha/yr	50% palm nut cake	27	466	6,578	6.3	1.2	17.9	367
21,000	TSP-540 kg/ha/yr AS-540/kg/ha/yr	50% palm nut cake, 50% cottonseed cake, 5% body wt/d	22	492	9,627	6.2	1.3	26.2	367
25,000	TSP-540 kg/ha/yr AS-540/kg/ha/yr	50% palm nut cake, 50% cottonseed cake, 5% body wt/d	23	444	10,000	5.9	1.1	27.2	367
31,000	TSP-540 kg/ha/yr AS-540/kg/ha/yr	50% palm nut cake, 50% cottonseed cake, 5% body wt/d	25	410	11,169	6.2	1.0	30.4	367
8,000	70 pigs/ha of water		25	205	1,290		1.0	6.8	189
10,000	120 pigs/ha of water		29	272	2,510		1.4	13.9	180
10,000	60 pigs/ha of water	cottonseed cake, 2% fish body wt/d	31	304	2,733	1.7	1.4	14.2	193
8,000	Chicken manure, 500 kg/ha/wk		25	186	1,150	10	0.9	6.1	189

[1]TSP = Triple Superphosphate
[2]AS = Ammonium Sulfate

chicken farm. The chicken manure was 79% organic matter. After 189 days, an average of 1,350 kg/ha of fish were harvested, averaging 186 g. The FCR for chicken manure to fish was 10. A summary of research results performed on the all-male tilapia hybrid in northeast Brazil is found in Table 2.

Collis and Smitherman (1978) raised all-male *S. niloticus* x *S. hornorum* hybrids in 400-m^2 ponds in Auburn, Alabama. Fish averaging 29 g were stocked at 10,000/ha. Three ponds were each fertilized with the equivalent of 28,381 kg/ha of fresh cattle manure (5,392 kg of dry matter) divided into daily applications over a 103-day culture period. Fish in three other ponds were fed a commercial catfish diet (36% protein) at 3% of their body weight per day. The average net productions in the manured and fed ponds were 1,646 and 2,663 kg/ha, respectively. The corresponding average fish weights at harvest were 200 g and 318 g. The FCR's for manure and catfish diet on a dry matter basis were 3.3 and 1.3.

Lovshin et al. (unpublished data) studied the effect of introducing *S. niloticus* females and the resulting recruitment on the growth and production of all-male *S. niloticus* x *S. hornorum* hybrids. Nine 350-m^2 earthen ponds were stocked with 10,000 all-male hybrids/ha averaging 11 g. Three ponds were then stocked with an additional 2.5% female *S. niloticus* and 3 other ponds with an additional 5% female *S. niloticus*. The female *S. niloticus* averaged 16 g. The fish were fed agricultural by-products at 5% of the body weight of the hybrids per day, 6 days a week over a 273-day culture period. Seine samples were taken monthly to determine the growth of the hybrids and recalculate feeding rates. The average weights of the hybrids from the 100% male, 2.5% female, and 5% female treatments were 481 g, 218 g, and 285 g, respectively. The corresponding average productions of all-male hybrids were 4,286, 1,809 kg/ha and 2,186 kg/ha. *S. niloticus* recruits increased the total fish production in the 2.5% female and 5% female treatments to 4,309 and 5,451 kg/ha, respectively. The growth of all-male hybrids was equal in the three treatments until the fifth month when the 100% male treatment showed a distinct advantage. It was possible to produce a 200-g fish in 6 months in the all-male treatment, but 7 months were required in the two treatments with females. While the 100% male treatment showed a significant difference ($P < 0.05$) in hybrid growth and production compared with the treatments containing females, harvestable hybrids were still obtained in the treatments with tilapia recruitment.

Greenfield et al. (1977) demonstrated the profitability of raising all-male hybrids using agricultural by-products as feeds in Northeast Brazil.

2. POLYCULTURE

In Israel, Tal and Ziv (1978) state that the majority of *S. niloticus* x *S. aureus* hybrids are raised in polyculture with common and silver carp. The tilapia assume the role of a pond cleaner, maintaining the water in good culture condition by consuming organic material and waste feeds that would otherwise decompose and pollute the pond environment. In most cases, the tilapia are able to increase total fish production without significantly reducing growth or production of the other species. The tilapia hybrids are normally 30 to 50% of the total fish population and their yield is 20 to 30% of the total.

In Brazil, Lovshin et al. (1977) tested the culture of the *S. niloticus* x *S. hornorum* all-male hybrid with mirror carp *(Cyprinus carpio)* to determine whether the addition of mirror carp would increase total fish production. Mirror carp raised alone were stocked at 2,240/ha, tilapia hybrids in monoculture at 8,960/ha and tilapia hybrids and mirror carp combined at 8,960/ha and 1,400/ha, respectively. All ponds received applications of cattle manure at 1,400 kg/ha/wk for 5 months after which applications were suspended. Rice polishings were fed throughout the 245-day culture period at 3% of the body weight of fish/day, 6 days a week. At harvest the average productions were: carp alone, 812 kg/ha; tilapia hybrids alone, 3,993 kg/ha and combined culture, 3,567 kg/ha. There were no significant differences in total production ($P < 0.05$) between treatments with the tilapia hybrid alone and the combined hybrid-carp cultures. However, these two treatments both produced significantly more harvestable fish than with carp alone. Moreover, the combined culture averaged 105 kg/pond of tilapia hybrids and carp raised on 295 kg of feed, while 108 kg of tilapia hybrids stocked alone required 441 kg of feed. Thus, less feed was required to raise an equal weight of hybrids and carps than was needed to raise hybrids alone. The average weight of tilapia hybrids raised with carp was 285 g, while that of the hybrids cultured alone was 353 g.

Da Silva et al. (1978) studied the influence of the all-male tilapia *(S. niloticus* x *S. hornorum)* in combined culture with tambaqui *(Colossoma macropomum)* a fruit-eating characid native to the Amazon River. Six 355-m^2 ponds were stocked with 25 g tambaqui at the rate of 5,000/ha. Three of the ponds were stocked with an additional 5,000 all-male tilapia hybrids per hectare, with an average weight of 18 g. The fish were fed daily on a pelleted chicken ration (17% protein) at 3% of the average body weight of tambaqui only in the afternoon, 6 days a week for 365 days. Feeding rates were recalculated monthly based on seine samples. The monoculture of tambaqui produced an average of 6,683 kg/ha with fish averaging 1.50 kg. The FCR was 2.8. The combined culture produced an average of 5,640 kg/ha of tambaqui averaging 1.20 kg and 3,299 kg/ha of tilapia hybrids averaging 0.75 kg. The FCR for the combined culture was 1.8. The addition of tilapia hybrids increased fish production by a total of 2,256 kg/ha compared to the monoculture of tambaqui without increasing the quantity of feed or the worsening the FCR.

To further test the influence of the all-male tilapia hybrid on tambaqui culture, Da Silva et al. (unpublished data) stocked the equivalent of 10,000 tambaqui per hectare together with 3,000, 4,000, and 5,000 all-male *(S. niloticus* x *S. hornorum)* hybrids/ha in 355-m^2 ponds. Each tilapia hybrid stocking rate was replicated three times. The average initial weights of the tambaqui and tilapia hybrids were 39 g and 13 g, respectively. The fish were fed a pelleted chicken ration (17% protein) at 3% of the average body weight of tambaqui in each treatment/day, 6 days a week for 360 days. Feeding rates were recalculated monthly based on seine samples.

The average tambaqui productions were 7,453, 7,201 and 7,779 kg/ha, with average weights of 760, 785 and 770 g for the 3,000, 4,000, and

5,000 all-male tilapia treatments, respectively. The corresponding tilapia productions were 2,224, 3,045, and 3,327 kg/ha with average weights of 770, 725 and 702 g and the total average productions were 9,677, 10,246 and 11,106 kg/ha. The FCR's for combined tambaqui and tilapia production were 3.4, 3.2 and 2.9. Increasing the stocking rates of the tilapia hybrid therefore increased the total fish production per pond without significantly affecting the growth or production of tambaqui. A summary of research results performed with tambaqui and the all-male tilapia hybrid can be found in Table 3.

Miscellaneous Aspects

1. Cold Tolerance

Chervinski and Lahav (1976) demonstrated that *S. aureus* native to Israel was more cold tolerant than *S. niloticus* introduced from Africa. The hybrid produced by crossing *S. niloticus* x *S. aureus* was as cold tolerant as *S. aureus*. *S. aureus* and the *S. niloticus* x *S. aureus* hybrid began dying at 9°C while *S. niloticus* died at 11°C.

Lee (1979) tested the cold tolerance of *S. aureus*, *S. niloticus*, *S. hornorum*, and their hybrids. All fish tested were acclimated to 21°C and the temperature was decreased about 0.8°C/hr until 50% mortality was recorded. For the purebred fish, *S. aureus* had the lowest thermal tolerance limit (6.7°C) and *S. hornorum* the worst (10°C). The cold tolerance limits of hybrids of *S. aureus* x *S. niloticus* were not significantly different ($P > 0.05$) from the pure *S. aureus* but they were significantly more cold tolerant than pure *S. niloticus* and the *S. niloticus* x *S. hornorum* hybrid. These results suggest that cold tolerance is a specific attribute of *S. aureus* and is probably transmitted to its hybrids.

2. Catchability

Lovshin et al. (1977) mentioned that the *S. niloticus* x *S. hornorum* all-male hybrid is easy to seine like its male parent *S. hornorum*, whereas *S. niloticus* is very difficult to seine and lies on its side in the bottom mud as the seine passes over.

Dunseth (1977) tested the catchability of male *S. aureus*, male *S. niloticus*, and the *S. niloticus* x *S. hornorum* all-male hybrid in replicated seine trials in 400 m^2 ponds. An average of 2% of the populations of male *S. niloticus* and *S. aureus* could be caught in the first seine haul. However, 50% of the all-male hybrid population was caught in the first seine haul.

Discussion

1. Fingerling Production

Fingerling production is a major constraint to commercial culture of tilapia hybrids, especially where 90 to 100% males are required. Maintaining pure genetic strains that give a high percentage of male hybrids takes great care and dedication on the part of hatchery workers. Large earthen ponds are not ideal units for holding pure genetic lines. Small, controllable earthen ponds, fiberglass, or concrete tanks are preferred.

A small number of pure broodstock couples can produce enough fingerlings to initiate even a large earthen pond tilapia hybrid fingerling production operation. If or when the stocks become contaminated, they can be eliminated and pure genetic lines reintroduced. Facilities for producing hybrids should be laid out so that ponds containing pure tilapia broodstock are isolated from each other as well as from hybrid spawning ponds. Hybrid nursery ponds should also be isolated from hybrid spawning ponds. In essence, at least three groups of fish are involved in any hybrid hatchery operation: the two parental stocks and the progeny. Care should be taken to eliminate any contact between groups except in the spawning ponds.

It is my opinion that the primary obstacle to producing commercial numbers of all-male tilapia hybrids is the low number of progeny produced per spawning. In Brazil, an average of 2,763 all-male hybrids were produced in 2.5 to 3.0 months when 50 female *S. niloticus* were stocked with 50 male *S. hornorum* in a 350-m^2 pond. It seems reasonable to assume that the average number of eggs produced per female was about 400. Thus, if survival of eggs to fingerlings was 100%, about 7 female *S. niloticus* spawned i.e. 14% of the females stocked. Even if the survival of eggs to fingerlings was not 100%, it seems unlikely that more than 20% of the females spawned. This, moreover, assumes that a female spawned only once per spawning period. If some of the females were able to spawn more than once then the percentage of spawning females would have been even less.

It appears at first glance that the number of hybrid fingerlings produced is small because the females are dying during some stage of development: hence the all-male survival. However, Hickling (1960) and Lee (1979) proved this to be untrue; females that spawn produce normal numbers of hybrid offspring. Lovshin (unpublished data) demonstrates that there is a relation between the number of females stocked in a 350-m^2 spawning pond and the number of hybrid fingerlings produced per female (Table 4). These data were collected over a 6-year period and do not consider the size of the female *S. niloticus* stocked, the variation in ratio of *S. hornorum* to *S. niloticus* stocked, or length of the spawning period (which varied from 71 to 111 days). The fewer the female *S. niloticus* per unit area of spawning pond the greater the number of hybrid fingerlings produced, calculated on a per female basis. Thus, it appears that the percentage of females that actually spawn increases with a decrease in the stocking density of females. It is not known why this happens. Increasing the stocking density of females increased the number of hybrids produced up to a value of 1 ♀/7 m^2, but further increases up to 1 ♀/4.7 m^2 and 1 ♀/3.5 m^2 failed to give hybrid increases. There appears to be some behavioral or chemical factor present that reduces the compatibility of female *S. niloticus* and male *S. hornorum* so that at high densities of female and/or male broodstock the percentage of females that will spawn is greatly reduced. The role of the male *S. hornorum* and the impact that surplus males or *S. niloticus* females may have on male territorial and sexual behavior must be considered. The densities of males given in

Table 3. Summary of results obtained culturing tambaqui, *Colossoma macropomum*, in monoculture and polyculture with the all-male tilapia (T.) hybrid (female *Sarotherodon niloticus* x male *S. hornorum*).

Species	Stocking rate/ha	Ration	Average stocking wt (g)	Average final wt (g)	Net yield kg/ha	Conversion ratio	Growth g/day	Net yield kg/ha/day	Culture period days
Tambaqui	5,000	Pelleted chicken ration (17% protein) 3% of body wt/d	25	1,496	6,558	2.8	4.0	18.0	365
Tambaqui	5,000	Pelleted chicken ration (17% protein) 3% of body wt/d of tambaqui only	25	1,189	5,515	2.8	3.2	15.1	365
T. hybrid	5,000		18	748	3,209		2.0	8.8	365
combined	10,000				8,724	1.8		23.9	
Tambaqui	10,000	Pelleted chicken ration (17% protein) 3% of body wt/d of tambaqui only	39	760	7,063	4.4	2.0	19.6	360
T. hybrid	3,000		15	770	2,179		2.1	6.1	360
combined	13,000				9,242	3.4		25.7	
Tambaqui	10,000	Pelleted chicken ration (17% protein) 3% of body wt/d of tambaqui only	36	785	6,841	4.7	2.1	19.0	360
T. hybrid	4,000		10	725	3,005		2.0	8.3	360
combined	14,000				9,846	3.2		27.3	
Tambaqui	10,000	Pelleted chicken ration (17% protein) 3% of body wt/d of tambaqui only	42	770	7,359	4.1	2.0	20.4	360
T. hybrid	5,000		12	702	3,267		1.9	9.1	360
combined	15,000				10,626	2.9		29.5	

Table 4. The effect of female *Sarotherodon niloticus* stocking density on the production of all-male hybrid fingerlings (*S. niloticus* x *S. hornorum*) in 350-m^2 ponds in Brazil over periods ranging from 71 to 111 days (after Lovshin 1980).

	Number of female *S. niloticus* in the spawning pond, i.e.,/350 m^2						
	6	10	15	25	50	75	100
No. of replicates	5	9	6	27	61	17	9
No. of male *S. hornorum*/pond	3	5	10	5-50	10	15	20
Average no. of fingerlings produced/pond	2,117	2,350	1,643	1,475	2,763	2,167	1,502
Range of the average no. of fingerlings produced	580 to 3,619	93 to 3,639	821 to 2,439	0 to 7,149	0 to 8,443	473 to 5,295	607 to 2,526
Average no. of fingerlings per female	353	235	110	59	55	29	15
Estimated no. of females spawning[a]/pond	5	6	4	4	7	5	4
Estimated % of females spawning	83	60	27	16	14	7	4

[a]Assuming 400 eggs per spawn, 100% survival of eggs to fingerlings, and females spawned only once in each spawning period.

Table 2 do not appear excessive for 350-m^2 ponds. Note should also be taken of the large variation in hybrid fingerlings produced when the same density of females is used (Table 4), especially the zero figures.

To what extent reduced fingerling production exists in other hybrid crosses is not known. Tal and Ziv (1978) state that the production of *S. niloticus* x *S. aureus* hybrids is much lower than from single-species crosses. Lessent (1968) also had problems obtaining all-male hybrid fingerlings by crossing *S. macrochir* x *S. niloticus* in ponds. However, Hickling (1960) stated that he had little problem producing *S. mossambicus* x *S. hornorum* all-male hybrid progeny in ponds.

I have observed many cases of the all-male hybrid of *S. niloticus* x *S. hornorum* backcrossing with the female *S. niloticus*. In a pond containing female *S. niloticus*, male *S. hornorum*, and the all-male hybrid, the fingerlings produced are fathered almost exclusively by the all-male hybrid. The sexual behavior of the all-male hybrid appears to present fewer compatibility barriers with the female *S. niloticus* than the male *S. hornorum*.

Whatever the causes, the low numbers of fingerlings produced and the level of technology needed for pure-strain maintenance place restrictions on the commercial culture of the *S. niloticus* x *S. hornorum* hybrid. It is my opinion, based on present knowledge, that the culture of all-male hybrid tilapias is not to be recommended for the majority of farmers in tropical developing countries where the financial resources to construct properly designed hatcheries and hire qualified hatchery staff are lacking. Contamination of pure genetic strains of tilapia broodstock and backcrossing in spawning ponds are likely to occur. The governments in most tropical developing countries do not have the money to build and staff hybrid tilapia hatcheries to produce and distribute the fingerlings needed to culture this fish on a wide scale. In most cases, for tilapia culture to have a wide economic and nutritional impact in a country, the private sector has to become involved in fingerling production.

