

Applied Genetics of Tilapias

Giora W. Wohlfarth
and Gideon Hulata



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INTERNATIONAL CENTER FOR LIVING AQUATIC RESOURCES MANAGEMENT
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**G.W. WOHLFARTH
AND G. HULATA**

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Cover: Red tilapias, Taiwan. Photo by R.S.V. Pullin.

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Foreword to the Second Edition

This review has evidently been welcomed by aquaculturists. The first edition of 1,000 copies found its way to many laboratories and libraries in both developed and developing countries.

The authors have maintained their close interest in the subject and provided new material and 15 new references for this second edition.

Since the first edition was printed, Dr. E. Trewavas, senior tilapia taxonomist, has made revisions to the genera following observations in Kenya that the mouthbrooder genus *Sarotherodon* includes two behavioral groups, and that the differences merit separate generic

status. Accordingly, the maternal mouthbrooders will become *Oreochromis* (e.g., *O. niloticus*, *O. mossambicus*) while *Sarotherodon* is retained for *S. melanotheron*, the paternal mouthbrooder and *S. galilaeus* in which both parents brood. However, in this review, the previous nomenclature has been retained for convenience.

Its publication coincides with the International Symposium on Tilapia in Aquaculture in Israel, May 1983. It is hoped that this revised edition will be a useful reference document for the symposium as well as for tilapia workers worldwide.

R.S.V. PULLIN
March 1983

Foreword

Tilapias are a major protein source in the developing countries and important cultured species in, for example, Israel and Taiwan. Their excellent growth rates, disease resistance and high market acceptability recommend them for culture on a wider scale and suggest that they could become prime domesticated species in the tropics and subtropics.

Within the genera *Tilapia* and *Sarotherodon*, there are numerous species of which only a few have been used for culture work. The literature from field biology and experimental culture work on tilapias is extensive, and to some extent confusing, with cases of misidentification of species and changes in nomenclature. It is hardly surprising that there has been no major research on the genetics of tilapias to screen species and hybrids for culture potential and to accelerate the domestication of promising strains, as for example has been achieved for the common carp.

This review was commissioned by ICLARM to collate existing information on the applied genetics of tilapias so as to assess the usefulness of previous work and to

suggest future research directions. Drs. Wohlfarth and Hulata were natural choices for this difficult task as the Fish and Aquaculture Research Station at Dor, Israel, has been a leading institution on tilapia research for years. They have taken a very broad view of applied genetics, and their review summarizes much of the information on the biology and distribution of tilapias which the culturist must appreciate before assessing an approach to genetic manipulation.

It is clear that the availability of a few species of tilapias, which were spread from Africa throughout the tropics and subtropics, and the search for reliable methods of producing all-male hybrid progeny on a commercial scale have limited genetic studies so far. It is also clear that more fundamental research is required on, for example, the sex determination mechanism in tilapias and their hybrids, and the use of electrophoretic genetic markers to label cultured stocks. It is hoped that this review will stimulate such work and will provide a useful source of reference for those attempting to accelerate the development of tilapia culture.

R. S. V. PULLIN
February 1981

Applied Genetics of Tilapias

G.W. WOHLFARTH AND G. HULATA

Abstract

Wohlfarth, G.W. and G. Hulata. 1983. Applied Genetics of Tilapias. ICLARM Studies and Reviews 6, 26 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

The present world production of tilapias is relatively low, despite their high potential for aquaculture. Most research efforts towards their husbandry have been aimed at solving the major problem in tilapia culture, uncontrolled reproduction. Other attributes of potential importance, such as temperature and salinity tolerance, feeding habits and growth capacity have been largely neglected. Real attempts at genetic improvement in tilapias have been restricted to the production of all-male hybrid progeny. A rational choice of species or isolates, according to economically important traits, instead of locally available species could be a first step in increasing production by genetic methods.

Introduction

Tilapias are of great potential importance in aquaculture in the tropics and subtropics, including most of the areas suffering chronically from a lack of animal protein (Hickling 1963). The attributes which make the tilapias so suitable for fish farming are general hardiness, resistance to diseases, high yield potential due to resistance to crowding and ability to survive at low oxygen tensions. They also grow on a wide range of foods both natural and artificial, utilize manure well, and withstand a wide range of salinities. They are excellent table fish, with firm white flesh and no inter-muscular bones.

In spite of these qualities, the annual world production of tilapias is low, less than 200,000 t in 1977 (FAO 1978). This represents about 16% of the total inland production of fish in countries producing tilapias (about 1.23 million t) and less than 2% of the world's total production from inland waters (close to 11 million t). Since FAO statistics do not differentiate between fish caught in lakes and rivers and the products of fish farming, the yield of farmed fish must be much lower than these figures.

The potential benefit of tilapias is shown in countries like Senegal and Papua New Guinea, whose total

inland catch consists entirely of these fish (FAO 1978). In Taiwan, where traditional fish farming was based on Chinese carps, tilapias have become the most important species in freshwater aquaculture. The tilapia yield in Taiwan reached close to 13,000 t in 1974 (Chen 1976) and over 22,000 t in 1977 (Schoonbee 1979).