It is my opinion that some system of culturing a pure tilapia species is better suited to most developing countries because the production of pure species fingerlings can be accomplished with few problems by most farmers.

2. GROWOUT

If the low production of fingerlings is the major disadvantage in culturing all-male tilapia hybrids then the growout of hybrids to marketable size is the major advantage. Stocking all-male tilapia without having to hand-sex is very advantageous. The hybrids grow rapidly and uniformly when fed a wide range of commercial and agricultural by-product diets. The addition of chemical or organic fertilizers to pond water further increases production and improves food conversion efficiency. Most tilapia hybrids are resistant to disease and to low levels of dissolved oxygen. This allows high rates of feeding and fertilizing resulting in elevated productions.

The culture of tilapia hybrids that are less than 100% male can also be very profitable depending on the percentage of males and the size of the fish to be marketed. Fish of about 200 g can be raised in 6 to 7 months with feeding or addition of organic fertilizer even if a small percentage of females are present. If larger fish (⩾ 400 g) are needed, then additional hand-sexing or a predatory fish may have to be stocked with the less than 100% male hybrids to control recruitment and allow a longer growing period.

3. The Evaluation of Tilapia Hybrids

The evaluation of hybrids for culture performance is not easy because few comparative data on fingerling production and growout are available. Only two crosses, *S. niloticus* x *S. hornorum* and *S. mossambicus* x *S. hornorum* are known to consistently produce all-male offspring. The male *S. hornorum* appears to be the most dependable male parent of 100% male tilapia offspring. Several other crosses will, however, produce more than 75% males consistently.

The maintenance of pure genetic lines is easier for some hybrid crosses than for others. The *S. niloticus* x *S. hornorum* hybrid, when 10 to 15 cm long, is relatively easy to distinguish from either parent on physical appearance alone by a trained biologist. Differences in physical appearance allow hatchery workers to easily determine the presence of contaminated broodstocks or mature hybrids in spawning ponds. The hybrids produced by crossing *S. mossambicus* x *S. hornorum* and *S. niloticus* x *S. aureus* are difficult to distinguish from their parents even by the trained eye. The chances of pure broodstock becoming contaminated with these hybrids are therefore increased. However, it is known that female *S. niloticus* crossed with male *S. hornorum* produces a low number of hybrid offspring. *S. hornorum* and *S. mossambicus* are close relatives as are *S. niloticus* and *S. aureus.* These pairs of species have similar reproductive behavior and coloration which may result in increased spawning and hybrid fingerling production, than, for example, *S. hornorum* with *S. niloticus.*

In countries where winter temperatures are low enough to threaten the survival of tilapias, hybrids with *S. aureus* as a parent should be considered because of their superior cold tolerance.

Future Research Needs

Fingerling production is the area in most need of research. If all-male hybrid tilapia culture is going to have an increased impact, then improved methods of consistently and economically producing all-male hybrid fingerlings on a commercial scale will have to be worked out.

A further pressing need is for information concerning the genetics, reproductive behavior and physiology of tilapias in relation to hybridization. What exactly is the genetic mechanism that produces all-male progeny from some crosses? Why are reduced numbers of fingerlings produced in some hybrid crosses when compared with pure species fingerling production? What are the visual and/or chemical cues which determine spawning compatibility between species? What other factors may be influencing the frequency with which two tilapia species hybridize? Does close taxonomic proximity of two species to be hybridized mean similar spawning behavior resulting in increased spawns and hybrid fingerlings?

Fish culture researchers have traditionally tried to answer these questions with practical research that often solved the problem without explaining why the result was obtained. Seven years of such work with the *S. niloticus* x *S. hornorum* hybrid has not provided the required increase in hybrid fingerling numbers on which to base large commercial cultures. I believe that the answer, if one exists, is to be found in basic research by knowledgeable behavioralists and physiologists aimed at understanding the barriers to tilapia hybridization and then discovering methods to overcome them.

Further investigation is needed to determine the best installations for producing tilapia hybrids. What are the comparative advantages of producing hybrids in small units, where a high degree of control is possible, over a well-designed pond hatchery? Which system is more economical and technically feasible?

Other areas still in need of further research are the optimum stocking densities and sex ratios of broodstock, the length of time for which they can be used before replacement, and the influence of broodstock nutrition on fecundity and fingerling survival.

Other tilapia species should be hybridized to discover new crosses that will produce 100% male offspring. The discovery of an all-male herbivorous hybrid would be very valuable.

Little comparative data is available on the growth and production of hybrids. Studies are needed to determine which hybrid crosses respond best to feeding and which to fertilizing so that intelligent choices of hybrids can be made.

The vast majority of cultured tilapia hybrid crosses give less than 100% male progeny. These fish are often marketed at a small size (Taiwan) or the males are hand-sexed so that larger fish can be raised (Israel). The commercial culture of all-male hybrids presents problems that have still to be researched. The consistent production of 100% all-male hybrid fingerlings in sufficient numbers to stock a large growout operation has not been worked out.

The level of technology needed to raise all-male hybrids is beyond the reach of most farmers in tropical developing countries and great care should be exercised in introducing all-male hybrid culture into countries with no fish culture tradition. Culture of pure species appears to be the logical first step in introducing tilapia culture to such countries. However, in countries with a tradition of fish culture, where trained biologists are available and money exists to build hybrid fingerling hatcheries, culture of all-male tilapia hybrids may hold great potential if researchers are able to improve fingerling production techniques.

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Discussion

BOWEN: Can you tell us if you have any idea of the fate of the agricultural products or by-products which you used as feed? Did the fish consume these readily?

LOVSHIN: There is no doubt about it. They consumed them immediately. You could see the feeding activity and when you examined the guts they would be crammed with the materials. Now, as far as digestibility is concerned, that is another matter. They can probably digest some of them—at least a certain percentage of the available nutrients—but a lot of their growth comes from the incorporation of nutrients into bacterial detrital feeds. We found that to really get the best growth in the pond culture of tilapia hybrids, we had to reach a certain level of pond fertility.

BOWEN: Is there any correlation between that level of fertility and feeding habits? Do the feeding habits change at that level of fertility?

LOVSHIN: That is a good question. I don't know. All I can say is that we always used extra supplemental food until pond fertility reached a certain point, and lowered the feeding rate thereafter because we knew that the fish were getting a lot of natural feed from the pond.

BOWEN: Secondary plant substances have been mentioned as obstacles to the utilization of some agricultural by-products. Did you ever note anything that could be suspected as a toxic effect from any of these substances which you used?

LOVSHIN: No. We used a castor bean meal which can be toxic, but ours had been detoxified by roasting. It was a good product for us because the animal husbandry people, pig and cattle raisers, do not like to use castor bean meal because it gives their animals intestinal problems. It does not kill them, but it irritates the intestines and causes diarrhea. We could get this particular material very cheaply. In my paper, there is a comparison between castor bean meal, cottonseed cake and palm nut cake, and the castor bean meal is by far and away the best because it has the highest protein level. We used the whole, ground castor bean seed which has an outer shell which is very hard and indigestible. In an aquarium, the bottom would be literally covered with these hulls, but we never had any toxicity problems.

PULLIN: You have already touched on the problem of compatibility between crosses of different species. What do you think about the technique of premaxilla clipping to reduce male aggression in confined environments?

LOVSHIN: In a confined environment, male aggression can be a problem, but we have never had any such problem in a pond environment which allows the females to escape from aggression. We never had any mortality from male aggression in the ponds we used, which were about 350 m^2 but when we brought fish into more confined environments, 3 to 4 m^2, the problem did occur. During the time I was in Brazil, I did not know about Lee's technique of cutting off the premaxilla, but at Auburn University, it works fine and we have been using it quite a bit. The male fish is still aggressive. It still chases the female but, because the premaxilla has been removed, he cannot wound her as easily. Sometimes he will still run her around so much that I think she could die of exhaustion, but he cannot break the skin.

JALABERT: What evidence do you have for the purity of the males which you used?

LOVSHIN: The only evidence I have is that we consistently got 100% all-male progeny. We have been doing this in Brazil now for seven or eight years.

JALABERT: In group spawning or single pair spawning?

LOVSHIN: Group spawning in Brazil, but 100% males have been obtained from single pair spawning using stocks which we sent to Israel. Also, our stocks have produced 100% males in Panama, in the United States and in Puerto Rico so I am pretty certain of the purity of the strains.

HENDERSON: You mentioned the problems of the reduced fry production with the hybrid crosses. Do you think this is a problem of reduced fecundity or incompatibility?

LOVSHIN: I don't think it is basically fecundity, that is an egg production problem. The number of eggs produced by actual spawning females is not abnormally low. I am convinced that the problem is compatibility. There are certain females that will spawn readily and repeatedly both in aquaria and tanks in normal pure species crosses. Now the question is, can you select for this, i.e., take those females out, mate them with a normal male, take the offspring, test them, select good females again, etc. Can we select genetically for good spawning in pure species crosses and for compatibility in hybrid crosses? These are questions for the geneticists.

GUERRERO: Is there any evidence of hybrid vigor when you compare the growth performance of hybrids with pure species progeny?

LOVSHIN: A good question and the answer is not clear from the literature because most hybridization has been to produce all-males from pure stock male and female. Comparisons between the growth of an all-male population and mixed sex or female populations are complicated because we know that males grow faster than females—both hybrid and pure species males. Where we compared all-male hybrids with the *males* of the other species, we found that the differences in growth were not very great. In Brazil, we found a difference, although I am talking here of a 10% to 15% advantage for the all-male hybrid at best and sometimes this was not statistically significant. In Israel, we found several cases where there was no difference at all.

ROBERTS: At the Institute of Aquaculture in Stirling, we have been producing very pure lines using normal and sex-reversed (hormone-treated) sibling crosses. We found a very significant growth promotion effect from the anabolic steroid treatment used for sex reversal. More important, by crossing pure lines, we can produce hybrid all-male progeny which, after 6 months or so, are very much larger than the pure lines. The performance of these hybrids cannot be due to any residual effects of anabolic steroids.

HENDERSON: The question is, is the growth improvement which you observe for the hybrids comparable to that for the sex-reversal treatment alone?

GUERRERO: We found significant differences in growth of normal males and those which are sex-reversed females. The latter remain slower growers compared with the normal males and with all-male hybrids.

JALABERT: Dr. Lovshin, in your maintenance of pure strains, have you seen any signs of adverse affects of inbreeding?

LOVSHIN: It is difficult to say. We suspect a reduction in growth rate but we have to check this. The *Sarotherodon niloticus* and *aureus* used at Auburn University, elsewhere in the USA and some of the Latin American work all stem from an initial introduction to the USA of about 25 individuals of each species from the Ivory Coast. Over the years, we kept about 25 or 30 broodstock of each species and we let them reproduce. Every six months to one year, we would clean everything out and replace the broodstock with 25 or 30 younger fish.

JALABERT: This is not a large enough population.

LOVSHIN: I agree with you.

HENDERSON: Incidentally, there was a consultation meeting in Rome in June 1980 sponsored by UNEP on the conservation of genetic stocks of fish. One thing that did come out of this was a recommendation on the minimum size of the stocks which you need keep to avoid the problems of inbreeding. I can provide an overview of this meeting to anyone who is interested.

EDITORS: In Panama, the cross *S. niloticus* ♀ x *S. hornorum* ♂ male has now been abandoned for all-male hybrid production in favor of the *S. mossambicus* ♀ x *S. hornorum* ♂ cross. This gives very high fingerling production and 100% males. Fry are reared in earthen ponds and then grown to fingerling size in open concrete ponds as in the Ivory Coast (see Coche, this volume). This information was received from R. Pretto Malca.

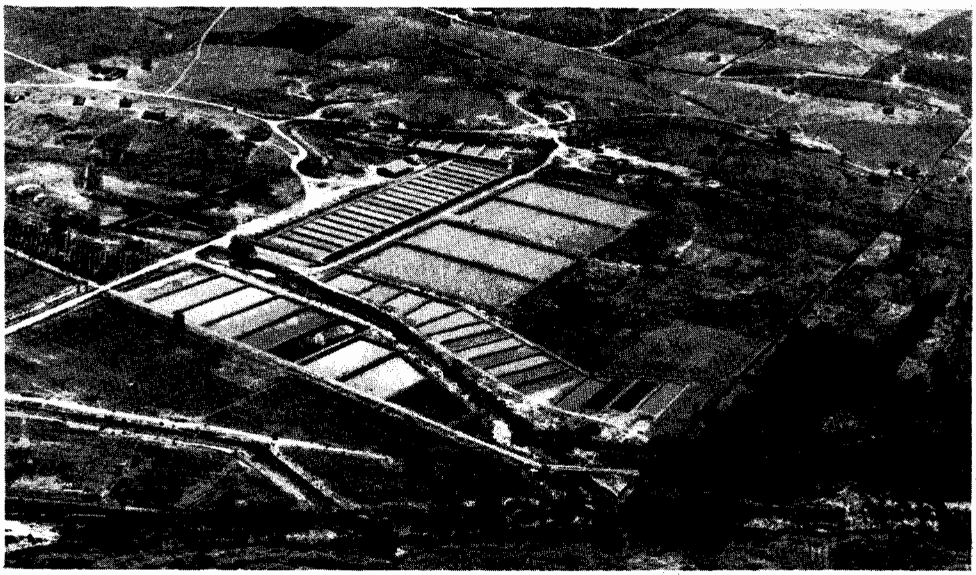

Plate 1. Phase I of the Rodolpho von Ihering Fish Culture Research Center, Pentecost, Brazil. (Reprinted by kind permission of the International Center for Aquaculture, Auburn University.)

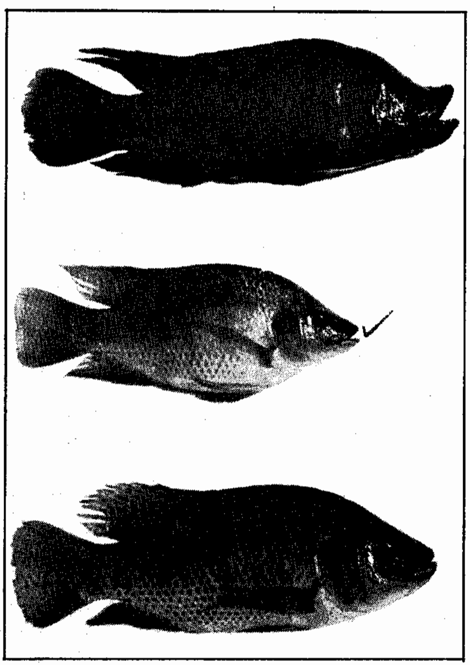

Plate 2. *Sarotherodon hornorum* male, all-male hybrid *(S. niloticus* x *S. hornorum)* and *S. niloticus* female (top to bottom).

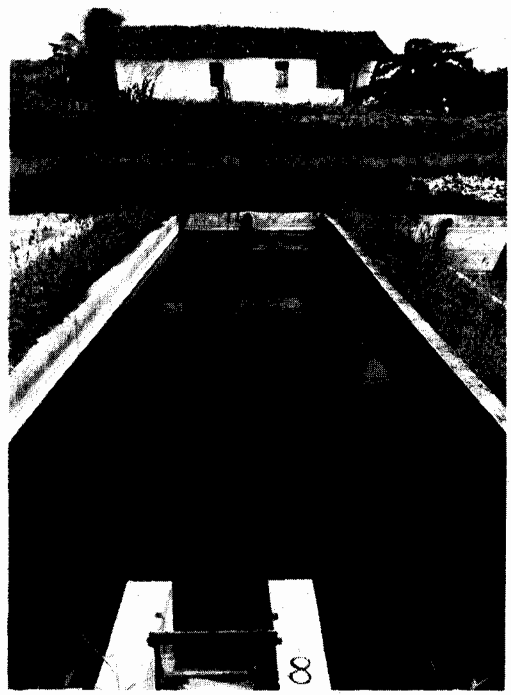

Plate 8. A 36 m^2 concrete-sided, earthern-bottomed tank used to maintain pure strains of tilapia for hybridization in Northeast Brazil. When in use, the tank has a filtered water supply and is covered with a net to avoid contamination from wild stocks. (Reprinted by kind permission of the International Center for Aquaculture, Auburn University.)

Control of Tilapia Reproduction

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Uncontrolled reproduction gives excessive recruitment and low yields of harvestable-size tilapias from culture ponds. Several effective methods have been developed and applied for controlling this in commercial farms including monosex culture, the use of predators and cage culture. Each method, however, has its advantages and disadvantages. Other methods that have been tested are stock manipulation, the use of irradiation and chemosterilants, reproduction inhibitors such as methallibure, salinity, light and temperature. Further research is needed to determine the practicality of these methods for commercial culture.

Introduction

Tilapias are an important foodfish in many tropical and subtropical countries. More than 20 species of tilapia have been cultured in developing countries where animal protein is lacking. Tilapias are considered suitable for culture because of their high tolerance to adverse environmental conditions, their relatively fast growth and the ease with which they can be bred.

The main drawback to the worldwide culture of tilapias is their excessive recruitment in ponds which results in low yields of harvestable-size fish. Where the acceptable market size is 150 g or more, this becomes a critical problem.

In general, tilapias have high breeding rates. Their fecundity ranges from a few hundred eggs to several thousands per spawning. Under pond conditions, precocious breeding and stunting have been reported (Fryer and Iles 1972; Cridland 1962) which assist excessive recruitment.

The various methods for controlling the reproduction and recruitment of tilapias are reviewed in this paper with a brief discussion on the advantages and disadvantages of each method. To be practical, a method must be easy to apply, effective and economical.

Monosex Culture

1. RATIONALE

In the tilapias, the male in general grows faster than the female (van Someren and Whitehead 1960a, 1960b; Fryer and Iles 1972; Guerrero and Guerrero 1975; Anon. 1979b). This appears to be genetically controlled. Monosex male culture therefore gives faster growth and eliminates reproduction. Monosex tilapias are obtained by manual or mechanical (grader) separation of the sexes or by production of monosex broods through hybridization or sex reversal.

2. MANUAL SEXING OR GRADING

Manual sexing of tilapia has been suggested and tested by several workers (Hickling 1963; Meschkat 1967; Shell 1967; Guerrero and Guerrero 1975). The sexes are distinguished by examination of the urinogenital papillae. Two orifices are present in the female papilla and one in the male (Vaas and Hofstede 1952). Although manual sexing is laborious and requires some skill, it is applied commercially in Israel. Sexing of 50 g or larger fish is easily done. One man can segregate about 2,000 male tilapias in a working day (Lovshin and Da Silva 1975). In many countries where the method has been introduced, however, it has failed. The major disadvantages of the method are human error in sexing and the wastage of females. Bardach et al. (1972) reported that hand sexing is 80 to 90% accurate. The use of mechanical graders for separating larger sized males was tried by Pruginin and Shell (1962) and Bard et al. (1976). The accuracy of this method, however, has been questioned by Balarin and Hatton (1979).

3. MONOSEX HYBRIDS

The production of all-male progeny from *Sarotherodon mossambicus* (female) x *S. hornorum* (male) hybridization was first described by Hickling (1960). Five other crosses have been reported to produce all-male F_1 hybrids: *S. niloticus* x *S. hornorum* (Pruginin 1967), *S. niloticus* x *S. macrochir* (Jalabert et al. 1971), *S. niloticus* x *S. aureus* (Fishelson 1962) and *S. niloticus* x *S. variabilis* and *S. spilurus niger* x *S. hornorum* (Pruginin 1967). Other crosses that have yielded 93 to 98% males are male *S. niloticus* x *S. leucostictus* (Pruginin 1965) and *S. niloticus* x *S. spilurus niger* (Pruginin 1965).

Several theories have been proposed to explain these ratios. Hickling (1960) and Chen (1969) suggested that the sex-determining mechanisms XX female-XY male and WZ female-ZZ male are both found in tilapias. However, not all the sex ratios of tilapia hybrid progeny can be explained by these. Hammerman and Avtalion (1979) have presented a model which takes into account the possible sex-determining effects of autosomes as well as sex chromosomes.

Culture of tilapia hybrids has resulted in high yields of harvestable-size fish (Hickling 1960; Pruginin 1967; Lovshin et al. 1977; Avault and Shell 1967). Although hybrid vigor has been reported by Hickling (1960) and Avault and Shell (1967), the findings of Pruginin (1967) and Lovshin et al. (1977) showed otherwise. One other advantage of using crosses which give monosex hybrid progeny is that the wastage of females from manual sexing is eliminated.

The main disadvantages of such crosses are: difficulty in maintaining pure parental stocks that consistently produce 100% male offspring (Pruginin et al. 1975), poor spawning success (Lee 1979) and incompatibility of breeders resulting in low fertility (Lovshin et al. 1977).

4. Sex-Reversal

The use of steroid hormones for production of monosex broods has proved effective in many tilapias. Artificial sex-reversal of genotypic females of five species has been achieved using methyltestosterone and ethynyltestosterone (Table 1) and feminization of genotypic males has been induced with estrogens: ethynylestradiol, estrone and diethylstilbestrol (Table 2). Treatment is *per os* for periods ranging from 15 to 60 days in tanks or aquaria. Survival of fry under hormone treatment does not differ significantly from controls indicating no differential mortality (Guerrero 1974). Effectiveness of the sex reversal treatment depends on the kind and dosage of steroid used, the method of administration, time and duration of treatment, and on the species (Yamamoto 1969). Shelton et al. (1978) recommend oral treatment of 9 to 11 mm *S. aureus* fry at a density of 2,600/m^2 or less with ethynyltestosterone dosage of 60 mg/kg of feed for 6 weeks at 25 to 29°C for production of all-male broods.

Sex-reversal using androgens on a commercial scale has been shown to be feasible by Guerrero (1979b) and Koplin et al. (1977). The disadvantages of the method are the need for holding facilities for treatment of large numbers of fry (Mires 1977) and the sophisticated skill needed for its application.

Hopkins (1979) produced all-male progeny of *S. aureus* with sex-reversed females (genotypic males) treated with ethynylestradiol. He also produced all-female fry with sex-reversed males of *S. niloticus* treated with androgens. The low percentage of spawns with monosex fish, however, points out that further research is needed to establish the practicality of the method.

Table 1. The treatment of tilapia fry with androgens to produce all-male broods (M = methyltestosterone; E = ethynyltestosterone).

Species	Compound	Treatment Level of food incorporation (mg/kg)	Duration (d)	% Males	References
Sarotherodon mossambicus	M	10-40	60	95-100	Clemens and Inslee (1968)
	E	50	40	100	Guerrero (1979b)
S. niloticus	M	40	60	100	Jalabert et al. (1974)
	M	15-50	42	96-98	Guerrero and Abella (1976)
	M	30-60	25-29	99-100	Tayamen and Shelton (1978)
	E	30-60	25-29	98-100	Tayaman and Shelton (1978)
S. aureus	M	30	18	98	Guerrero (1975)
	E	30-60	18	98-100	Guerrero (1975)
	E	30	22	90-100	Sanico (1975)

Table 2. The treatment of tilapia fry with estrogens to produce all-female broods.

Species	Compound	Treatment Level of food incorporation (mg/kg)	Duration (d)	% Females	References
Sarotherodon mossambicus	ethynylestradiol	50	19	100	Nakamura and Takahashi (1973)
	estrone	200	56	99	Guerrero and Guerrero (1976)
S. niloticus	diethylstilbestrol	100	25	91	Tayamen and Shelton (1978)
S. aureus	ethynylestradiol*	100	42	90	Hopkins et al. (1979) Jensen and Shelton (1979)

*With 100 mg/kg methallibure

The Use of Predators to Control Recruitment

Effective predators on young tilapias include many piscivorous fishes, such as *Elops hawaiiensis*, *Megalops cyprinoides*, *Micropterus salmoides*, *Ophicephalus striatus*, *Cichla ocellaris*, *Lates niloticus*, *Clarias lazera*, *Hemichromis fasciatus* and *Cichlasoma manguense*. In most cases, predator-prey stocking ratios have been determined (Table 3). Where effective predators are used, high yields of harvestable-size tilapia are reported (Swingle 1960; Lovshin 1975; Dunseth and Bayne 1978). Total production of tilapias, however, is significantly reduced as the recruits are eaten (Maar et al. 1966; Lovshin 1975). Moreover, difficulty in obtaining stocks of the desirable predator has limited application of this population control method (Balarin and Hatton 1979).

Table 3. Fish predators used for the effective control of recruitment of tilapias.

Prey	Predator	Stocking Ratio (Predator:Prey)	References
Sarotherodon mossambicus	*Elops hawaiiensis*	1:10 and 1:20	Fortes (1979)
	Megalops cyprinoides	1:10	Fortes (1979)
	Micropterus salmoides		Swingle (1960)
S. niloticus	*Cichla ocellaris*	1:15	Lovshin (1975)
	Clarias lazera	1:10	Bard et al. (1976)
	Lates niloticus	1:20-1:84	Planquette (1974)
S. shiranus	*Clarias* sp.	1:10-1:20	Meecham (1975)
T. rendalli			
S. aureus	*Cichlasoma managuense*	1:4-1:8	Dunseth and Bayne (1978)
Not specified	*Hemichromis fasciatus*	1:48	Bardach et al. (1972)

The Use of Stock Manipulation Methods

Reproduction of tilapias appears to be inhibited by high stocking densities (Allison et al. 1979). Swingle (1960) reported that increasing stocking rates of fingerlings decreased rates of reproduction. He suggested the presence of a repressive factor affecting reproduction. In *S. mossambicus*, a substance believed to be present in the mucus has been found to cause an autoallergic response at high densities (Henderson-Arzapalo et al. 1980).

Culture of tilapia in cages at high densities has limited reproduction (Pagan 1975; Coche 1979; Guerrero 1980a). Pagan (1969) suggested that failure of tilapia to reproduce in cages is due to an alteration of reproductive behavior that prevents fertilization or that the eggs pass through the cage.

The Use of High Stocking Densities

The continuous harvesting of tilapias from ponds to reduce their population has been proposed by Hickling (1960). A similar method suggested is harvesting before the fish become sexually mature (Swingle 1960). No data are available to evaluate such methods for tilapias but Payne (1970) reported that regular seining of ponds with *S. esculentus* and *T. zillii* reduced the fry population. Mortalities were believed to have occurred from physical damage or deoxygenation.

The Use of Irradiation, Chemosterilants and Reproduction Inhibitors

Al-Daham (1970) observed a decrease in the gonadosomatic index and growth rate of *S. aureus* fry exposed to high doses of ^{60}Co gamma ray irradiation. Nelson et al. (1976, as cited by Balarin and Hatton 1979) found no obvious effects on the germ cells of 7 to 8 week old *T. zillii* fry treated with ^{60}Co gamma radiation for 35 days.

Destruction of the gonads of *S. aureus* fry was induced by Eckstein and Spira (1965) using estrogens at concentrations of 50 and 100 μg per liter of aquarium water for a period of 3 to 4 weeks. Al-Daham (1970) inhibited brood production in tilapias with the chemosterilants metepa and tetramine administered at concentrations of 20 ppm for 2 and 3 months and 0.8 ppm for 2 and 3 months, respectively. Sterile male tilapia were produced with the treatment of ^{90}Sr at 10^{-10} and 10^{-6} Ci/liter (Voronina 1974, as cited by Balarin and Hatton 1979).

Using methallibure, a compound which blocks synthesis or release of pituitary gonadotropins, Dadzie (1974) suppressed gonadal development in *S. aureus*. The treatment enhanced the growth of female fish and delayed spawning. A major constraint in the future development of methallibure for controlling reproduction is the discovery of its teratogenic effect in swine (see discussion in Balarin and Hatton 1979).

The reproduction of tilapias also appears to be affected by salinity. Chimits (1955) reported that *S. mossambicus* did not reproduce in salinities above 30‰. Similarly, Chervinski and Yashouv (1971) found that *S. aureus* did not reproduce in saltwater ponds with salinities of 36.6 to 44.6‰. *S. niloticus* fry were not found in brackishwater ponds in salinities of 15 to 30% (Dureza, pers. comm.). Ang (pers. comm.) observed that no hatching of *S. niloticus* eggs occurred in aquaria in salinities of 18‰ and higher.

Light and temperature strongly influence the spawning of tilapias. Cridland (1962) showed in laboratory experiments that sexual maturity of *T. zillii* was delayed by "strong periodic illumination for 12-hr periods" and by low temperatures. The sexual precocity of tilapias in ponds and swamps has been related to light (Chimits 1955; Lowe (McConnell) 1958). Mires (1974) indicated that temperature influenced the sex ratio of *S. aureus*: a higher percentage of females was associated with low temperatures.

Conclusion

It is evident that three methods can be used for the control of tilapia reproduction: monosex culture, the use of predators and stocking at high densities. Each method, however, has disadvantages.

The use of stock manipulation techniques, irradiation, chemosterilants and reproduction inhibitors have shown promise in limiting tilapia reproduction on an experimental scale, but further research is needed to determine the practicality of these methods for commercial use.

Discussion

HENDERSON: Dr. Guerrero, do you have any idea of the comparative cost of sex reversal by hormone treatment compared with that of manual sexing?

GUERRERO: For manual sexing in the Philippines, we pay twenty centavos (US$0.03) per fish and a worker can sex 2,000 fish per day. The daily wage is up to US$3/day, on average about $2.60. Sexable size is taken as 10 g or above. Hormone sex-reversal is of course labor saving, but you can see that our labor costs are low. Moreover, we have to use alcohol for dissolving the hormone for food incorporation. For every kilogram of feed, with hormone we use one liter of alcohol. This is quite expensive unless you can recycle the alcohol. We consider that it costs about 20 Philippine pesos (about US$3) to treat about 1 million fry. These costs would be only for feed and labor, ignoring the depreciation cost of facilities. If we sell these sex-reversed fingerlings, we get about 150 Philippine pesos (which is about US$20) per thousand so we still make a good profit. Sex-reversal techniques are fine if you have practical experience, but in general, I would not recommend them in a developing country like ours because of the relatively high capital requirements and the need for skilled workers. There are no commercial hatcheries using sex-reversal in the Philippines at present.

ROBERTS: We use similar methods to yours but with a 35-day treatment period and 30 ppm dose regime. Going back to the anabolic steroid growth promotion effects, we find that this anabolic effect is so significant and gives the fry such a head start that it is worth doing quite irrespective of any sex-reversal objectives. Recently, we had indications that sex-reversed females grew better than normal females and normal males. We are also studying the residence time of steroids in our fish after cessation of treatment using radioactively-labelled compounds. They are generally undetectable after 5 days. This is important as many of the developing countries are borrowing their food and drug legislation direct from the USA and we have to show that this short-term fry treatment is very different from caponisation in the poultry industry which uses long-lasting steroid implants. We have had our best sex-reversal results with *S. mossambicus* and *S. spilurus* and our worst with *T. zillii.*

It may be of interest that the black coloration of species like *S. mossambicus* does not produce sales resistance in Africa—unlike in Southeast Asia.

HEPHER: I wonder whether space is a severe limiting factor on the whole sex reversal operation. If you talk in terms of raising 2,000 fry/m^2 then you will need 15 of such tanks to serve 1 ha of monoculture pond with a normal stocking ratio of about 30,000/ha. Therefore, think how many tanks you would need for a whole farm. Won't this be a bottleneck?

GUERRERO: Our systems are as yet experimental but the production per unit area could probably be improved by using raceways with a flow-through system.

HEPHER: The second bottleneck which I can envisage is obtaining sufficient numbers of fry at exactly the right age for sex-reversal treatment.

GUERRERO: Using our net enclosure (hapa) system, we can produce 10,000 fry/ 500 m^2/day.

MORIARTY: Has anyone tried treating with hormones in the tank water? I believe that aquarists have done this with other species.

GUERRERO: Some people have tried this with tilapias but it has not been effective. Of course hormone injections are effective—more so than food incorporation but this is not practical for sex-reversing fry.

MORIARTY: What about a large quantity of hormone in the water?

GUERRERO: The hormones are not water soluble.

CHERVINSKI: I think I am right in saying that *S. aureus* has never been sex-reversed by hormone treatments.

GUERRERO: It has been done successfully for *S. niloticus, aureus* and *mossambicus.*

PHILIPPART: Regarding the use of flow-through systems, we succeeded last year in producing sex-reversed *S. niloticus* in such systems. We had to regulate food input very carefully. We treated the fish for 29 to 30 days.

A Study of the Problems of the Mass Production of Hybrid Tilapia Fry

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Comparative data on the spawning capacity and spawning frequency of female tilapias demonstrate successful spawning in intraspecific and interspecific crosses. There is, however, great variability in the fecundity of individual females. Spawning incompatibility exists between tilapia species, the degree of incompatibility varying with the species combination. The influence of the sex ratio of the parental stock and other factors which reduce male aggressiveness are discussed. There are three main influences on the production of tilapia fry: genetic, behavioral and environmental.

Introduction

For the last ten years or so, fish farmers in various parts of the world have searched for efficient ways of rearing all-male broods of tilapias (Hickling 1960; Fishelson 1962; Pruginin 1967; Chen 1969; Mires 1973; Lovshin and Da Silva 1975; Mires 1977), yet the problem of mass-rearing these fish remains. After many years of hard work, some of the Israeli fish hatcheries have succeeded in making a major breakthrough in this field (Mires 1977) but this young industry still has to overcome the problem of the low fry production from interspecific spawns. This paper discusses various aspects of this problem.

Possible Reasons for the Low Production of Tilapia Fry in Spawning Ponds

There are quite a few possible reasons for the low production of tilapia fry in commercial spawning ponds. The main ones are probably: too low a density of broodstock; incompatibility in interspecific crosses; inappropriate broodstock sex ratios; inadequate spawning techniques and high fry mortality. More information is needed on each of these possibilities.

The production of tilapia fry in spawning ponds depends on three main factors: the spawning frequency of each female in the parental stock, the number of eggs produced in each spawn, and the survival of the fry. These aspects will be considered for intraspecific and interspecific crosses.

Egg and Fry Production: General Considerations

It is important to define the term 'fecundity'. Lowe (McConnell) (1955b) defined fecundity as "the number of young produced during the life time of an individual". This definition is perfectly acceptable for natural conditions, but it is very hard to use in culture or in experimental conditions. In this paper it is proposed to change the time limit from "life time" to 12 months starting from the first spawning.

It has been stressed that the number of eggs in each spawn depends on the length and/or weight of the spawner (Fryer and Iles 1972) but Peters (1959) and Lee (1979) found different results. Lee (1979) found that for some individual spawners there was a trend of increasing clutch size through successive spawns, but this was not uniform (see also Tables 1 and 3). Babiker and Ibrahim (1979) showed correlations between the length or the weight of *S. niloticus* and the number of oocytes in the ovaries, but there are doubts as to whether these correlations can forecast the actual quantities of eggs or fry obtainable from a given female during a given period under various conditions.