Most of the world's tilapia haul (about 163,000 t) is not classified according to species (FAO 1978). The most important classified species is *Sarotherodon mossambicus*. In 1977, production of this species was 19,500 t in Indonesia and 12,000 t in Papua New Guinea. Much lower *S. niloticus* hauls were recorded from Indonesia and Kenya (FAO 1978). In Taiwan, the species originally cultivated was *S. mossambicus*, but *S. niloticus* was introduced in 1966 (Chen 1976).

The main reason that tilapias make a relatively small contribution to fisheries production in most countries, in spite of their desirable traits, is their early sexual maturity. Tilapias reproduce when they are only a few months old, often below market weight. Uncontrolled spawning in production ponds often results in gross overcrowding and reduction of fish growth. Early sexual maturity may also have a negative influence on growth rate. A major proportion of the yield may then consist of unmarketable fish. Hence, the main research effort on tilapias has been aimed at investigating different methods of reproduction control, which has probably led to a neglect in researching other traits, e.g., fast growth rate and cold resistance.

The fish popularly termed tilapias have been divided into two genera mainly according to their breeding behavior (Trewavas 1973). The substrate breeders retain the generic name *Tilapia*, while the mouthbrooders have been defined as the genus *Sarotherodon*. A classification of tilapias, according to breeding behavior results in four groups (Goldstein 1970; Rothbard 1979):

1. Substrate breeders.
2. Maternal mouthbrooders, including nearly all species of *Sarotherodon*.
3. The one known paternal mouthbrooder, *S. melanotheron*, previously referred to as *T. macrocephala* (*S. macrocephalus*) and *S. heudeloti* (e.g., Aronson 1951).
4. The one known biparental mouthbrooder, *S. galilaeus* (Ben Tuvia 1959).

In the present review, fish of both genera are collectively termed tilapias. Their taxonomy is extremely confused, being based on morphological traits, such as color, which may change according to environment, season or state of sexual maturity. Misidentification has

also occurred. Several cases of synonymy are known, e.g., *T. melanopleura* is generally synonymous with *T. rendalli*. On the other hand, *S. homorum* was recognized as a species distinct from *S. mossambicus* (Trewavas 1967) due to sex ratios very different from 1:1 in their interspecific hybrid progeny. For years, *S. aureus* was misidentified in Israel as *S. niloticus*, and this was only cleared up by the skewed sex ratios of the interspecific hybrid between true *S. niloticus* females and *S. aureus* males (Fishelson 1962; Trewavas 1965). Some of the unlikely cases of supposed interspecific or intergeneric hybrids found in nature are also due to misidentification, e.g., the supposed hybrid between *T. nigra* (*S. spilurus niger*) and *T. zillii* (Whitehead 1960), which was later recognized as *S. leucostictus* (Elder et al. 1971). It is probably indicative that at least two cases of misidentification (i.e., *S. homorum* and *S. aureus*) were cleared up by genetic methods. A new monograph on the genus *Sarotherodon* should clarify the situation (Trewavas, in press).

Tilapia production could be greatly improved by a number of methods, such as increase in the total area under culture and improvement of management methods and broodstock. These improvements are interrelated. An improvement in broodstock performance may permit better management, and any other improvements could result in an increased area under culture.

The aim of this review is to summarize the little that is known of the applied genetics of tilapias in order to stimulate research towards breed improvement. We are dealing with a large number of species, belonging to two genera, and not a single species as in most branches of livestock husbandry.

A first step towards improving the characteristics of cultured tilapias is the proper choice of species. The culture of locally existing species can prove highly unsatisfactory. An example is the widespread use of *S. mossambicus* in the Far East, resulting from the chance discovery of a small number of individuals in Java (Schuster 1952). Not only is it doubtful whether *S. mossambicus* is particularly suitable for fish culture in the Far East, but the stock used may suffer from inbreeding depression due to the small number of original progenitors. Presumably, stock improvement in the Far East could be achieved simply by introducing either a different *S. mossambicus* stock from Africa or other species for use alone or in hybridization work. The introduction of *S. niloticus* appears to have achieved this aim in Taiwan (Chen 1976).

Geographical Distribution of Tilapias

The family Cichlidae, with about 700 species (Fryer and Iles 1972), is naturally distributed throughout Africa, Central America up to Mexico, the northern half of South America and part of India (Sterba 1962). Tilapias, the most important group of this family, are mainly indigenous to Africa. The one exception of natural occurrence of tilapias outside Africa is their presence in the Middle East, as far north as Syria (Chimits 1957). Present world distribution of tilapias covers the area between the 20°C winter isotherms, and extends to southern U.S.A., Europe and the Far East (Balarin and Hatton 1979). This includes areas into which tilapias have been transplanted or introduced for fish culture. The present distribution of the more important tilapias is shown in Table 1.

The wide distribution of some species is due to their transplantation by man. *T. zillii* and *T. rendalli* were introduced into many countries for weed control (Chimits 1957). *S. niloticus* and *S. aureus* have also been widely

distributed due to their reported good growth rate (Bardach et al. 1972). *S. mossambicus* became spread over wide areas of the Far East for fish culture during and after World War II (Chimits 1955). It was also introduced to Hawaii for live-bait production for tuna fishing, because of its high fecundity and euryhalinity (Chimits 1957). Its distribution in many New World countries is not well documented. In recent years, *S. hornorum* became a popular species for transplantation because of its suitability for the production of all-male hybrids (Lovshin and Da Silva 1975). The presence of a tilapia species in a given country does not imply its economic importance there. Thus, Malaysia, a pioneer in tilapia research in the Far East (Hickling 1960), has no recorded commercial production of tilapias (FAO 1978). On the other hand, tilapia culture is being developed in some Latin American countries and their present low yield is expected to increase.