Tables 1, 2, 3, and 5 show a big variability not only in the spawning frequency between spawners of different species but also in the total number of eggs produced by the females within the groups. Moreover Lee (1979) showed a 20 to 30% difference in the number of eggs produced within female groups of two different species, stocking three females per aquarium.

Peters (1959) showed an exact correlation between the weight of the clutches and the body weight of the females; he also stressed that "fish either produce relatively few large eggs or relatively many small eggs". It seems possible therefore that on an annual basis small but more fecund females can and will probably produce more eggs than big but poor spawners.

Spawning procedures and conditions can also influence the production of fry in the spawning ponds: for example the rate of water changes. There is no substantial data on the influence of this factor on fry yields from spawning ponds, but for aquaria most of the hatchery operators in Israel believe firmly that periodical water change will usually cause a renewal of spawning activity. Commercial fry producers also believe that the change of water in spawning ponds has a beneficial effect on spawning frequency. This is probably due to the flushing out of metabolites. It seems that overcrowding in ponds, tanks, etc., may induce earlier maturity than in nature and a larger production of smaller sized eggs (Fryer and Iles 1972).

Feeding conditions also have an influence on egg and fry production (Miranova 1977). For example, *S. mossambicus* females spawned more frequently when they were underfed, and the total amount of eggs was higher than when they were fed abundantly. This response to unfavorable conditions has probably permitted many tilapia species to adapt to harsh and changing environment during their evolution (Fryer and Iles 1972). Lately, the Ein Hamifrats fish farmers (unpublished) have observed that when a spawning pond becomes overcrowded with fry, the spawning activities of parent fish cease completely. In these conditions, there are no mouthbrooding females and the few nests present seem to be unattended.

Intraspecific Spawning

A lot of work has been published on the reproductive behavior of tilapia spp., but very little has been said about the individual spawning potential of females. The only possible way to study this closely is under aquarium conditions, where the females are kept in separate aquaria or in separate compartments of the same aquarium, because in spawning groups a hierarchy may become established in aquaria and cause some dominant females to spawn more than others (Fishelson 1966a; Mires 1973; Rothbard 1979).

During the first working period in the Ein Hamifrats hatcheries, some valuable data were gathered on the individual spawning potential of *S. niloticus* B and *S. vulcani* (Mires 1977). A few females weighing 400 to 500 g were introduced into separate compartments in aquaria and kept at a constant temperature of 25 to 28°C year-round, fed with 25% protein pellets. The day on which each female was ready to spawn was recognized by the form of the genital papilla being much larger and more erect than usual. Such a female was transferred to an aquarium where one male of the same species was held. If the female was ready to spawn, the male would immediately start courting her; but if not he would start chasing her around and eventually bite her severely. In such a case the female was removed and placed back in her compartment.

After spawning, the female was separated from the male by a screen, and was left to mouthbrood her eggs for a few days. The larvae were then removed from her mouth, and cared for in Zuger bottles for the rest of their larval development. When a female spawned without the presence of a male the spawn was recorded, but unfortunately the eggs were not counted. The results for one group of *S. vulcani* and another group of *S. niloticus* B are given in Tables 1 and 2. Although the females were kept in separate compartments of the same aquarium, it is possible that slight environmental differences existed (corners versus center). Their spawning frequency was very variable and they did not spawn year-round despite the controlled temperature. In both groups the maximum number of individual spawns was 7: represented in both cases by only one female. It is interesting that the proportions of prolific and poor spawners were similar for both *S. niloticus* and *S. vulcani.* The same phenomenon exists with interspecific spawns.

McBay (1961) gathered data on the spawning of what was then called *T. nilotica*, later re-identified as *S. aureus*. The fish were paired in 40-liter aquaria and the egg or fry production was recorded and counted. Out of 17 females, one spawned 6 times, two spawned 5 times, one spawned 4, and all the rest spawned three times or less.

Table 1. The spawning frequency and egg production of isolated individual *Sarotherodon vulcani* females (400-500 g each) studied from February 1, 1973 to January 1, 1974 (after Mires 1977 and Mires unpublished data).

Female no.		Date of spawning							Total egg count	Average eggs/ spawn*	No. of spawns	Average interval (days)
	Date	24/3-	24/4-	15/5-	3/6-	24/6-	26/7-	5/9-				
1	No. eggs	1,600	**	**	**	**	**	**	1,600	1,600	7	
	Interval (days)	31	21	19	21	32	40					27
	Date	10/3-	8/4-	27/5-	24/6-	3/7-	5/8-					
2	No. eggs	1,400	**	1,500	1,200	**	1,000		5,100	1,275	6	
	Interval (days)	39	47	28	9	33						31
	Date	25/3-	4/4-	9/5-	7/8-							
3	No. eggs	1,000	**	1,150	**				2,150	1,075	4	
	Interval (days)	10	35	90								45
	Date	27/3-	28/4-	18/7-								
4	No. eggs	**	**	**					—	—	3	
	Interval (days)	32	81									56
	Date	25/3-	21/9-									
5	No. eggs	**	**						—	—	2	
	Interval (days)	150										150
	Date	14/3-										
6	No. eggs	**							—	—	1	
	Interval (days)											

*Based on the number of eggs in fertile spawns only.
**Infertile spawns: eggs not counted.

Unfortunately, some of the females died during the experiment and the times of death were not recorded. It is therefore impossible to know whether the spawning of some of the females ceased because of their death or because of other reasons. It is, however, interesting to observe that here again, although an optimal temperature was maintained throughout the experiment, the spawning frequency of the females differed.

In the Kibbutz Ein Hamifrats fish hatcheries, where several families of *S. niloticus* and *S. aureus* are kept in 500-liter aquaria, individual females of both species have never spawned more than six or seven times in one year and the average spawning frequency of any given group of females in a family has not exceeded four. Moreover the period over which spawning occurs is restricted to five or six consecutive months even when the temperature is optimal year-round.

In other intraspecific spawns in aquaria (Lee 1979) very big differences were observed in the spawning frequency and fecundity of various females.

Out of ten *S. aureus* females, one spawned 8 times, one 7 times, two 6 times, one 5 times, four 4 times and one 3 times. Out of nine *S. niloticus* Ivory Coast one spawned 5 times, five 4 times and three 3 times. Yashouv (1958) stated that in Israeli fish ponds, two-year old *S. aureus* usually spawn three or four times from May to October.

Table 2. The spawning frequency and egg production of isolated individual *Sarotherodon niloticus* B (400-500 g each) studied from February 1, 1973 to January 1, 1974 (after Mires 1977 and Mires unpublished data).

Female no.		Date of spawning	Total egg count	Average eggs/ spawn*	No. of spawns	Average interval (days)
	Date	7/2- 4/3- 3/5- 5/6- 6/7- 30/7- 5/9-				
1	No. eggs	200 1,600 ** ** ** 1,000 **	2,800	933	7	
	Interval (days)	25 57 33 31 24 35				34
	Date	26/2- 24/4- 2/5- 29/5- 23/7- 20/8-				
2	No. eggs	900 ** ** ** 1,300 **	2,200	1,100	6	
	Interval (days)	57 8 27 56 28			35	
	Date	20/5- 9/6- 13/7- 4/8-				
3	No. eggs	** ** ** 1,000	1,000	1,000	4	
	Interval (days)	15 34 21				23
	Date	4/3- 29/3- 4/5-				
4	No. eggs	** ** 700	700	700	3	
	Interval (days)	25 36				30
	Date	24/5- 18/6- 2/9-				
5	No. eggs	1,090 1,600 **	2,690	1,345	3	
	Interval (days)	25 76				50
	Date	21/6- 26/7-				
6	No. eggs	** **			2	
	Interval (days)	35				35

*Based on the number of eggs in fertile spawns only.
**Infertile spawns: eggs not counted.

Interspecific Spawning

1. Aquaria and Tanks

The successful crossing of two different tilapia species in aquaria has always been a serious challenge to researchers and hatchery operators. It was made easier with the help of induced spawning techniques (Rothbard and Pruginin 1975) but it seems improbable that this can be used widely. Recently interspecific spawns have been obtained in tanks (Hulata et al. 1980). Hulata and co-workers have been studying interspecific spawns in 600-liter tanks since 1978 and have kindly permitted the use of some of these data (Tables 3, 4 and 5). As in Tables 1 and 2, there is an enormous variability in fecundity between females of the same group, even with constant environmental conditions year-round.

Table 3. The spawning frequency and egg production of *Sarotherodon niloticus* Ghana females in interspecific spawning crosses with *S. aureus* males weighing 50 g each over a 12-month period (Hulata et al. 1980 and Hulata unpublished data).

Female nc		Date of spawning								Total egg count	Average eggs/ spawn*	No. of spawns	Average interval (days)
1	Date	6/4-	7/5-	21/6-	8/7-	23/8-	14/9-	9/10-	26/10-				
	No. eggs	82	41	**	230	171	298	220	399	1,441	205	8	
	Interval (days)	31	45	17	46	22	25	17					29
2	Date	10/6-	8/7-	12/8-	6/9-	2/10-	26/10-						
	No. eggs	274	375	360	467	158	172			1,806	301	6	
	Interval (days)	28	35	24	26	24							27
3	Date	18/7-	15/8-	6/9-	2/10-	22/10-	26/11-						
	No. eggs	283	55	**	247	368	272			1,225	245	6	
	Interval (days)	27	22	28	20	35							26
4	Date	8/7-	15/8-	6/9-	2/10-	22/10-	26/11-						
	No. eggs	251	298	451	214	449	383			2,046	341	6	
	Interval (days)	38	21	27	20	34							28
5	Date	5/8-	17/9-	6/11-									
	No. eggs	254	390	284						928	309	3	
	Interval (days)	42	49										45
6	Date	26/8-	24/9-										
	No. eggs	414	200							614	307	2	
	Interval (days)	26											26
7	Date	14/9-											
	No. eggs	210								210	210	1	
	Interval (days)	—											—
8	Date												
	No. eggs									0	0	0	
	Interval (days)												
9	Date												
	No. eggs									0	0	0	
	Interval (days)												

*This figure represents only the average amount of eggs in fertile spawns.
**Infertile spawns: eggs not counted.

2. PONDS

For interspecific spawning in ponds, it is practically impossible to obtain any information on the fecundity of individual spawners and only the total fecundity of the broodstock can be studied. Crosses between 3 groups of nine *S. niloticus* Ivory Coast females and three *S. hornorum* males (mean individual weight of both sexes, 45 g) in triplicate experimental ponds yielded 223, 280, and 404 fry/pond for a 72-day period (Lovshin and Da Silva 1975). The same authors reported no significant difference in hybrid fry production from two spawning groups: *S. niloticus* Ivory Coast females x *S. hornorum* males (10 ♀♀:5 ♂♂ and 6 ♀♀:3 ♂♂). There was a high variability in fry production within the replicates of the same group: 93 to 2,981 for the 10:5 group and 580 to 3,619 for the 6:3 group. The spawning period in both cases was 72 days. Two factors could have caused this big variability: some of the females could have spawned more often than others (thus causing a temporary higher yield) and some of the spawning groups may have had a greater number of more fecund females than others.

3. The Effect of the Sex Ratio of the Parental Stock

In a field experiment (Mires, unpublished) done in two spawning ponds (0.4 and 1.0 ha) at the Kibbutz Ein Hamifrats, two different parental sex ratios were tested over a whole spawning season: *S. niloticus* B females x *S. aureus* males, 1:1 and 3:1. The basic assumption was that in this kind of spawn, the females do not have a strong urge to spawn with males of a different species and therefore a stronger "male pressure" could improve the situation. This assumption was based on the fact that in aquarium conditions it often happens that two or more females are ready to spawn at the same time, while there is only one male available. In such cases it often happens that the eggs of one of these females are not fertilized. The 1:1 ratio gave higher fry production than the 3:1 (800 fry per female in the 3:1 ratio compared to 1,100 in the 1:1 ratio).

The beneficial effect of the "male pressure" ratio has again been shown recently (Lovshin 1980) when for *S. niloticus* Ivory Coast females x *S. hornorum* males, a 1:2 sex ratio gave significantly higher fry production than 2:1 or 1:1.

4. Differences in Spawning Behavior; Incompatibility Problems

Differences in spawning behavior have been described for various species of tilapias (Fryer and Iles 1972; Lee 1979). The incompatibility between the species used in interspecific crosses have usually been studied in aquaria or in tanks, but not in nature.

Tables 3, 4 and 5 show that *S. niloticus* Ghana females do not have any incompatibility problems in crosses with *S. aureus* males. In the last experiment (Table 3), the average spawning frequency was just as high as in individual intraspecific spawns (Tables 1 and 2). However, *S. aureus* and *S. niloticus* Ivory Coast females did encounter serious problems while spawning with *S. niloticus* Ivory Coast and *S. aureus* males respectively, and therefore, the number of spawns obtained from these crosses was very low.

In interspecific crosses in tanks between *S. niloticus* Ivory Coast females and *S. hornorum* males, some of these incompatibility problems can be overcome by surgical removal of the male premaxilla (Lee 1979). However, male aggression is only one of the problems. Other factors that may cause low fry productivity in interspecific crosses include differences in courting behavior, in mating color display and in the form of the nest. All these problems and others may exist separately or simultaneously and are very hard to overcome in ponds.

Table 4. The spawning frequency and egg production of *Sarotherodon aureus* females in interspecific spawning crosses with *S. niloticus* Ivory Coast males 50 g each over a 12-month period (after Hulata et al. 1980 and Hulata unpublished data).

Female no.		Date of spawning			Total egg count	Average eggs/ spawn*	No. of spawns	Average interval (days)
1	Date	16/6-	4/7-	16/8-				
	No. eggs	**	348	88	348	348	3	
	Interval (days)	18	43					30
2	Date	7/8-						
	No. eggs	**					1	
	Interval (days)							
3	Date	5/7-						
	No. eggs	**					1	
	Interval (days)							
4, 5, 6,	Date							
	No. eggs						0	
	Interval (days)							

*Based on the number of eggs in fertile spawns only.
**Infertile spawns: eggs not counted.

Table 5. The spawning frequency and egg production of *Sarotherodon niloticus* Ivory Coast females in interspecific spawning crosses with *S. aureus* males 50 g each over a 12-month period (after Hulata et al. 1980 and Hulata unpublished data).

Female no.		Date of spawning				Total egg count	Average eggs/ spawn*	No. of spawns	Average interval (days)
1	Date	27/7-	19/8-	7/9-	5/10-				
	No. eggs	341	273	460	464	1,538	384	4	
	Interval (days)	23	18	18					19
2	Date	3/2-							
	No. eggs	136					136	136	1
	Interval (days)								
3, 4, 5, 6,	Date								
	No. eggs							0	
	Interval (days)								

*Based on the number of eggs in fertile spawns only.
**Infertile spawns: eggs not counted.

Table 6. Fry production (*Sarotherodon niloticus* ♀ x *S. aureus* ♂ hybrids) from 3 spawning ponds at Ein Hamifrats fish farm over the four month summer spawning season, harvested with a 5 mm mesh net.

Pond no.	1	2	3
Area (ha)	1.5	1.3	0.7
Parental stock			
Females	1,400	1,057	579
Males	900	1,084	300
Removal of fry			
End of July	650,000	600,000	160,000
End of August	230,000	192,000	220,000
Total	880,000	792,000	380,000
No. of fry/♀	628	749	656

The Mass Production of Hybrid Tilapia Fry

Five or six million hybrid tilapia fry per year are now being cultured commercially within the Israeli fish farming system, produced by a few farmers who have acquired a lot of recent experience. However, only a part of these produces pure-strain tilapias. It seems, therefore, that the future of the Israeli tilapia culture industry lies in the hands of a few specialist hatchery operators.

The problem of low fry production per spawner has been solved by holding more parental stocks. Low productivity of spawners is, however, only one of the problems that have an influence on the mass production of fry. In countries with a warm temperate climate, like Israel, overwintering of the fry is another problem. In Israel today, this has been recognized as a serious limiting factor, and many farmers are experimenting with various facilities which will help overcome it.

Tilapia fry under 20 grams are hardly able to survive the Israeli winter temperatures. To overcome this problem, young fry must be introduced into the nursing ponds early enough to reach or exceed this weight before the winter. This takes about 60 days and the growing season ends at the beginning of November. Therefore, the last date at which it is still worthwhile to start nursing is September. This restricts the usable spawning period to four months only: from May to the end of August.

In addition to these restrictions, the Israeli hybrid fry producers prefer to harvest with nets of at least 5 mm mesh, because smaller mesh nets collect a lot of mud and cause big fry losses. At the end of the spawning season, therefore, hundreds of thousands of the small fry are left unharvested and are not recorded as part of the total production of the spawning ponds. During the four-month spawning period, not more than two or three spawns can be expected from each female. Therefore a 400 g *S. niloticus* female cannot produce more than about 2,500 fry per season. In practice, the best yields obtained from females of this size in the Kibbutz Ein Hamifrats fish ponds, using a 1:1 sex ratio and counting all small fry, never exceeded 1,500 fry/female. The normal average production, using a 5 mm mesh net, is usually less than 1,000 fry/female (Table 6). Therefore, we could only expect to increase production by about 100% from existing facilities, even if all the problems cited above were solved.

Discussion

With this information we can attempt a new synthesis of the interrelationships of the various factors influencing intraspecific and interspecific spawning in tilapias and point out the factors that will have to be studied in order to overcome the problem of low fry production. The various factors fall into three main categories: genetical, behavioral and environmental.

1. Genetic Improvement

There is a very big phenotypical individual variability in the fecundity of the various tilapias. This variability exists within individuals of the same species as well as between the different species. Therefore, females whether from the same or from different species, will not necessarily produce the same amount of eggs even when crosses occur under identical conditions. This big variability has probably been the cause of some of the discrepancies between results of previous experiments. It seems that the smaller the number of spawners in a spawning pond, the bigger the chances will be of obtaining inconsistent results. If more fecund genotypes can be selected for cultured strains then higher yields of fry can be expected from both intraspecific and interspecific crosses.

2. Behavioral Factors

The different behavioral patterns that exist between the various species cannot be altered, although techniques like the removal of the male premaxilla may reduce behavioral incompatibility in some cases. Other solutions to this problem may be altering the conventional parental sex ratios, especially by using a higher male to female ratio, or using species with a closer behavioral pattern.

3. Environmental Factors

In normal environmental conditions female tilapias of any species will always spawn according to their natural individual spawning capacity, but the number of fertilized eggs and the production of fry seem to be mainly determined by behavioral factors. The improvement of environmental factors will most probably have a beneficial effect on fry production from any kind of cross.

In the immediate future it seems that the mass production of hybrid tilapia fry will still depend on the number of spawners used for any given cross.

Acknowledgments

I would like to thank Dr. G. Hulata and the genetic team in Dor station, for allowing me to use some of their data. I would also thank Dr. Hulata, Dr. Ernesto and Mr. Aldridge for reading the manuscript and for their remarks.

Discussion

NOAKES: In your Tables 1 to 3 giving the spawning performance of females, are these individual females in isolated aquaria or are they all in the same tank?

MIRES: Tables 1 and 2 refer to individual females in individual cells.

NOAKES: Then these were in separate water bodies with no contact between them?

MIRES: No, they were separated by partitions but in a common water body. There would be the possibility of chemical contact.

NOAKES: The reason for my question is that the apparent pattern suggested to me some kind of hierarchical arrangement, or some kind of inhibition of spawning of some females by others. Whatever the reason, the pattern of spawning by females is quite repeatable.

MIRES: I would say that there was no hierarchical arrangement. A hierarchy would probably show in the amount of eggs spawned, whereas here, successful spawning females always showed full spawning aggression and spawned normally.

NOAKES: It just occurred to me that the other females may sense chemically that a given female has spawned close by and may be inhibited by this.

MIRES: If this is so, I have no knowledge of it. There was of course a water change in this system.

PHILIPPART: Have you found differences in the number of spawn obtained from different-sized females?

MIRES: The data we are discussing here were from comparisons with females of equal size. They show a big variability in spawning frequency. I can say, however, that within a spawning family in aquaria in my hatchery it always happens that a few of the females are doing all the work and the remainder are not doing very much.

CHERVINSKI: Do you think that by draining your spawning ponds you are getting higher fry production than by not draining?

MIRES: I believe definitely yes, and I would like to suggest why. We know that there are definite differences in fecundity between species. Also *within* a species there are differing individuals with higher or lower fecundity. Pond drainage and water change will therefore improve production both from inter- and intraspecific spawning.

CHERVINSKI: Perhaps by doing this we are getting rid of some waterborne chemical factor produced during reproduction which at high fry densities inhibits further reproduction?

MIRES: I don't believe so.

LOVSHIN: What is your source of water?

MIRES: In the hatchery, it is the city water supply; in outdoor ponds it is a mixture of irrigation water, well water and water reclaimed from sewage effluent.

LOVSHIN: I was just thinking that even if you do keep wild tilapia out, they could be a source of chemical factors in the water, but I do not really think this is important. What is very significant in my view is that by draining the pond and removing the small fry you are greatly reducing the scope for cannibalism and this is probably the basis of your improved production. Partial selective harvesting or draining on a one- or two-month basis is always a good thing. I would not discount the possibility of a chemical stimulatory effect of water change on spawning or vice versa on an inhibitory effect by chemical factors at very high fish densities, but I have experienced continuation of spawning at very high densities (see Henderson-Arzapalo et al. 1980—Editors).

ROBERTS: Much of our hatchery work is done in Edinburgh prison by long-term prisoners. They take great pride in keeping the fish and preparing high protein diets, such as earthworms, for them. We maintain there pure lines of *S. niloticus*, *S. mossambicus* and *S. spilurus.* We can get regular spawning virtually every month (say 28 to 35 days) from given broodstock of all these species over an 18-month period. After this, they are less effective as broodstock and we choose to replace them although they are still fecund. These are fish which receive very careful attention and the best possible diet in small aquaria. I realize that this would not be economical on a commercial scale and that our situation is very different from Mr. Mires' hatchery. Our results suggest, however, that you can smooth out the variability in spawning by optimizing all conditions.

MIRES: Do your results apply to all your fish on an individual basis?

ROBERTS: To virtually every fish.

MIRES: Are they in separate tanks?

ROBERTS: They are kept in tanks in groups of 3 or 4 females per male.

HENDERSON: This suggests that we know very little about optimum husbandry methods in commercial hatcheries.

ROBERTS: I think that the main factor with our fish is their good husbandry and diet, including live food.

LOVSHIN: Regarding the age of broodstock and the length of time for which you can use them, we found in Brazil that after 1 year of spawning activity, i.e., after 3 or 4 spawnings (after which time our fish would be one to one-and-a-half years old) the number of fry produced per unit body weight would fall by about 50%. We therefore began to replace such fish, which were about 300 g in weight, with smaller fish, say 60 g, and we found that such continuous replacement gave better production than carrying on with the big fish. I cannot altogether explain this as of course larger fish produce larger total numbers of fry per spawning than small fish. I suspect that it is a question of spawning frequency. The smaller fish are more active and frequent spawners.

NASH: Does the fecundity decrease in the larger older spawners, or does the viability of the eggs decrease?

LOVSHIN: I have no way of telling from pond work. We should expect larger numbers of eggs from larger fish.

MIRES: I have observed in aquarium spawnings that the viability of eggs is just as good from 6-year old fish as from younger broodstock.

LOWE-McCONNELL: In the wild, with batch-spawning species such as *S. esculentus* and also *S. leucostictus* in Lake Victoria, the number of eggs per batch gets lower with successive batches in females of comparable size. Robin Welcomme has demonstrated this.

MIRES: I know this, but in aquaria we have not observed a similar situation. On the contrary, the number per batch sometimes goes up.

General Discussion on the Biology and Culture of Tilapias

Compiled by R.S.V. Pullin

Abstract

A report is given on a wide ranging discussion on the biology and culture of tilapias. The topics covered include speciation, species for aquaculture, establishment and conservation of pure strains, the concepts of stunting and a switch between somatic growth and gametogenesis/spawning, the physiology of digestion in tilapias, detritus and detritivory, feed formulation, food presentation, broodstock nutrition, broodstock management, mass seed production, recruitment control, integrated farming and wastewater reuse, and diseases of tilapias.

Classification and Speciation

Dr. Trewavas began by outlining the classification and interrelationships of the tilapias. It is generally accepted that the mouthbrooding species arose from ancestral substrate-spawning *Tilapia* and from a narrow group of these. Prof. Peters thinks that this may have happened several times, including the comparatively recent evolution of the species of the Cameroon crater-lake, Barombi Mbo. For this reason he thinks it inappropriate to unite those of more ancient origin with the more recent ones in one genus separate from *Tilapia*. He would retain the generic name *Tilapia* for all of them. But the mouthbrooders are alike, not only in their reproductive arrangements but also in their feeding habits and structures, and the *Sarotherodons* in Barombi Mbo are in Dr. Trewavas' opinion derived from species that were already mouthbrooders and microphagous feeders. This is not to say that there are no mouthbrooders derived independently from *Tilapia*, but these have not developed the same feeding structures as *Sarotherodon*.

There is more than one way of expressing such opinions in the nomenclature, and it is proposed to adopt the name *Sarotherodon* for all the mouthbrooding tilapias (but see Preface and Addendum, p. 11-12). There is no doubt that the east and central mouthbrooding species belong to a branch or branches that have long been separated from the west African. This may be expressed by regarding them as separate subgenera, a rank that may be disregarded by those not specialists in taxonomy.

Methods of speciation were discussed and the main point emerging was that speciation among the tilapias has been almost exclusively by specialization following geographical separation, i.e., allopatric. Among the notable exceptions where sympatric speciation is thought to have occurred, that in Lake Barombi Mbo is the most interesting. This 2.5 km diameter lake has 11 species of endemic cichlids, including four which are arguably

Sarotherodon spp., although their reproductive behavior has not been fully described. Dr. Trewavas speculated that the present situation had probably arisen from more than one source species, and included some fascinating scenarios requiring successive introductions of local riverine species with extreme spates and specialization/radiation/changing lake conditions in the intervals between spates. The Malawi species flock is another interesting example.

The difficulty of detecting modes of speciation was also apparent from studies on Lake Jipe in which it was not clear whether the present lacustrine species had arisen sympatrically from incursions of *S. pagani* from the Pagani River or whether *S. jipe* was itself originally present in the river. Also in west Africa, the lower Nile and Israel, *S. niloticus* and *S. aureus*—which are so alike that some museum workers have confused them in the past—are sometimes found together. Whether this is a secondary coming-together or a result of some sympatric speciation is difficult to say. These species do have slightly different ecological niches, for example in feeding habits, and sexual dichromatism and dimorphism are more marked in *aureus* than in *niloticus*.

Allopatric speciation has been the general rule for tilapias. For example, *S. mossambicus*, which occurs in the lower Zambezi and Limpopo Rivers, *S. spilurus* in Kenya (this species is so similar to *mossambicus* that they are difficult to separate in preserved material), *S. urolepis* in the Rufigi River and *S. hornorum* in Zanzibar, are all part of the same group. They are of similar appearance with a long snout and long jaws especially in breeding males. *S. hornorum* is particularly easy to distinguish on characters such as fin-ray counts.

The species living in the east African alkaline lakes, such as Lake Magadi, were also discussed. These species, e.g., *S.a. alcalicus* share a common problem with tilapias inhabiting river systems that are prone to severe drying, namely, a very restricted environment. In the alkaline lakes, the waters habitable by fish are restricted to those after the hot spring waters (about 42° C) have cooled slightly and before their salt content becomes too elevated by evaporation. Such species have many things in common. They generally have low number of gill rakers, vertebrae and fin-rays; they are very aggressive and active despite their high population density and restricted space, and they breed at an early age and small size. In Lake Natron, very small *S.a. alcalicus* males set up their breeding pits adjacent to those of mature males but in Lake Magadi small *S.a. grahami* interfere with larger spawning fish. Such populations show in natural waters the early breeding characteristics that tilapia culturists would like to avoid. They merit much fuller study. It would be a mistake, however, to call these wild fish 'stunted' as they are often in good condition.

The total number of species of *Tilapia* and *Sarotherodon* is a matter of opinion. Dr. Trewavas estimated that there are approximately 30 *Tilapia* and 46 *Sarotherodon* species. She pointed out that Thys van der Audenaerde regards as species populations of *S. melanotheron* that she considers subspecies. Dr. Trewavas has also recognized 7 subspecies of *S. niloticus*, some of which have yet to be named.

It is obvious that transplantation of species into natural waters, dams and aquaculture systems has further complicated an already complex situation.

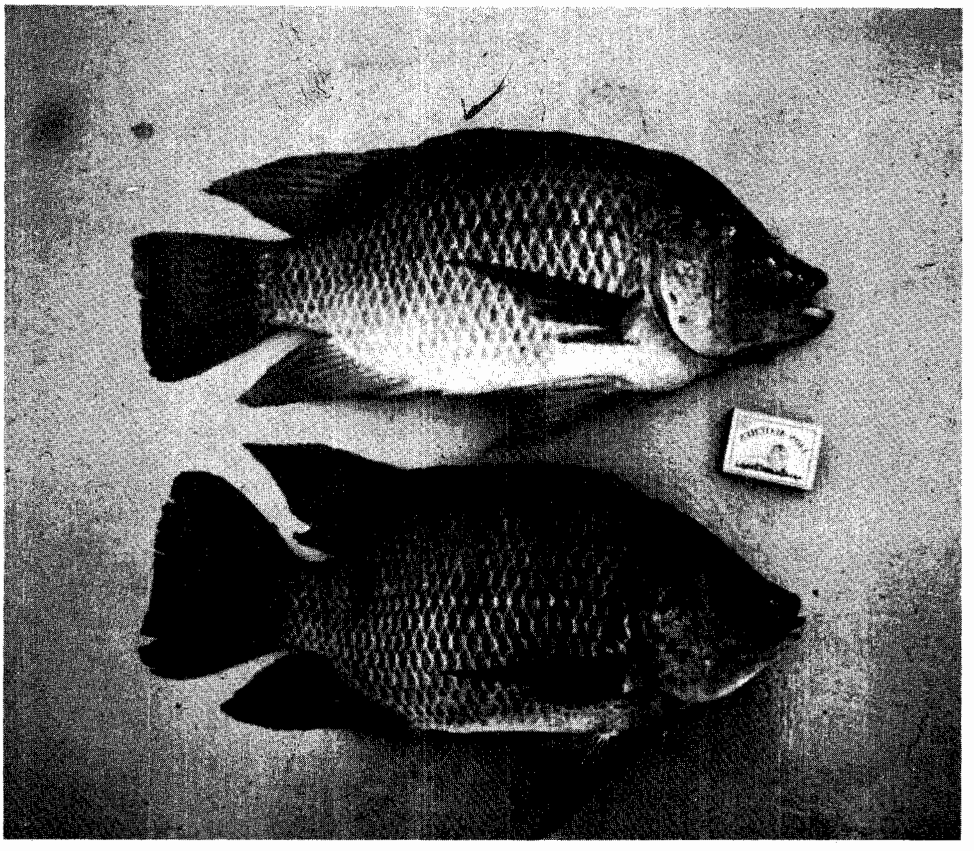

Plate 1. Typical *S. mossambicus* from lower/middle Zambezi. Photo by M.S. Caulton.

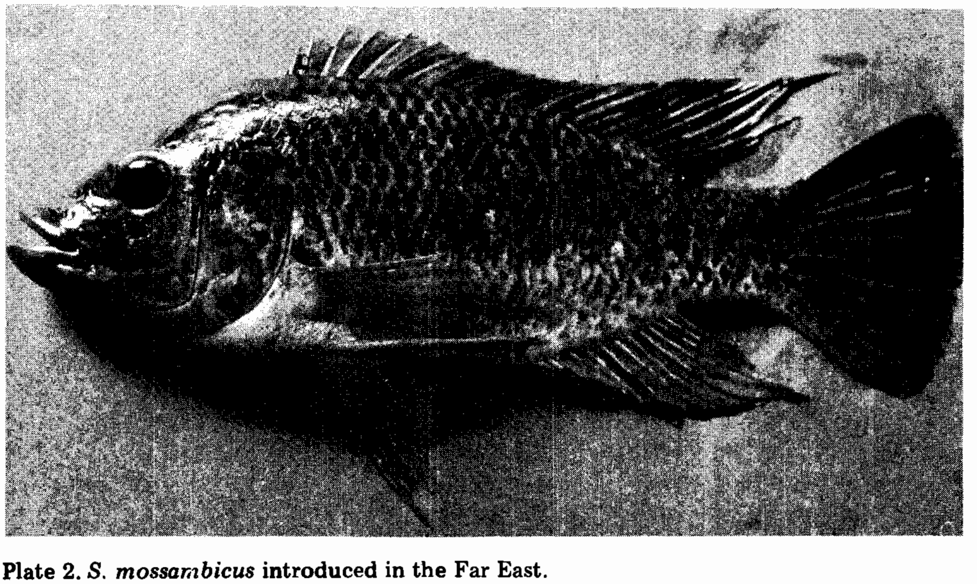

Plate 2. *S. mossambicus* introduced in the Far East.

In some natural waters which have received multiple introductions, e.g., Lake Naivasha, the tilapia populations have changed year by year through hybridization and interspecific competition. The classic definition of a species, based on reproductive isolation, is obviously of limited use for tilapias, especially in aquaculture where so many different hybrids have been produced. There is a need to distinguish between postulational and operational definitions of species. For aquaculturists, an operational definition is required, i.e., a species must be recognizable either from morphology or biochemical tests.

There was a brief discussion on whether species developed through allopatric speciation would be incompatible with respect to reproduction if brought together. The consensus of opinion was that tilapias usually hybridize relatively easily. Differences in reproductive behavior are probably the most important factor where interbreeding is difficult. It is possible that bringing species together in an artificial lake or culture environment may facilitate hybridizations which would not occur in a natural environment.

Several speakers commented on the change in appearance of transplanted species. To illustrate this, Dr. Caulton showed a picture of typical *S. mossambicus* from the lower/middle Zambezi (Plate 1). These large deep-bodied fish are much larger at first maturity (around 500 g for breeding males) than is commonly seen in introduced populations in the Far East (Plate 2).

Species for Aquaculture

The species currently being used for aquaculture are a good representative group of the tilapias. The use of additional tilapia species for aquaculture is controversial. It could be justified where, for example, a previously unoccupied niche in a polyculture system could be filled or where additional species could outperform existing cultured species in growth and/or reproductive performance. Additional species would also open up new possibilities for hybridization work, but the maintenance of genetically pure lines is not an easy task. Hybridization work has concentrated largely on the production of all-male progeny rather than on demonstration of hybrid vigor, production of new hybrids for brackishwater culture, etc.