Variation Between Species

Temperature and salinity tolerance, feeding habits and growth capacity are the major biological characters to be considered when tilapia species are evaluated for their suitability for aquaculture.

TEMPERATURE TOLERANCE

Temperature requirements of the more important tilapias are reviewed by Balarin and Hatton (1979) who also discuss the effects of temperature on their physiology. For ease of comparison, the available data are summarized in Table 2. The normal water temperature range for tilapias is 20 to 30°C, but they can withstand lower temperatures. The only species able to survive at 10°C are *T. zillii*, *S. aureus* and *S. galilaeus* at the northern limit of their distribution (Syria and Israel) and *S. mossambicus* and *T. sparrmanii*, at the southern limit of their distribution in Africa (Jubb 1967). Nevertheless, *S. aureus* (referred to as *S. niloticus* by McBay 1961) is cold-affected at 13°C, while the orientation of *S. mossambicus* is disturbed at 11°C (Allanson et al. 1971). In spite of its cold tolerance (some individuals can survive at 6.5°C), *T. zillii* is not found naturally in areas where water temperatures below 13°C occur for more than two consecutive weeks (Hauser 1977).

Most tilapias do not eat or grow at water temperatures below 15°C (e.g., Bardach et al. 1972; Dendy et al. 1967) and do not spawn at temperatures below 20°C. The optimal temperature range for spawning is 26 to 29°C for most species (e.g., Rothbard 1979). The only

known exception is *T. sparrmanii*, with a minimum spawning temperature of 16°C (Chimits 1957). Upper thermal tolerance varies between 37 and 42°C, with little variation between species. *T. rendalli* appears to be the only exception. According to Spass (1960; cited by Balarin and Hatton 1979), its optimum temperature for maximum growth is between 19 and 28°C. Caulton (1975), however, demonstrated its preference for temperatures between 35 and 37°C, close to the upper temperature limit of 37°C (Whitefield and Blaber 1976) or 41°C (Caulton 1976; cited by Balarin and Hatton 1979).

SALINITY TOLERANCE

Tilapias are freshwater fish, generally assumed to have evolved from a marine ancestor (Kirk 1972). It is thus not surprising that many of the tilapias are euryhaline species. The available data (see Balarin and Hatton 1979) are tabulated to enable direct comparisons (Table 3).

S. mossambicus (e.g., Popper and Lichatowitch 1975) and *T. zillii* (Chervinski and Hering 1973) survive, grow and reproduce in the sea. *S. galilaeus*, *S. niloticus* and *T. zillii* were found in the Great Bitter Lakes of Egypt (Kirk 1972) at salinities between 13.5 and 22.4‰, but only *T. zillii* survived after the salinity rose above 22.4‰ (Bayoumi 1969). *S. shiranus*, indigenous to Lake Chilwa (Malawi) where salinity ranges between 12.5 to 28‰ "can just withstand 100% sea water" (Morgan

Table 1. Present distribution of the more important tilapias.