There are some other cases in which new species could prove useful. For example, Prof. Roberts stated that *S. spilurus spilurus* performs very well in brackish and seawater culture unlike *S. spilurus niger*. Small decorative species, such as *S. alcalicus grahami*, could have a future in the aquarium trade, although sex-reversal or other sterility-inducing techniques are needed to make this a continuing commercial proposition. Attempts to sex-reverse *S. alcalicus* fry have so far been unsuccessful and it is possible that such small, early maturing tilapias have fry whose sex is determined before release from the parental mouth and are therefore not easily treated with sex-reversing steroids.

T. rendalli merits more attention in culture where vegetation is available for feeding. Although *S. hornorum* x *S. mossambicus* hybrids produce all-male progeny, *S. spilurus* x *S. mossambicus* crosses do not. This is probably indicative of a closer relationship between the latter two species.

Establishment and Conservation of Pure Strains

Very few pure strains of tilapias are available to culturists. Only where stocks are continuously tested by electrophoretic markers and selected can genetic purity be ensured, e.g., the *S. aureus* stocks at Mr. Mires' hatchery at Kibbutz Ein Hamifrats, Israel, tested by Prof. Avtalion. Elsewhere, culturists are relying on wild stocks, often contaminated by hybridization with introduced species, or on introductions made many years ago from very restricted gene pools, e.g., about 30 *S. aureus* individuals sent from Israel to Auburn University, Alabama, have been the ancestors of widespread introductions for culture in Southeast Asia and Latin America, where it is not surprising that they are showing signs of inbreeding depression.

There is a clear need for collections of known strains of tilapias for research and culture work. The establishment of such collections was discussed and the following points were made:

1. Collections would have to be very carefully maintained by painstaking workers in high-security premises and replicated at several different locations.
2. Tilapia broodstock collections are probably not a function for regional aquaculture centers in tropical developing countries where such work would be difficult to carry out and would normally take lower priority than production-orientated research.
3. The location of some collections in colder countries could prove advantageous as escapees would not survive to cause environmental problems.
4. The facilities needed to accommodate large numbers of broodstock of different species and strains would be very costly.
5. Tilapia researchers have much to learn from domestic animal and plant breeders in planning such collections.

It was agreed that the methodology for maintaining pure strains needed further development. Cryopreservation of semen could prove a useful future technique for storing male genetic material. At present, the collections of tilapias maintained in Israel, the United Kingdom (Stirling University), the Philippines (Central Luzon State University) and the U.S.A. (Auburn University) were recognized as the most significant. In the absence of funding or plans for larger collections, it was stressed that natural populations of tilapias in African waters should be carefully protected. Transplantations should be avoided wherever possible to assist in the conservation of genetic material for the future. For example, the natural populations of *S. hornorum* are probably uncontaminated at present. There is a clear need for cataloguing critical sites, such as the small lakes in the Cameroons and possibly Lake Bosumtwi. The International Union for the Conservation of Nature (IUCN) is aware of the vulnerable nature of these populations.

Three main objectives were identified concerning the genetic improvement of cultured tilapias: 1. The guaranteed supply of high quality pure strain or hybrid fry for farmers; it was recognized that these would be expensive and that restriction of distribution to monosex progeny may be desirable. 2. Conservation of wild tilapia stocks. 3. The absolute necessity for *all* researchers to work with known material.

Prof. Roberts gave a very useful example of the confusion which can arise if the last of these objectives is not fulfilled. At Stirling University, experimental infections of *S. mossambicus* with a monogenean (*Cichlidogyrus* sp.) would take only in a strain known as 'B' from a type location in Africa. *S. mossambicus* strain 'A' which had come via Singapore and was slightly contaminated was resistant to infection. A parasitologist working with 'A' only would have drawn the erroneous conclusion that this particular *Cichlidogyrus* sp. was not a parasite of *S. mossambicus.*

The Concept of 'Stunting' and a 'Switch' Between Somatic Growth and Gametogenesis/Spawning

(The concept of a simple 'switch' is perhaps false, as somatic growth demonstrably does not cease during gametogenesis. The greatest growth check occurs from the onset of spawning through to mouthbrooding—Editors.)

The phenomenon of stunting was discussed in relation to the concept of a switch from somatic growth to gametogenesis leading to first maturity. The phenomenon of maturation at a small size is common to both guarders and mouthbrooders and to riverine and endemic lacustrine species. For example, *S. esculentus* normally take about three years to mature as 20-cm fish in Lake Victoria, but will mature after only five months as 10-cm fish in aquaria. This ability to shift the timing of the 'switch' has great adaptive value particularly in lakes which dry up periodically, e.g., Lake Rukwa and Lake Chilwa, where fish migrate to inflowing streams as the lakes dry, breed at a small size, and then repopulate the lakes when they fill again.

Dr. Lowe-McConnell's data for *S. niloticus* suggest that breeding size is low if condition factor is low in the population. This suggests that the quantity and/or quality of available food may be a factor. Other possible factors include water chemistry, temperature, salinity, dissolved oxygen and parasite burdens.

There are further clues in results of field biology studies. For example, the *S. niloticus* population in Lake George remained unfished from the 1920's to 1952 because of tsetse fly infestation of the area; their minimum breeding size was about 28 cm. With increasing fishing pressure from 1952 to 1972, the minimum breeding size fell to about 18 cm. Field studies have shown that the majority of the fish have always concentrated around the lake margins. Beyond 100 m offshore the bottom becomes a loose flocculent ooze which is unusable for tilapia nests. This suggests that there is a severe limitation on breeding sites and that the removal of large fish by the fishermen has allowed smaller individuals to come in and occupy these sites. The mesh size of fishing (gill) nets has been reduced from 15 cm to about 10 cm. In the early days of this fishery (1950's), very few females smaller than 28 cm had ripe ovaries, and therefore it was gametogenesis, not just spawning, that was restricted to larger individuals.

In Lake Sibaya, it was stated that only the large males can find breeding sites when the lake is at a low level: the smaller individuals take up sites when the water rises. In Lake Valencia (Venezuela), again the cichlid population is found only around the periphery where they form nesting arenas. Diving observations indicate that much wider areas offshore have suitable substrates, but perhaps behavioral factors are involved in the selection of inshore sites.

In Lake Kariba (total area 5,000 km^2), fish have experienced the change from a riverine to a lacustrine environment, and for *S. mortimeri* and possibly some *S. mossambicus* this has involved a change from a situation with relatively scarce to one with abundant breeding sites. In the fast-flowing Zambezi, fish were able to breed only in bays and backwaters; now it has about 2,000 km^2 of lake waters of appropriate depth. With this change, the minimum breeding size has increased from 3-400 g to 600 g. Middle Zambezi fishes in the Kariba area are now called *S. mortimeri* although some *S. mossambicus* may have been moved around and hybridization may have occurred.

S. a. grahami introduced to Lake Nakuru has changed the whole ecology of the lake. For example, the population of birds has increased from a few casual visitors to vast numbers of residents feeding on the fish. *S. alcalicus* has thrived in this lake and appears to breed at a larger size than in its more restrictive alkaline lake habitats, although the breeders are probably still very young. This is perhaps analogous to the situation with milkfish *(Chanos chanos)* in hypersaline lagoons on Christmas Island, which mature late and at a small stunted size compared to open sea fish. *S. a. grahami*, however, may grow quickly in restricted, high temperature alkaline lakes and breed when small and *young*. The fast growth could explain its low vertebral counts. These questions will not be resolved until more data are collected on growth rates for 'stunted' and other populations in restricted and open habitats.

The above examples were discussed at length but there was no general agreement on their implications for culturists. The fact that culturists have frequently observed mouthbrooding species spawning in cages suggests that the hypothesis concerning shortage of breeding sites in lakes may be incorrect. A cage does, however, provide a solid substrate, with visual cues. In the Lake George example, it was felt that there was insufficient knowledge of the simple effects of fishing selection and the genetic make up of the population: apparently, a few 40 cm fish are still catchable far offshore.

There were also conflicting reports on the effects of environmental factors on maturation and spawning. For example, nest building is rarely seen below 60 to 70 cm depth in Israeli tilapia culture but *S. mossambicus* breeds normally at 2 m in Lake Sibaya. Indeed, the preferred depth for mating pits seems to be a specific character, c.f. the Malawi species flock. It was suggested that culturists could test the Lake George hypothesis in ponds by adding large fish to outcompete the cultured crop for breeding sites. The idea here is that the large fish would inhibit spawning by the cultured crop which would therefore keep growing. This idea was not received very enthusiastically as it would still mean accepting recruitment from successful large breeders. An alternative suggestion was the development of weak or non-functional males which would fail to fertilize eggs and cause these to be rejected by the females thereby reducing the females' non-feeding period.

Many plants and animals adjust their life-history strategy to maximize the intrinsic growth rate of the population ('r'). The 'decision' when to produce gametes and breed involves a tradeoff with respect to any individual's contribution to the population. By delaying breeding, the individual increases its size and energy stores for the future whereas by breeding early, it reduces its exposure to mortality risks and shortens the generation time.

This theoretical framework can be fitted to all the tilapia examples given. For example, in Lake George, there is a classical response of earlier breeding with exploitation (fishing mortality). In Lake Sibaya, *S. mossambicus*, when they reach about 8 cm, are exposed to heavy predation from birds and *Clarias* if they remain in the rich feeding grounds inshore and here they breed at a small size. The theoretical framework, however, does not tell us the mechanism for the switch to breeding. The mechanism is probably some sort of energy constraint rather than a simple behavioral or ecological factor such as competition for breeding sites or mates.

The theoretical framework does, however, tell us where to look for the mechanism or at least for ways to manipulate it without having to unravel all the detailed behavioral, endocrinological and other physiological interactions. The basic theories of population dynamics and natural selection tell us to look for correlations between environmental changes and reproductive output.

Dr. Jalabert proposed a model of a balance beam between somatic growth and gonad development with genetic and environmental factors controlling its swing. It was generally agreed that the difficulty, expense and complexity of endocrinological and other physiological research made it unlikely that more research in these fields would bring rapid payoffs for aquaculture in the form of techniques to manipulate the switch. The best approaches were identified as behavioral studies, environmental manipulation and work on the genetics of maturation age and size. It was felt, however, that some useful techniques for culturists could emerge from attempts to identify and synthesize pheromones or other waterborne factors. There was further discussion of the existing experimental evidence and the best possible clues for environmental studies.

The question of available oxygen was debated and it was pointed out that 1 kg of small-sized tilapias (say individual weight about 10 g) require about twice as much oxygen as 1 kg of, say, 200 g fish. It is possible, therefore, that in a pond situation with densely crowded small fish, the available oxygen for digestive/oxidative processes becomes so reduced that metabolic pathways are affected. Perhaps, as a result of this, nutrients begin to be channelled into gonadal products. Also, as the gill surface area of fish limits their ability to take up oxygen, the relative growth of this to the overall size of the fish could be involved in the 'switch' in environments with variable oxygen availability (see Pauly 1981—Editors).

There are two factors that could encourage a fish to continue to channel all its assimilated nutrients into somatic growth rather than gonadal products, unlimited food supply and a low risk of mortality. In culture, the questions of food supply and quality are relatively easy to investigate. The risk or 'expectation' of mortality is more difficult, however, and can only be expressed in vague terms as stress factors, e.g., oxygen stress, salinity stress, thermal stress, density stress.

The possibility of genetic determination of age at first maturity was then discussed. It was stated that if age at first maturity is genetically controlled, then the problem for a culturist is how to get the maximum growth within this period. Evidence was cited against genetic determination of first spawning age in the tilapias. The example of *S. esculentus* breeding at two to three years of age in natural waters and five months in captivity was repeated, but the prospect of genetic selection for later spawning was not dismissed.

The consensus was that gross environmental changes are the overriding factors determining age/size at spawning. The examples of *S. mossambicus* breeding at 6 g after five months in aquarium conditions and the fished population of *S. niloticus* in Lake George now spawning at 18 cm (estimated age 1 yr) as opposed to 28 cm (estimated age 1.5 yr or older) were repeated. Dr. Caulton also cited some personal observations on *S. mossambicus* which bred two or three times over a two-year period in aquaria and were about 50 g in weight. When transferred to a more spacious environment—in this case a *Macrobrachium* farm raceway—the fish stopped further breeding until they reached about 250 g and were 3 yr old. This suggests that the flexibility of timing maturation and spawning extends beyond the age/size at first maturity and effects spawning frequency as well. In Lake Sibaya, *S. mossambicus* reaches first maturity in one or two years.

The experiences of experimental culturists in Israel, the Philippines and the U.K. indicate that the age at first maturity for a given species is relatively constant, i.e., to within a matter of a few weeks at a given location, but that great variability occurs between different populations at different experimental stations. *S. niloticus* and *S. aureus* are later spawners than *S. mossambicus*.

In the Philippines, the age for first spawning of *S. mossambicus* is about two months and for *S. niloticus* about three months in pond systems. Stunted fish of 5 to 10 g spawn after two to three months as well as larger fish. It has also been observed that *S. andersonii* in Zambia, living at relatively low temperatures, breed fairly late (at about 15 months in ponds) and at a large size. In natural waters here they also take 3 years or more to reach first maturity. When this species was transferred to Tanzania, maturation was noted as early as two to five months at a very small size.

In Israel, it was of note that the necessity to overwinter fish gave very little scope for trying to alter the age at first maturity. The greatest potential appears to be in tropical locations where 'young of the year' are cultured in shorter production cycles.

It was also noted that while manipulation of stocking density, salinity, temperature and other environmental factors may be biologically feasible as a means to influence gametogenesis and spawning, any method chosen for commercial application must be economically feasible also. For example, it may be possible to delay or suppress reproduction by lowering the temperature to 18 to 20°C, but this would be expensive and growth rates would be severely reduced.

The effects of light and daylength were discussed and it was pointed out that a given species usually spawns at a fixed time within a 24-hour cycle in aquarium conditions. There could be scope for further investigation in this, especially as gametogenesis in trout has been suppressed experimentally by continuous illumination. The effect of temperature may be different for fish of different ages or sizes and more important than the effects of feed quality and quantity. If so, then *S. mossambicus*, first spawning at four months in a relatively cool location, could spawn at, say, two months at a hotter location, irrespective of the feeding regimes.

Nutrition

1. THE PHYSIOLOGY OF DIGESTION IN TILAPIAS

Dr. Moriarty summarized the digestive physiology of microphagous tilapias, i.e., those feeding on phytoplankton, blue-green algae (cyanobacteria) and detritus (including bacterial proteins). Previous studies have shown that although the stomach in these fish is structured such that some food can pass from esophagus to intestine through the anterior end only, it is a true stomach with a pyloric sphincter and a very important cycle of acid secretion.

The sequence of events observed in large individuals having a relatively large stomach is as follows. In the early morning (6:00 A.M.), when feeding commences, the stomach is collapsed (contracted) and secretes little or no acid. For the first few hours of feeding, therefore, some of the food passes through the anterior end of the stomach straight from esophagus to intestine. As feeding increases, however, the stomach becomes progressively distended and takes in food. It also begins to secrete acid. By 10:00 A.M., acid secretion is maximal and over the next 1 or 2 hours the pH in the ventral portion of the stomach falls below 1.8, at which point acid lysis of bacterial and algal cell walls commences. Over the 6-hour feeding period from 10:00 A.M. to 4:00 P.M. ingested food can either pass into this very acidic portion of the stomach for complete lysis or pass through only the acidic portions (pH > 2.0) or bypass the stomach more or less completely. After feeding stops, the rate of movement of food through the stomach slows down, thus allowing all the food material to be exposed to a low pH. Complete lysis and digestion of all food occurs, whereas bacterial or blue-green algal cells that pass rapidly through the stomach and thus are not exposed to a high acid concentration are incompletely digested. The assimilation efficiency may be as high as 80% for blue-green algae ingested during the period of peak acidity, but it is near zero at the commencement of feeding and variable at other times. The mean assimilation efficiency over the whole feeding period is probably 40 to 50%. For small tilapias and for *Haplochromis nigripinnis*, which has a similar digestive physiology, the overall assimilation efficiency is higher, probably because the acid concentration is high throughout their small stomachs.

Fish culturists were advised to take note of the very slow passage of food through the tilapia intestine during non-feeding periods (4:00 P.M. to 6:00 A.M.) in systems where natural or *ad libitum* feeding is available. The assimilation efficiency is very high during non-feeding periods. This suggests that the most efficient utilization of food in cultured fish could probably be obtained by a series of feeding/non-feeding cycles, i.e., a feeding period sufficient to distend the stomach and stimulate maximum acidity followed by a non-feeding period to allow maximum lysis of the ingested food and slow passage through the intestine. With controlled feeding, perhaps two or three such cycles could be applied each day. Further work is needed to determine the effect of rate of movement through the intestine on assimilation rate and efficiency, and thus whether such feeding cycles are advantageous.

Dr. Bowen's work on *S. mossambicus* in Lake Valencia was discussed. It was noted that high-quality proteinaceous material is usually completely assimilated within the first quarter of the intestine whereas the peptidic fractions of detrital agregates (see below) are digested and assimilated all along the intestine. It was agreed that although such tilapias do produce a pepsin (pepsinogen has been demonstrated) there is probably no proteolytic digestion in the stomach. The stomach function in *S. niloticus* has become specialized and restricted to acid lysis: proteolytic digestion is confined to the intestine.