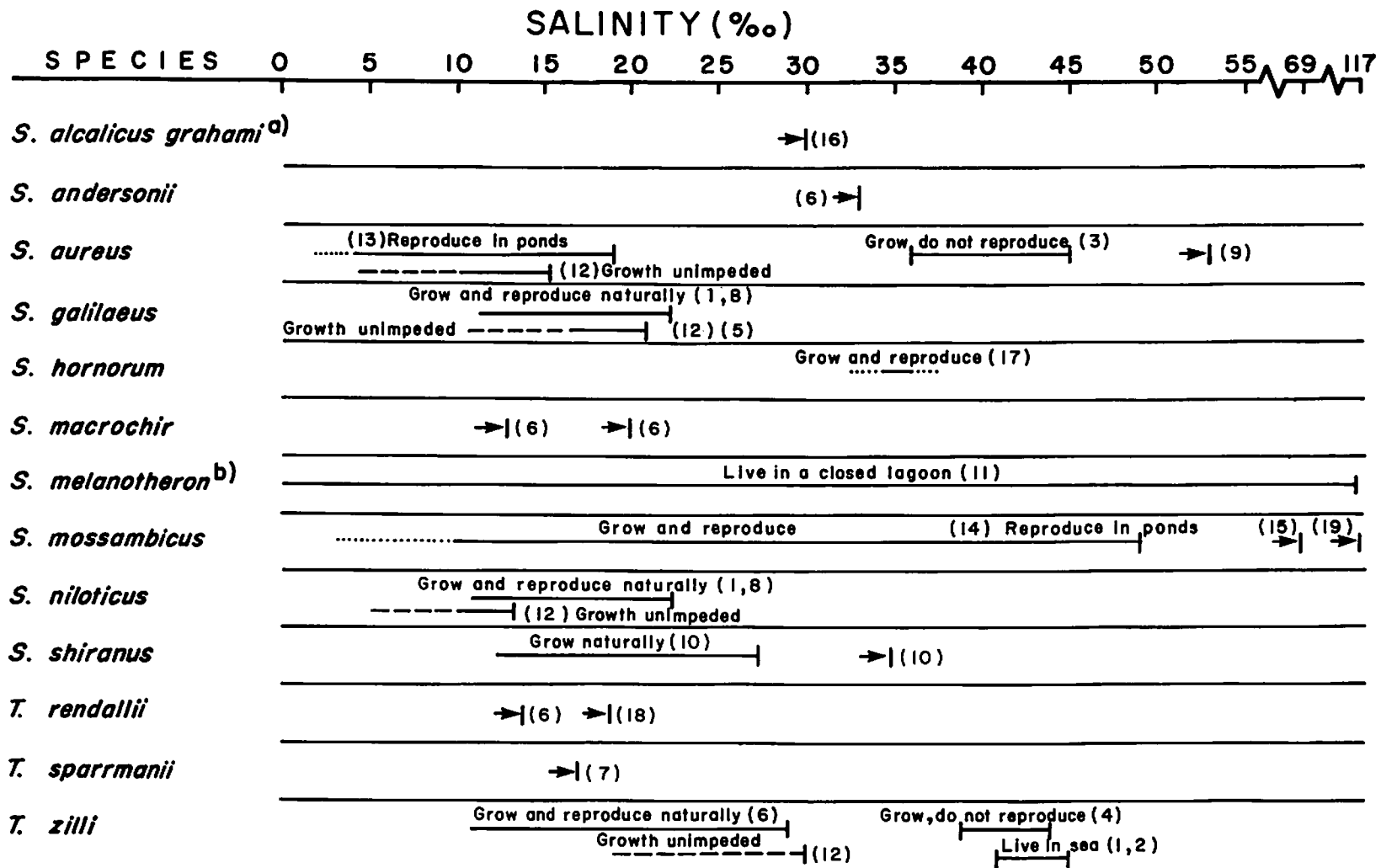
Species	Natural distribution	Distribution by man	Sources
<i>T. rendalli</i> ^a	West Africa (Senegal and Niger River systems), Central Africa (Congo River system), and Eastern South Africa (Zambezi River system as far as Natal)	Sudan, Malagasy Republic, Southern U.S.A., Mexico, Puerto Rico, Brazil, Colombia, Pakistan, Thailand and Malaysia	Balarin and Hatton 1979; Chimits 1955, 1957; Jubb 1967; Ruwet et al. 1975
<i>T. sparrmanii</i>	Africa, south of the Equator (Zambezi River), down to the Orange River system	Tanzania, Japan, U.S.A. (California)	Balarin and Hatton 1979; Chimits 1957; Ibrahim 1975; Jubb 1967; Sterba 1962; Pelzman 1972
<i>T. tholloni</i>	Tropical West Africa, from Cameroon to the south of Congo		Ruwet et al. 1975; Sterba 1962
<i>T. zillii</i>	Africa, north of the Equator (Nile River system and Western Africa up to Morocco), Middle East (Jordan Valley, Syria)	East Africa, U.S.A. (California, Florida, Hawaii), Southern U.S.S.R., Japan, Malaysia, Philippines	Balarin and Hatton 1979; Chimits 1957; Ruwet et al. 1975; Sterba 1962
<i>S. andersonii</i>	Upper Zambezi River system	Congo, Zambia, South Africa	Hickling 1967; Jubb 1967
<i>S. aureus</i>	West Africa (Senegal and Niger River systems), Nile River system, Middle East (Jordan Valley, Syria)	Uganda, U.S.A. (Alabama, Florida, Texas), Puerto Rico, Taiwan	Balarin and Hatton 1979; Trewavas 1965
<i>S. esculentus</i>	East Africa (Lake Victoria)	Tanzania, Malagasy Republic	Lowe (McConnell) 1956
<i>S. galilaeus</i>	From Jordan River system over East and Central Africa to Senegal, north of the Equator	South Africa	Balarin and Hatton 1979; Chimits 1957; Johnson 1974; Sterba 1962
<i>S. hornorum</i>	East Africa (Zanzibar)	Uganda, Ivory Coast, Latin America (Brazil, Mexico, Panama), U.S.A. (Alabama, Florida), Malaysia	Balarin and Hatton 1979; Lovshin and Da Silva 1975; Trewavas 1967
<i>S. leucostictus</i>	East Africa (Lakes Albert, Edward and George)		Elder et al. 1971
<i>S. macrochir</i>	Southern part of Central Africa (Upper Zambezi River system)	Congo, French Equatorial Africa, Ivory Coast, Liberia, Malagasy Republic	Balarin and Hatton 1979; Chimits 1955; Jubb 1967; Vincke 1979
<i>S. melanotheron</i> ^b	West Africa (coastal districts from Senegal to Congo)	U.S.A. (Florida)	Balarin and Hatton 1979; Pauly 1976; Sterba 1962
<i>S. mossambicus</i>	East and South Africa as far as Natal	South East Africa, South East Asia, Pakistan, India, Sri Lanka, U.S.A. (Florida), Latin America (Mexico, Guatemala, Brazil), India, Hawaii	Balarin 1979; Chimits 1955; Jubb 1967; Sterba 1962; Devedas et al. 1953; Neil 1966
<i>S. spilurus niger</i>	East Africa (Lake Rudolf)	Mozambique, Malagasy Republic, Zambia	Balarin and Hatton 1979; Elder et al. 1971
<i>S. niloticus</i> ^c	East Africa (Nile River system), Congo and West Africa (Senegal and Niger River systems)	Israel, South East Asia (e.g., Indonesia, Philippines, Taiwan, Thailand), U.S.A. (Alabama, Florida), Latin America (Brazil, Mexico, Panama)	Balarin and Hatton 1979; Sterba 1962
<i>S. variabilis</i>	East Africa (Lake Victoria)		Lowe (McConnell) 1956

^a=*T. melanopleura*. Jubb (1967) and Ruwet et al. (1975) claim that the area of origin of this species is Central Africa, from Congo and Zambezi River system southwards to Natal. Chimits (1955) and Balarin and Hatton (1979) suggest that *T. melanopleura* is also indigenous to western Africa.