Dr. Bowen pointed out that *S. mossambicus* differs from the above pattern (which was largely taken from studies on *S. niloticus* in Lake George, feeding on lake plankton) in that it can fill its stomach within 10 minutes to one hour, depending on the size of the fish. Observations on trawled specimens of *S. mossambicus* (size range 4 to 25 cm) from Lake Sibaya and Lake Valencia show that the degree of stomach acidity depends on stomach fullness. The pH of an empty (resting) stomach is from 4 to 7 whereas that of a full stomach is around 1.5. Therefore, with *S. mossambicus*, there is no long lag period to reach maximum efficiency. The first batch of diatoms ingested can still pass through the gut without lysis, but the very rapid stomach filling and acid secretion mean that the system can work at close to 100% assimilation efficiency thereafter.

There are perhaps some lessons here for culturists. Phytoplankton feeding *S. niloticus* in ponds would largely resemble the Lake George situation and operate well below maximum assimilation efficiency. Any species that can fill its stomach rapidly, however, such as fish receiving supplementary feed or *S. mossambicus* ingesting large quantities of detritus will be much more efficient. Of course economics will dictate what is possible in a commercial situation: phytoplankton is cheaper than supplemental feed!

There was further discussion on the functional anatomy of the tilapia gut. *S. mossambicus* was said to have a relatively muscular stomach which maintains its shape and size when empty better than *S. niloticus* in which the stomach shrinks to a very small size. Dr. Moriarty showed, however, that the stomach of *S. niloticus* at maximum distension holds about 50% of the total ingested material: the other 50% is spread out along the very long intestine. In *S. mossambicus*, the distended stomach holds only about 10% of the total ingested food, the remainder being in the intestine.

Dr. Caulton described the digestive physiology of *T. rendalli* for comparison. The most important aspect of this is the rasping of plant material by the pharyngeal teeth. Within one hour from the commencement of feeding the entire gut of *T. rendalli* can be found packed with plant material of which virtually none is digested, despite pharyngeal teeth disruption. At this time, the stomach pH is about 4. This suggests that *T. rendalli* wastes a lot of food, but it should be noted that not only does it normally have an overabundant food supply but also it can consume very large quantities very quickly, e.g., 3 g in 10 minutes even for very small fish. After about one hour of feeding, the stomach pH falls to about 1.4, lysis begins and assimilation efficiency increases. The overall assimilation efficiency is probably around 50%.

The stomach residence time for food is very important in *T. rendalli* not only because gastric acid assists lysis of the plant cells, but also because denaturation of the protein by acid seems to be a necessary pretreatment for its digestion by enzymes in the intestine. It is well known that trypsins, which are present in tilapias, act better on previously denatured proteins so the acids here could be assisting proteolytic digestion. This is possibly analogous to the action of renin coagulating milk protein in the mammalian gut before digestion.

2. Detritus and Detritivory

Detritus is a very complex mixture of living and non-living components. It is erroneous to regard the food value of detritus (including plant wastes, such as straw and grass clippings) as merely the production of microbial protein built from the waste substrate. Non-living organic matter plays the principal role in nutrition of many detritivores.

The methodology available to sort out the various components of detritus was discussed. Light microscopy is useful to give rough estimates of bacterial numbers and sizes, especially with epifluorescence techniques. Bacteria and blue-green algae can be easily counted when they are made to fluoresce against the non-living matrix. Electron microscopy (EM) has revealed the complexity of detritus. Bacterial slime layers and capsules are visible using EM and include proteinaceous material (stainable with osmium tetroxide), polysaccharides (stainable with Ruthenium Red) and lipids. These are all presumably of some nutritional value to detritivores. Bacterial populations can also be estimated by determining the muramic acid content of detritus. However, even simple analysis into living and non-living material is difficult. ATP measurements will give some idea of this but say nothing of the types of organisms present. It is well known that plant material decomposing in aquatic ecosystems first suffers a drop in N-content for a few days and then the N-content increases. This has always been assumed to be entirely due to the obvious colonization of the material by microorganisms. As the material ages, however, some of its N-content derives from chemical processes, e.g., precipitation/complexing and is found as refractory nitrogenous compounds in the detrital aggregate.

Dr. Bowen's work in Lake Valencia shows that well-established detritus contains very significant amounts of these nitrogenous compounds in addition to microbial protein. Dr. Moriarty questioned the methodology used to estimate these compounds and also Dr. Bowen's conclusion that they were not protein. The extraction methods used to estimate these compounds—6N HCl for 24 hr at 100° C—would in fact hydrolyze all peptidic material to its constituent amino acids. It was also considered significant that while these compounds in Dr. Bowen's work were not extracted by 0.1 N KOH and were therefore not considered proteins, this method does not always give complete protein extraction. Their exact nature must await further study with improved methodology. Dr. Bowen accepted that methodology needed improvement but emphasized that even with the existing crude methodology, his work had demonstrated that microbial protein could account for only a portion of the N-content of detritus. The food value of the refractory nitrogenous compound requires further study.

Detritus and detritivory are very important in pond aquaculture. It was suggested that agricultural wastes could stimulate microbial production in ponds by providing large surface areas for bacteria. The use of animal manures to give high concentrations of suspended colloidal particles for bacterial colonization was considered very important as well as the development of benthic detrital aggregates. This discussion centered on Israeli experience with cow and chicken manure in which the main thesis was that as yields from anaerobic bacterial production are only about 10% of those from aerobes, a system of suspended colloidal material for aerobic bacteria to work on is the best. Frequency of manuring is very critical in the maintenance of sufficient dissolved oxygen for aerobic bacteria and for normal fish growth. Pond aeration can help here. Daily manuring is recommended and rates as high as 180 kg dry matter/ha/day have been used. Therefore, pond management techniques are already being used to maximize bacterial production. Tilapias are the most responsive of all fish to such techniques.

Dr. Lovshin recalled that pretreatment of fish ponds with manure was a long established technique designed to build up plankton populations. It was recognized that this technique must also encourage detrital production as well and that perhaps the recommended time lags between manuring and stocking should be re-examined. This requires a full investigation, i.e., not only how to pretreat to get maximum bacterial and detrital production but also how to continue treating to maintain these through growout. The food value of such sources was also debated. Obviously, before culturists are encouraged to develop detrital systems to feed their fish, it must be demonstrated that these will supply all the required dietary components especially essential amino acids, essential fatty acids, vitamins, etc. The consensus of opinion was, however, that high bacterial diversity and the chemical complexity of detritus made it unlikely that deficiencies in essential nutrients would arise in well-managed detrital-based culture: for example, in manured ponds. Experience with marine fish larval rearing has shown that some long-chain polyunsaturated fatty acids present only in some phytoplankton species are essential for growth and survival, but this situation was not considered comparable to detritivorous adult fish feeding in a pond where the diversity of food items is very high.

Dr. Bowen pointed out that detritivorous fish are very selective feeders in natural waters and suggested that a painstaking approach to defining the essential dietary requirements of tilapias (as had been done for example for salmonids with test diets deficient in individual amino acids and vitamins) was probably not required in this context. Why not just characterize the physical and chemical nature of their selected types of detritus? This approach would help to determine whether it is the microbial biomass or the other components of detritus that are most important in detritivore nutrition in different situations. It was stressed that the nutritional requirements and feeding habits of juvenile fish are often different to those of adults. For example, the juveniles of the microphagous tilapias, up to about 5 to 10 cm, often feed on copepods. As they switch to microphagy, mucous glands develop at the back of the buccal cavity and pharynx. The mucus captures microorganisms for passage to the gut. This switch from zooplankton feeding to microphagy has been observed in culture and in natural waters, e.g., Lake George, and indicates a high requirement for animal protein in juvenile life. The changes in digestive physiology associated with this change in diet have yet to be investigated.

3. Feed Formulation

Prof. Roberts stated that the optimal protein levels, protein/energy ratios and essential amino acid requirements for *S. aureus* and *S. mossambicus* had recently been determined by work at Stirling University for the formulation of complete, pelleted diets. Information was also being gathered on the nutritional value of locally available agricultural products in the tropics. These studies show essentially that these tilapias need the same essential amino acids as other fish but that their requirements for individual amino acids are different. In some control feeding trials using high protein commercial trout diets, tilapias showed a hyperproteinosis syndrome: loss of orientation, swollen bodies and death. The histopathology of this condition was acute circulatory collapse and histamine release from mast cells. Conversely, Dr. Lovshin reported that trout chow with 40% protein is fed routinely to tilapias in ponds and cages with very satisfactory results and no deleterious effects.

Tilapias can accept very high levels of carbohydrates in supplemental feeds. For example, Dr. Coche described work with *S. niloticus* in the Ivory Coast in which diets with up to 45% carbohydrate were accepted.

The use of growth promoters was discussed. It was generally agreed that anabolic steroids could not be incorporated into feeds on a large scale because of cost. Prof. Roberts repeated, however, that sex-reversed fry gain a useful growth boost over non-treated fish from the steroids used: the treatment lasts for 35 days. This effect, and the steroid residues, disappear within 5 days of cessation of treatment when the fry are transferred to growout tanks. The use of virginiamycin (e.g., Biazon) was also discussed. This has been used as a growth promotor in grouper culture in Malaysia, but not apparently with tilapias. Despite its name, it is not an antibiotic.

4. FOOD PRESENTATION

Dr. Coche noted that some pond culture work, for example, Miller's work with tilapias in the Central African Republic, has shown that powdered supplemental feed could give yields as high as pelleted feeds. This suggests that the high cost of pelleting can be avoided. Dr. Lovshin supported this observation from studies in experimental ponds at Auburn University, Alabama, in which meal diets gave comparable yields to pelleted diets. It was agreed, however, that pelleted feeds were desirable for cage culture.

Dr. Coche reported that very good results have also been obtained in the Ivory Coast with mixed feeds presented as a "mash" shaped into large balls, placed in the middle of cage covering nets and lowered underwater. For mariculture, unpelleted wet feeds are generally used.

The problem of food wastage in cage culture was discussed. Although a variety of chemical binders is available for pellets, these can cause problems, for example, the kidney disorders observed in experimental marine flatfish culture in the U.K. Prof. Roberts mentioned that freshwater-moistened diets are preferable for tilapias cultured in seawater as these supply dietary water and reduce osmotic work below that required for salt regulation following seawater drinking. Dr. Caulton commented that in the tropical developing countries, 2% dried green banana powder is the best and cheapest binder available and is used in commercial feeds for *Macrobrachium* culture. However, other materials such as boiled plantains, potatoes, manioc or any other starch source can be used as cheap binders at 10 to 20% of the diet. They would be cheaper and more available than 2% dried green banana powder in many developing countries.

The extent of food wastage from commercial tilapia cages does not appear to have been quantified. All commercial growers use sinking as opposed to the more expensive floating pellets. The ability to manufacture floating pellets may be absent in many of the developing countries. Food wastage seems to depend on the degree of powdering of the pellets during storage and handling (this powder is easily washed from the cage), the pattern of water currents and the rate of feeding. Water currents are particularly important. Dr. Nash pointed out that elongated cages which set parallel to the current can be useful in maximizing food retention if suitable end baffles can be fitted: there are, however, structural limitations to this in strong tidal streams.

It was agreed that tilapias in cages can be very voracious feeders similar to salmonids. Feeding at a very slow continuous rate seems, however, to be very advantageous. Dr. Coche reported that Campbell in the Ivory Coast has used a very slow feeder in which a rope hanging down into the water below the hopper is moved by gentle water currents to allow a trickle of pellets to come out. This simple device could have advantages over more sophisticated automatic and demand feeders. Dr. Philippart stated that in experimental tank trials in Belgium, tilapias in excess of 200 g fed five or six times/day grew better than those fed more frequently, e.g., twice/hour. It was agreed that juvenile fish require more frequent feeding than larger fish: usually about 10 feeds/day.

5. BROODSTOCK NUTRITION

It was agreed that there is very little information available on the nutritional requirements of tilapia broodstock. There is, for example, no information on the effects of nutrition on fecundity in tilapias apart from general observations that well-fed fish have higher counts of oocytes at all stages than poorly-fed fish. Prof. Roberts reported work at Stirling University which indicates that the dietary protein requirements of broodfish are significantly lower than those of immature fish in the most active phase of somatic growth. The *quality* of protein required for broodstock diets is, however, very high. Earthworms are an excellent protein source. For a number of species, it has been shown that broodstock can be spawned at approximately monthly intervals for as much as 18 months given good nutrition. Also, for *S. mossambicus* in tanks, all the animal protein, for example fish meal, in the diet can be replaced with high quality algal protein. For spawning ponds, however, broodstock pelleted diets should contain animal protein.

Dr. Guerrero reported that a commercial animal feed company in the Philippines is developing a diet for *S. niloticus* broodstock. The starting point for this is a salmonid-type diet with high energy content and 25% protein, at least half of which is animal protein, largely from fish meal. The natural foods present in spawning ponds are a very important part of broodstock nutrition.

6. SUMMARY ON NUTRITION

To summarize on nutrition, it is clear that vastly different approaches are needed to optimize the nutrition of tilapias in extensive and intensive culture systems. The feeding niches in extensive systems need fuller definition, particularly the microbial ecology of detrital aggregates, while for intensive culture, least cost formulation of complete diets is still awaited for most culture situations.

Seed Supply

1. BROODSTOCK MANAGEMENT

In spawning tanks, the territorial aggression of males is the major factor limiting stocking density. In Israel, however, as Mr. Mires pointed out, mixed sex broodstock are overwintered in extremely dense conditions (50 kg fish/m^3 of water) at 15 to 17°C. This does not affect their reproductive performance when put out to ponds. Presumably, the low winter temperatures suppress aggressive behavior.

Dr. Lovshin mentioned the possible advantages of sexing broodstock while they are still immature and then keeping the sexes in separate ponds until they are ready to spawn, as is done for carp breeding. This method gives a high degree of control for handling pure stocks and for hybridization work.

The best sex ratios to use for high broodstock performance were then discussed. Experimental work in the Philippines has shown that a ratio of one male to one female gives better results than one male to two or three females for *S. niloticus* and *S. aureus* broodstock in plastic pools and aquaria. This result is, however, in conflict with some other work, for example Campbell working in the Ivory Coast has found that high female:male ratios of 5 or even 7 or more to one has given very intensive reproduction of *S. niloticus* in shallow raceway-type ponds. The best sex ratio varies with specific breeding behavior. For example, in *S. melanotheron (T. heudelotii)* in the Ivory Coast, in which the male is the mouthbrooding parent, it is 1:1 in ponds.

In contrast to this, Dr. Lovshin's work in Brazil and the concept of 'male pressure' suggests that even higher numbers of males may be advantageous. Dr. Lovshin pointed out, however, that there is a difference between intraspecific or pure strain crosses, in which sex ratios of about one male to three females seemed to be generally accepted, and the interspecific hybrid crosses where he had harvested more fingerlings from ponds with 'male pressure': two males to one female. This may be due simply to the constant availability of males to court any ripe female, but more work on sex ratios in ponds and restricted environments is urgently needed.

It is not clear whether chemical stimuli play an important part in the reproductive behavior of tilapias. In salmonids, males use chemical recognition to select females that are ready to spawn. If such chemical stimuli are also produced by tilapias, they could be major factors in mate selection and in reducing male aggression against ripe females. Dr. Noakes pointed out that there were fundamental differences between the salmonids and the lek breeding tilapias and similar groups, like the centrarchids. In the salmonids, the female excavates the nest and the male undoubtedly recognizes and chooses his mate partly by chemical recognition. In the lek breeding tilapias and centrarchids, however, it appears to be the female that makes the choice, and of course, the male that excavates the breeding pit. For the centrarchids, it has been shown that a male will attempt to court any fish or object that comes into his breeding territory. If this also applies to the tilapias, it argues against chemical stimuli having importance over behavioral cues. Dr. Lowe-McConnell added the observation that *S. karomo* in the field wander through the breeding arenas and appear to inspect not only the males but also their breeding pits before selecting a mate. This was observed in very clear water.

The problem of male aggression appears to be very different in restricted environments, such as tanks and aquaria, from the situation in ponds. In the former, males can kill females or cause ovarian regression by repeated attacks, whereas in ponds, the females have space for escape and are rarely adversely affected. Mr. Mires described aquarium observations in which ripe females were keen to enter the males' breeding territories and the males pushed and encouraged them to enter. If this also occurs in ponds with a preponderance of males, it means that ripe females are continually bombarded by courting males. This could have a stimulatory effect and help to account for the good results of hybrid crosses with 'male pressure'. The question of breeding coloration was raised but it was felt that this had little relevance in ponds, where visibility was often very low.

2. Mass Seed Production

The discussion centered first on the possible alternatives to spawning ponds for mass fry and fingerling production. The example of mass fry production using cages (hapas) was described by Dr. Guerrero. Prof. Roberts commented that a commercial farm in Kenya was producing large numbers of pure strain, hybrid and sex-reversed tilapia fry for sale within Kenya, Nigeria, other African countries and the Middle East. Details of the system used were not available.

Dr. Philippart mentioned that an experimental system of 4-m^2 fiberglass tanks had also been developed using recirculated heated effluents in Belgium. The system, with 15 to 16 spawners/tank produces about 500 fry/tank/day for short periods (5 to 7 days) of intense reproductive activity and about 150 fry/tank/day on average over longer periods (50 days). Small females of around 100 g perform better than larger fish. The development of intensive recirculatory raceway systems for fry production was discussed but it was felt that these would be costly both in construction and energy requirements.