^b=*S. macrocephalus*.

^c=*S. niloticus*. The erroneous mention of Syria and Jordan River (e.g., Sterba 1962) as part of the natural distribution of this species stems from the misidentification of *S. aureus* and *S. niloticus* (Trewavas 1965), the northern natural limit of *S. niloticus* being Egypt. *S. niloticus* in Israel (Fishelson 1966) is suspected to be a translocation from Egypt. *S. niloticus* was first imported to Alabama (U.S.A.) from Brazil in the early 1970s and not in the 1950s as mistakenly reported (Tave and Smitherman 1980).

Table 3. Salinity tolerance of tilapias (partially after Balarin and Hatton 1979). (→| symbolizes lethal salinity. Figures in parentheses refer to list of sources below).



Sources: 1. Bayoumi 1969. 2. Chervinski and Hering 1973. 3. Chervinski and Yashouv 1971. 4. Chervinski and Zorn 1974. 5. Chervinski 1982. 6. Fryer and Iles 1972. 7. Fukusho 1969. 8. Kirk 1972. 9. Lotan 1960. 10. Morgan 1972. 11. Pauly 1976. 12. Payne and Collinson 1983. 13. Perry and Avault 1972. 14. Popper and Lichatowich 1975. 15. Potts et al. 1967. 16. Reite et al. 1974. 17. Talbot and Newell 1957. 18. Whitefield and Blaber 1976. 19. Whitefield and Blaber 1979.

^{a)} = *S. grahami*

^{b)} = *S. macrocephalus*

1972). *S. melanotheron* (*S. macrocephalus*) thrives naturally in West African coastal lagoons where the salinity may range from almost 0‰ (during heavy rain falls) to 72‰ (Pauly 1976; Pauly, pers. comm.). *S. hornorum* has been reared in marine ponds on Zanzibar Island (Talbot and Newell 1957), though it is not known if it can also reproduce at this salinity. The maximum salinity for reproduction of *S. aureus* is 19‰ but it can be acclimatized to grow in salinities between 36 to 45‰ (Chervinski and Yashouv 1971), or even 53.5‰ (Lotan 1960). Several species are sensitive to salinities over 20‰. *T. sparrmanii* hardly survived 17‰ and could not tolerate 26‰ salinity (Fukusho 1969). *S. macrochir* cannot generally tolerate salinities above 13.5‰, though it was found in Zambia at 20‰ (Fryer and Iles 1972). *T. rendalli* died at 13.5‰ (Fryer and Iles 1972), though Whitefield and Blaber (1976) claim it can tolerate up to 19‰ salinity. On the basis of these data, Kirk (1972) suggested the use of *S. mossambicus*, *S. aureus* and *T. zillii* for culture in ponds filled with sea water used for cooling power stations. *S. aureus* seems the most suitable of these species since it does not reproduce in these conditions.

FEEDING HABITS

The tilapias are very heterogeneous in the food items they consume. The food spectrum of different species (Table 4) enables a division of the tilapias into three major categories:

1. Omnivorous species—e.g., *S. mossambicus*, the species with the most diversified food spectrum (Man and Hodgkiss 1977), *S. niloticus*, *S. spilurus niger*, *S. andersonii* and *S. aureus*—the only documented zooplankton consuming species (Spataru and Zorn 1978).

2. Phytoplankton feeders—e.g., *S. esculentus*, *S. galilaeus*, *S. leucostictus* and *S. macrochir*. Other species, e.g., *S. melanotheron* (*S. macrocephalus*) and *S. shiranus*, consume dead phytoplankton deposits. *S. alcalicus grahami* utilizes algae growing on stones.

Several species possess a special gastric mechanism enabling the lysis of blue-green algae. The importance of this mechanism in digestion by tilapias is not clear and may vary with species (Bowen, in press).

3. Macrophyte feeders—e.g., *T. rendalli*, *T. sparrmanii* and *T. zillii*. The feeding mechanism of *T. rendalli* is composed of specifically adapted pharyngeal teeth and a stomach capable of secreting strong acids (Caulton 1976) as in *S. niloticus*.

GROWTH CAPACITY

Growth capacity is obviously a major economic characteristic for culture. Most comparisons between growth rates of different tilapias consist of observations

in natural waters (Fryer and Iles 1972). Relative performance under culture may be very different from that in the wild. Furthermore, differences in stocking rates, feed quality and quantity, water quality and other management factors may have an influence on the relative growth of different tilapias even under culture, as shown by Van Someren and Whitehead (1959a, b; 1960a, b; 1961) with *S. spilurus niger*.

Available data on growth differences among tilapias are given in Table 5. For most species, only maximum size was recorded, while information on growth rate was usually lacking. Maximum size is of relatively little value, since it is attained by fish much older than those generally used in fish farming. Some indications of species unsuitable for fish culture may be obtained from Table 5. *T. sparrmanii* (Van Schoor 1966), *T. tholloni*, *S. melanotheron* (*S. macrocephalus*) and *S. leucostictus* (Biribonwoha 1975) cannot be widely recommended as they rarely exceed 100 to 200 g. *S. niloticus* has been suggested as suitable for fish culture, both for its fast growth rate and its good utilization of natural and supplemental food (Shehadeh 1976).

Only a few growth comparisons between different tilapias have been carried out, some of which were not replicated (e.g., Van Schoor 1966; Swingle 1960). Yashouv and Halevy (1971) found a small growth advantage of *S. vulcani* over *S. aureus* (2.9 and 2.4 g/d, respectively). Yashouv (1958b) also showed the superiority of *S. aureus* over *S. galilaeus* as pondfish. No significant difference in growth rate was found between *S. aureus* and *S. niloticus* (Pruginin et al. 1975; Anderson and Smitherman 1978). Bowman (1977) showed that *S. aureus* grows faster than *S. mossambicus* in manured ponds. No real difference in growth rate was found between the all-male hybrid *S. niloticus* x *S. hornorum* and *S. aureus* males (Lovshin et al. 1977). The female parent is given before the male parent in all crosses throughout this text. A comparison between the hybrids *S. niloticus* x *S. aureus* and *S. vulcani* x *S. aureus* did not reveal a difference in growth rate (Pruginin et al. 1975). Growth rates of the hybrids *S. niloticus* x *S. aureus* and *S. niloticus* x *S. hornorum*, when stocked in polyculture with common and Chinese carps, were similar and faster than that of *S. mossambicus* x *S. hornorum* (Hulata and Wohlfarth, unpublished results).

COLORATION

Traits other than growth capacity are also important in choice of species or hybrids. Some tilapias, e.g., *S. hornorum* and *S. vulcani*, have a dark colored skin, which is also expressed in their hybrids. Consumer resistance to dark colored fish may lessen their acceptability in some areas (Bardach et al. 1972). Nevertheless,

Table 4. Food spectrum of different tilapias. (Figures refer to list of sources below).

Species	Omnivorous	Zooplankton	Natural food				Detritus	Benthos	Artificial food	
			Phytoplankton Blue-greens	Diatoms	Microphytes	Macrophytes			Oil cakes mill wastes	Plants
<i>S. alcalicus grahami</i> ^a			11							
<i>S. andersonii</i>	3, 14					3	3			
<i>S. aureus</i>	14, 18	14, 28					27			1, 5
<i>S. esculentus</i>				3, 9, 10, 12			3			
<i>S. galilaeus</i>				12, 14, 16	16		16			
<i>S. leucostictus</i>				12, 25			12			
<i>S. macrochir</i>				3, 14						3
<i>S. melanotheron</i> ^b		14		8		26	7, 8, 21, 26	7, 22	26	26
<i>S. mossambicus</i>	14, 17, 19	14, 21		11, 21	21, 29	3, 21	3	3	3, 19	3
<i>S. niloticus</i>	12, 14		14, 20	11, 25			11, 12, 25	13	6, 30	1
<i>S. shiranus</i>							11			
<i>S. s. niger</i>	4, 14		11		4			4, 11		
<i>S. variabilis</i>							10, 12			
<i>T. rendalli</i>		14, 21								
<i>T. sparrmanii</i>	15	23						21	3, 26	3, 26
<i>T. zillii</i>					12		4	23		
							12, 14			24

Sources: 1. Anderson and Smitherman 1978. 2. Caulton 1976. 3. Chimits 1955. 4. Chimits 1957. 5. Davis and Stickney 1978. 6. De Kimpe 1971. 7. Fagade 1971. 8. Finucane and Rickney 1965. 9. Fish 1951. 10. Fryer 1961. 11. Fryer and Iles 1972. 12. Greenwood 1957. 13. Harbott 1975. 14. Jauncey and Ross 1982. 15. Lowe (McConnell) 1955. 16. Johnson 1974. 17. Man and Hodgkiss 1977. 18. McBay 1961. 19. Mironova 1969. 20. Moriarty 1973. 21. Munro 1967. 22. Pauly 1976. 23. Pelzman 1972. 24. Payne 1971. 25. Semakula and Makoro 1967. 26. Sivalingam 1975. 27. Spataru 1976. 28. Spataru and Zorn 1978. 29. Swingle 1960. 30. Tondo 1972.

^a=*S. grahami*

^b=*S. macrocephalus*

Table 5. Growth and reproduction characteristics of several tilapias in pond culture. (Figures in right hand column refer to list of sources below).