It was agreed that most of the large-scale commercial production of tilapia fry was still done in spawning ponds. Mr. Mires stated that in Israel, producers have changed from small to large spawning ponds because the demands of buyers were constantly changing with respect to size and numbers of fish. Large spawning ponds become essentially early nursery ponds as well. Fry or fingerlings can be harvested and graded to meet demands with less labor and management than from numerous small ponds. At the Kibbutz Ein Hamifrats hatchery, the use of large spawning ponds has reduced the monthly labor requirement for fry/fingerling harvest to four hours work by a team of five to six people.

The development of tilapia hatcheries was felt to be the key to expansion of the culture industry. A small number of large hatcheries with well-trained personnel was considered to be a better prospect than large numbers of hatcheries scattered throughout the rural areas of developing countries. This would allow controlled production of good strains, hybrids, etc. It was recognized, however, that distribution difficulties could arise in island systems like the Philippines and in areas where roads and communication systems are very poor and fuel prices high. In these cases, local hatcheries would be essential. Tilapias are among the hardiest of fish and survive transportation very well. Prof. Roberts commented that tilapia fry brought overland from Israel to Scotland in fruit lorries suffered no mortality despite exposure to cold temperatures.

Several participants expressed the view that private sector hatcheries afforded the best hope for a rapid and efficient increase in tilapia seed production. However, the economic viability of tilapia seed production has been tested in very few countries, such as Israel and Taiwan. Government hatcheries or government subsidies to private sector producers may be needed in the future.

Culture Techniques and Systems

1. Recruitment Control

The discussion concentrated on methods of recruitment control other than monosex culture of sex-reversed or hybrid progeny, which it was felt were adequately discussed elsewhere. Attention was drawn to the high success (84%) of male fry production by size selection alone in the Ivory Coast. There was also a brief discussion on the destruction of urinogenital papillae. This has been accomplished at Auburn University, Alabama, by hot wire cautery, but the papillae regenerate and the fish spawn normally.

The main method discussed was the use of predators to remove unwanted recruits. It was recognized that although tilapia recruits have different feeding preferences to their parents, they do compete for food and oxygen in culture ponds.

Dr. Pullin commented that *Channa striata* was being studied at Central Luzon State University in the Philippines to control tilapia recruitment in an *S. niloticus* (85%):*Cyprinus carpio* (15%) polyculture system. Very low numbers of this predator (20 to 30 stocked as fingerlings) could obliterate tilapia recruitment in 0.1 ha ponds containing 850 or 1,700 *S. niloticus* stocked at average weight 3 g and grown for 90 days, during which first maturity is reached and spawning occurs. If the culture period is extended to 180 days, however, the predators are unable to cope with the increased level of recruitment and up to 200 to 300 kg of tilapia recruits/pond can be present at harvest. Therefore, the size and fecundity of the breeding tilapias and the length of the culture period must be considered, not just numbers of fish. *Channa striata* is a very useful controlling predator and has a high value as a by-catch. It is used in commercial culture of tilapias in Taiwan—largely in monosex culture where it mops up any recruits resulting from inaccurate sexing or poor quality hybrid progeny.

Dr. Coche pointed out that smaller predators than *Channa* should also be considered. Although of negligible value as a by-catch, they have the advantage of always selecting the smallest recruits as prey and there is, therefore, no danger of them eating the cultured crop as well as unwanted recruits. He also reported work using *Clarias lazera* in the Cameroons. This species ceased to be an effective controlling predator when the water became very turbid and it was also useless in systems where high protein supplemental food was given to the cultured tilapias: it preferred to eat the supplemental food.

Dr. Lovshin reported that in his experience predator control was the most reliable method of controlling recruitment. He also voiced the opinion that there was a very great potential for managed fish production from the thousands of livestock watering/irrigation ponds in tropical developing countries by using predator-prey systems. Guidelines for stocking and harvesting would have to be worked out as for the bass-bluegill systems described by Swingle for the southern U.S.A.

2. Integrated Farming and Wastewater Reuse

It was agreed that tilapias were ideal species for integrated agriculture-aquaculture farming systems, particularly in tropical developing countries. It was recognized that the public health aspects of such systems needed fuller investigation.

The use of wastewater (sewage) to fertilize tilapia ponds was considered a very controversial topic. Dr. Hepher described Israeli work in which human bacterial pathogens had been shown to penetrate the muscle and internal organs of fish above certain threshold levels of bacterial populations in the water. The thresholds vary with species: silver carp are the most susceptible to contamination, common carp are intermediate and tilapias the most resistant. Tilapias have particularly high thresholds for *Salmonella* and *Shigella* penetration. The thresholds also vary greatly with stress. They become lowered in stressful conditions such as low dissolved oxygen and high ammonia. Fish which have become contaminated with pathogens in muscle and internal organs take a very long time to depurate in clean water: usually over one month. Fish which have taken pathogenic bacteria into their guts only can be depurated in 2 to 3 days.

Mr. Mires voiced great concern at the use of wastewater in aquaculture and drew attention to the adverse publicity that it could give to fish culture in general. It was his opinion that public attitudes would be strongly against this method of growing fish even if the health hazards could be controlled. It was pointed out, however, that fertilization of fish culture systems with human wastes has a long history in Asia and that human waste recycling through aquaculture should not be abandoned because of public attitudes in the developed countries.

The buildup of heavy metals in manured ponds was also discussed. Dr. Hepher stated that in Israel, both common carp and tilapias remained largely unaffected by heavy metal buildup. The levels of heavy metals in the pond sediments increase with heavy manuring but the fish are present in the ponds for such a short time that heavy metal levels in their tissues always remain well below World Health Organization recommended safe limits. In particular, common carp take up virtually no heavy metals at all, presumably because they lack the highly acidic stomach of the tilapias.

It was agreed that much more information was required on the public health aspects of the use of organic manures and wastewater in aquaculture.

Diseases of Tilapias

Dr. Roberts summarized the present importance of diseases in the commercial culture of tilapias. There are very few serious disease problems and these are localized in nature, for example, infestation with *Lernaea* in a few Southeast Asian and Indian locations. The myxobacterial diseases and bacterial septicaemias are generally diseases of bad husbandry and can be avoided but such disease problems will probably increase as tilapia culture expands. Vaccines may be available in the future for septicaemias.

Although only one virus has been isolated from tilapias at present and produces no serious pathological effects, more viruses are bound to occur in intensively cultured fish. There are also risks for the future with respect to public health. The misuse of antibiotics in fish ponds receiving human wastes could create antibiotic-resistant strains of human pathogens. Also, a parasite such as *Haplorchis* could ruin a culture industry if it can be shown that infection is caused by farmed fish.

The transportation of broodstock and fry has attendant risks of disease transfer. If a large fry supply industry develops, then control measures will have to be undertaken. These must be realistic, however, not like the extreme quarantine measures recently applied to the introduction of coho salmon to the U.K. for experimental work, which included complete confinement in recirculation systems for long periods and sterilization of effluents. A realistic series of measures is needed, including routine monitoring of broodstock health, disinfection of fry with formalin and malachite green both before despatch and on receipt, isolation from natural waters and other stocks on receipt (quarantine) and the destruction, preferably by burning, of all packing materials. All inspection, certification and licensing should be matters for official government scientists or other trained personnel. Stirling University has been involved in training fish disease experts from Southeast Asia and Africa and in liaison work with Thailand where the Government is developing a routine disease diagnostic system for the catfish industry.

Dr. Pullin asked whether the possibility of shipping disinfected tilapia eggs had been investigated as it was impossible to give whole fish a clean bill of health. The shipment of disinfected eyed ova is routine in the salmonid culture industry and greatly reduces the risks of transfer of all diseases apart from intraovarian viruses. It was agreed that tilapia eggs can be incubated in water provided that they are kept moving by slow aeration or agitation and that transportation of disinfected eggs in self-contained units could be viewed as a future method.

Dr. Lovshin drew attention to the difficulties of treating tilapia diseases, particularly in the rural areas of developing countries where even basic chemicals such as formalin and potassium permanganate are either unavailable or very costly. Prof. Roberts stated that the best treatments in any disease situation were usually improvement in water quality and reduction in stocking density. It was agreed that formalin is the most useful general chemical for disease treatment, but that salt can also prove useful against ectoparasites. Details of treatment methods applicable to tilapia culture in rural areas have still to be worked out.

Consensus Statement and Research Requirements

A. CONSENSUS STATEMENT

The conference participants agreed on the following:

1. The Value of Fundamental Research

Fundamental research on the taxonomy, genetics, physiology and ecology of tilapias has produced a large amount of information of direct benefit to the culture industry and merits increased and sustained financial support.

2. Standardization

The scientific nomenclature used for the tilapias remains a matter of controversy among taxonomic experts. For the sake of uniformity, the genera *Sarotherodon* for the mouthbrooders and *Tilapia* for the substrate-spawners are accepted for the published proceedings of this conference.

To avoid confusion, all descriptions of hybrid crosses should be given with the female parent first. The various laboratories establishing collections of so-called pure strains of tilapias should collaborate to standardize the nomenclature. The geographical origin and history of transplantation of strains should be documented and information on electrophoretic and other genetic markers exchanged on a regular basis. The present situation is very confused and should not be allowed to worsen.

Researchers should use fish of known origin and history and the fullest possible information on these should be given in the methodology of all published works. Ideally, all fundamental research should use pure strains of fish but this must be seen as a long-term objective, particularly in the developing countries.

3. Conservation of Genetic Material

Collections of pure strains of tilapias should be established both to improve the genotypes of cultured stocks and to supply standard material for research. It should be recognized that some strains and hybrids developed by commercial operators could be the subject of industrial patents. Collections should be replicated at several sites and should maintain sufficient numbers of broodstock to avoid inbreeding depression, except where inbred lines are developed intentionally.

Information should be collected on the sites at which pure wild stocks of tilapias can still be found. Aquatic reserves should be established at critical locations to conserve these stocks and any rare species, especially to protect them from any contamination by fish introductions.

4. Fish Introductions and Transfers

The continuing widespread introductions and transfers of tilapias are a cause for concern, and there is a clear need for the involvement of competent technical bodies to advise on and control these in the future. The possible adverse effects of introductions are ecological damage, contamination or elimination of endemic wild stocks and transfer of pathogens.

Introductions and transfers of tilapias will, however, be essential for the future development of the culture industry, especially as new strains and hybrids are developed. The risks of pathogen transfer can be minimized by moving only early life history stages (which are less prone to carry pathogens than broodstock) from reputable suppliers, by enforcing medication and inspection of fish and the destruction of packing materials on arrival.

5. Health Aspects

The use and abuse of antibiotics in fish culture requires urgent control *and legislation.* Control measures to contain the spread of fish diseases should also be considered by appropriate authorities, including the right of officials to inspect fish and farms for the presence of diseases, to restrict fish sales and movements as and when necessary, and to require farmers by law to notify the appropriate authorities of outbreaks of designated serious diseases.

6. Information Resources

Recent bibliographies and reviews have collated much of the large volume of literature on the biology and culture of tilapias but have missed a considerable amount of so-called "grey" literature, particularly reports and documents with a limited circulation from Africa, Asia and Latin America and material published in local languages.

There will be a continuing need for information collection and dissemination (for example, as special bibliographies) as the literature on tilapias continues to grow. To facilitate this and to lessen the volume of grey literature, published material should, wherever possible, be in a form for direct input into abstracting services and computerized data bases (i.e., having an abstract in English, ISSN number, key words etc., as appropriate. The following could have roles to play in the future collection and dissemination of information: the regional aquaculture centers of FAO, the International

Collection "Cichlid Papers" Reference Service (Parkstrasse 15, D-5176 Inden-Lucherberg, Federal Republic of Germany) and ICLARM.

B. RESEARCH REQUIREMENTS

Table 1 summarizes the research priorities identified by the Conference. The division into near-term and sustained work is arbitrary: all are worthy of sustained research support. Support for those in the left-hand column could result in rapid payoffs for the culture industry.

The following notes amplify some of the topics:

1. Genetics

Applied research on the applied genetics of tilapias can have rapid payoffs for the culture industry and merits sustained support as the industry expands. It should be recognized, however, that all work on genetic improvement is high-risk (high-investment) research.

Although some of the tilapias currently available have good culture characteristics, there is much room for improvement by selection of strains for fast growth, higher fecundity and later maturation. The screening of new species and hybrids for culture in freshwater could be beneficial; it is required urgently for brackish and seawater culture where there are few culturable finfish species available of which the life cycles have been closed in captivity. Future studies on hybridization should, therefore, include the development of hybrids which perform well in saline waters. Hybridization work should also include studies on hybrid vigor, and should not be restricted to the search for crosses resulting in all-male progeny. For the developing countries, however, the improvement of cultured strains should have priority over hybridization studies as the continuous development of hybrids requires elaborate facilities for the isolation and the characterization of parents.

The elucidation of sex-determination mechanisms in the tilapias is a pressing need in order to explain the sex-ratios of progeny from the various hybrid combinations either in current use or for future development. The greatest benefit to the culture industry from this would be the reliable production of 100% all-male progeny.

2. Reproduction

The design of systems for mass fry and fingerling production is the most important single requirement for the culture industry. The private sector is expected to develop such systems rapidly if given the necessary biological data and basic guidelines from researchers. This requires technological as well as practical extension work by leading aquaculture research centers.

The other important research areas related to reproduction can be summarized as behavioral studies. For example, broodstock performance is likely to be controlled by behavioral factors. Compatibility in hybrid crosses is one area in which near-term research and application of the existing published information on the reproductive behavior of tilapias would be useful.

Table 1. Summary of research priorities on the biology and culture of tilapias. A broken line between the columns indicates scope for both near-term and sustained work on the adjacent topic(s).

Near-term research priorities for both public-funded institutions and the private sector.	Priority research areas for sustained work, which would benefit from institutional collaboration.
1. Genetics	
Screening of new species and hybrids for freshwater and saltwater culture	
Selection for fast growth, higher fecundity and later maturation	
Elucidation of sex determination mechanisms	
2. Reproduction	
Design of mass fry and fingerling production systems	Variability in reproductive performance
Behavioral studies relevant to broodstock performance	Suppression of gametogenesis by environmental, behavioral or physiological manipulation
Chemical communication in reproductive behavior	
Cryopreservation of gametes	
Recruitment control by predators	
3. Growth and Nutrition	
Nutritional requirements of young, growing and mature fish	Feeding niche dynamics in polyculture
Incorporation of local materials in formulation of supplementary feeds	Metabolic pathways in relation to growth and gametogenesis
Feeding behavior in culture systems	
Digestive physiology in relation to feeding practices in culture	
4. Facilities and Equipment	
Development of integrated farming systems	
Pond and cage design	
5. Environment	
Pen, cage and pond effluent studies	
6. Fish Health	
Diseases and pathology	
Acclimation and stress reactions in culture systems	

Variability in reproductive performance has many causes, including possibly a genetic basis. Attempts should be made to explain the large differences in time to first maturation, fecundity, spawning frequency, etc. observed by different workers within a single species under different conditions. This work overlaps the narrower aim of suppressing gametogenesis by environmental, behavioral or physiological manipulation.

The importance of communication via dissolved organic compounds (pheromones) should also be investigated. If chemical communication is significant in the reproductive behavior of the tilapias, then the culturists could conceivably develop techniques either to encourage or suppress spawning by chemical means.

Cryopreservation of gametes is a useful technique for storing genetic material cheaply. Experience with other fish indicates that only spermatozoa are amenable to cryopreservation. Techniques for tilapia semen should be developed.

Control of tilapia recruitment, especially in pond culture, remains a difficult problem. Recruitment control by predators offers a viable solution for culture in both developed and developing countries. Research is needed to identify suitable predator species and to study predator-prey relationships to develop management techniques.

3. Growth and Nutrition

The dietary requirements of the important cultured species and hybrids must be defined so that supplemental feeds can be formulated on a sound technological basis. Because supplemental feeds are a major cost item in intensive or semi-intensive culture, studies on the physiology of digestion and assimilation in relation to feeding rate and frequency are important. The use of locally available dietary components can reduce feeding costs, but must be nutritionally adequate. More attention should be paid to *published information* on the feeding behavior and digestive physiology of wild fish and more research performed on these topics using fish in culture systems both with and without supplemental feeding. The study of feeding niches in polyculture systems is also important as there is evidence that some tilapias can cross from niche to niche which could reduce the number of species for a specific system and also maximize production.

4. Facilities and Equipment

The design of integrated agriculture-aquaculture farming systems is a high priority area for further research. While such developments must consider the public health aspects of producing human food from agricultural wastes, it is important that any apparent health hazards are assessed against those that exist anyway in normal agricultural and aquacultural practice. For example, by using animal manures to fertilize ponds, are more health hazards created than those already present in intensive animal production systems or in culture pond water?

5. Environment

Methodologies and standards are needed to assess environmental impact of effluents from aquaculture systems. This applies to pens and cages in enclosed or semi-enclosed bodies of water and to ponds, whether as periodic run-off or when draining to harvest (particularly in fertilized systems).

6. Fish Health

Sustained research on the parasites and diseases of tilapias and their pathology is essential as the culture industry continues to expand.

Acclimatization and stress reactions of fish in culture systems are poorly understood and have wide implications for growth, survival, reproductive performance and susceptibility to pathogens. Studies in both these areas are needed.