Species	Growth g/year	Growth Maximum	Age at maturity (months)	Fecundity (eggs/female)	Cultured in ^a	Sources
<i>S. andersonii</i>	200-250	1.8 kg	12-15	300-700/year	Central East Africa	8
<i>S. aureus</i>	2-3 g/day	31.5 cm	6	2,900-4,000/year	Israel ^b	3-14
<i>S. esculentus</i>		37.5 cm	5	up to 700/spawn	Tanzania	5,7
<i>S. galilaeus</i>		0.8 kg		5,000/year	Africa	3
<i>S. leucostictus</i>			6 (7.5 cm)	up to 400/spawn	Kenya and Uganda	7,12
<i>S. macrochir</i>	150-250	2.0 kg		up to 800/spawn	Africa	2,7,8,12
<i>S. melanotheron</i> ^c		0.3 kg			Africa	13
<i>S. mossambicus</i>	150-350	39 cm	2-3	up to 800/spawn (6-11 spawns)	Southern Africa, South East Asia	3,8
<i>S. spilurus niger</i>		1 kg	4		East Africa	6
<i>S. niloticus</i>	2-3 g/day	2.5 kg	4-5	700-2,000/spawn	Africa, Israel ^b , South East Asia, Latin America ^d	6,7
<i>S. shiranus</i>		39 cm			Malawi	3,10,11
<i>S. variabilis</i>		0.5 kg		up to 300/spawn	East Africa	7
<i>S. vulcani</i>	2-3 g/day		6	2,000-2,100/year 7,000-8,000/year	Africa, South East Asia	14 7,8
<i>T. rendalli</i>	150-200	1.3 kg			Colombia	2
<i>T. sparrmanii</i>		0.15 kg		up to 3,300/spawn		1,6
<i>T. tholloni</i>		0.15 kg			Cameroons	6
<i>T. zillii</i>		0.8 kg	5	300-12,000/year	Africa, South East Asia	4,5,12

^aAccording to Jhingran and Gopalakrishnan (1974).

^bMainly as female *S. niloticus* x male *S. aureus* hybrid.

^c= *S. macrocephalus*

^dMainly as female *S. niloticus* x male *S. hornorum* hybrid.

Sources: 1. Balarin and Hatton 1979. 2. De Bont 1949. 3. Fryer and Iles 1972. 4. Hauser 1975b. 5. Ibrahim 1975. 6. Jhingran and Gopalakrishnan 1974. 7. Lowe (McConnell) 1955. 8. Maar et al. 1966. 9. Marshall 1979. 10. Meecham 1975. 11. Ruwet et al. 1975. 12. Siddiqui 1977. 13. Sivalingam 1975. 14. Yashouv and Halevy 1971.

the culture of the *S. niloticus* x *S. hornorum* all-male hybrid is spreading in some Latin American countries, in spite of its dark appearance. Strains of red tilapia, with a characteristic white flesh and colorless mesentery, are cultured in Taiwan (Fitzgerald 1979), Philippines (Radan 1979) and Florida (Sipe 1979). These strains have great market potential in Japan and U.S.A. as a cultured substitute for red sea bream (*Chrysophrys major*).

Differences in appearance between species to be hybridized is important in distinguishing between parent species and their hybrids. The sustained production of all-male hybrids between *S. niloticus* females and *S. hornorum* males, compared to the eventual appearance of varying proportions of females in the crosses between *S. mossambicus* and *S. hornorum*, or between *S. niloticus* and *S. aureus*, may be due to the relative ease of distinguishing between *S. niloticus* and *S. hornorum*.

FECUNDITY

The fecundity of substrate breeders is generally much higher than that of mouthbrooding species (Fryer and Iles 1972), but little is known about differences in fecundity between species with the same breeding behavior. By choosing species with lower fecundity, the problem of uncontrolled reproduction in ponds may be reduced, but this may increase costs of fry production. In hybrid production, reduced fecundity may be a serious problem, and there appear to be considerable differences in fecundity when hybridizing different species. The fecundity of the *S. mossambicus* x *S. hornorum* hybrid is not less than that of pure bred *S. mossambicus* (Hickling 1960). This is not the case when either *S. vulcani* x *S. aureus* (Yashouv and Halevy 1971) or *S. niloticus* x *S. hornorum* (Lovshin and Da Silva 1975) hybrids are compared to their parental species. Differ-

ences in fecundity between reciprocal crosses were found when hybridizing *S. niloticus* and *S. macrochir* (Lessent 1968), hybrids being obtained only irregularly when *S. niloticus* was the female parent. Lee (1979), working with *S. aureus*, *S. niloticus* and *S. hornorum*, obtained fewer fry from hybrid combinations than from intraspecific spawns. He noted that "the clutch size of the hybrids apparently was not smaller than that of the

pure breeds, however spawning was less frequent in hybrid crossings."

A partial explanation of these apparently conflicting data may be the fact that the two species hybridized by Hickling (1960), i.e., *S. mossambicus* and *S. hornorum*, are more closely related to each other, as suggested by their more similar appearance (Trewavas 1967; Fryer and Iles 1972), than the other pairs of species hybridized.

Interspecific Hybridization

A large number of hybrids between *Sarotherodon* spp. and between *Tilapia* spp. as well as intergeneric hybrids between *Sarotherodon* spp. and *Tilapia* spp. have been found in the wild or produced intentionally. A list of almost 30 hybrids is shown in Table 6. In constructing this table we used summaries of interspecific hybrids from Elder et al. (1971) and Balarin and Hatton (1979). A number of hybrids included in these summaries are not included in Table 6, since we consider them to be doubtful or insufficiently documented (Table 7). In both Tables 6 and 7 there is no mention of which fish acted as female and which as male parent either because the original source fails to give details or to save space when both reciprocals have been produced.

Successes of interspecific crosses tend to be more readily reported than failures, though the latter may also be of interest. Table 8 gives a summary of attempts at hybridization which did not result in viable offspring. In some cases the same interspecific cross appears in both Tables 6 and 8. This is due to success in one reciprocal cross and failure in producing the other.

Most successfully produced hybrids (Table 6) are between different species of maternal mouthbrooders. This is expected, since the vast majority of tilapia species belong to this breeding type. However, most of the other combinations between different breeding types are represented by at least one hybrid. The only documented cross involving the biparental mouthbrooder *S. galilaeus* (*S. niloticus* x *S. galilaeus*, Yashouv and Chervinski 1959) was later doubted by its authors (see footnote in Peters and Brestowski 1961). However, crosses between *S. galilaeus* and maternal mouthbrooders have recently been carried out artificially (Fishelson, pers. comm.).

The number of successful hybrids obtained from some species is high, e.g., nine different hybrids were produced with *S. niloticus* as one parent and four with *S. hornorum*. This is presumably due to *S. niloticus* being regarded as a fast growing species and *S. hornorum* (when used as male parent) as a promising candidate for producing all-male hybrid broods. We suspect that many more hybrids, not yet attempted, could be produced.

It is also noticeable that the majority of the reports on tilapia hybrids were published in the 1960s. This may be due largely to three independent occurrences:

1. The majority of naturally occurring hybrids were discovered in Africa during this period by a group of British investigators. Since these people left Africa, emphasis in tilapia research has changed somewhat, from the ecology and taxonomy of natural populations in lakes, to their utilization in aquaculture.

2. Many of the hybrids between different breeding types were produced by members of the behavioral school at Tübingen University (Germany) during this period. Their interest lay in comparing the behavior of cross-bred fry between mouth and substrate breeders to that of their parents. In some cases the hybrid fry were apparently not grown to an age enabling differentiation between the sexes.

3. A large number of hybrids were produced by Pruginin (1967) during his stay in Uganda in the 1960s as an FAO Fisheries Officer. Some of these hybrids had previously been known only from natural hybridization in African lakes.

From a taxonomic point of view, production of interspecific hybrids, in some cases with ease, and in many cases with fertile offspring, is in conflict with the classical definition of *species*: "A group of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Mayr 1940). However, a similar situation also exists in some other groups of fish. In the centrarchids (Childers 1967), ictalurids (Sneed 1971), cyprinids (Bakos et al. 1978) and salmonids (Suzuki and Fukuda 1971), a large number of interspecific hybrids have also been produced, in some cases with relative ease. In most cases the fertility and sex ratio of these hybrids have not been examined.

The species concept in some taxonomic groups of fish appears to differ from the classical definition. It appears characteristic of interspecific crosses between tilapias, that the sex ratio of the hybrid broods deviates strongly from the 1:1 ratio found in intraspecific broods, a

Table 6. Hybrids between different tilapias. (Figures refer to list of sources below).

Breeding type	Species ^a	Observations		Deliberate crosses carried out		Sex of hybrid progeny in deliberate crosses
		in nature		in ponds or tanks	under lab. conditions	
Maternal mouthbrooder x Maternal mouthbrooder	<i>S. niloticus</i> x <i>S. spilurus niger</i> <i>S. niloticus</i> x <i>S. macrochir</i> <i>S. niloticus</i> x <i>S. aureus</i> <i>S. niloticus</i> x <i>S. variabilis</i> <i>S. niloticus</i> x <i>S. leucostictus</i> <i>S. niloticus</i> x <i>S. hornorum</i> <i>S. niloticus</i> x <i>S. mossambicus</i> <i>S. mossambicus</i> x <i>S. hornorum</i> <i>S. mossambicus</i> x <i>S. andersonii</i> <i>S. mossambicus</i> x <i>S. spilurus niger</i> <i>S. mossambicus</i> x <i>S. aureus</i> <i>S. vulcani</i> x <i>S. hornorum</i> <i>S. spilurus niger</i> x <i>S. hornorum</i> <i>S. spilurus niger</i> x <i>S. leucostictus</i> <i>S. amipheles</i> x <i>S. esculentus</i> <i>S. vulcani</i> x <i>S. aureus</i> <i>S. hornorum</i> x <i>S. aureus</i>	19 29,30 20 7,8 27	25 3,14,17 9,12,16,22,24,25,26 25 25 16,18,24,25 6,12,15,28 5,11 33 2,10,12,23 25 25 25 25 26 16,24,25			Surplus of males Only males when <i>S. niloticus</i> female parent Occasionally males only when <i>S. niloticus</i> female parent Only males when <i>S. niloticus</i> female parent Surplus of males Only males when <i>S. niloticus</i> female parent Surplus of males Only males when <i>S. mossambicus</i> female parent Surplus of males Surplus of males (<i>S. aureus</i> misidentified as <i>S. niloticus</i>) Large surplus of males Only males when <i>S. spilurus niger</i> female parent Surplus of males Large surplus of males Surplus of males
Maternal mouthbrooder x Paternal mouthbrooder	<i>S. melanotheron</i> ^b x <i>S. mossambicus</i> <i>S. melanotheron</i> ^b x <i>S. niloticus</i>				4,21 4,21	Only females when <i>S. melanotheron</i> female parent
Maternal mouthbrooder x Substrate breeder	<i>T. tholloni</i> x <i>S. mossambicus</i> <i>T. tholloni</i> x <i>S. niloticus</i> <i>T. zillii</i> x <i>S. mossambicus</i> <i>T. zillii</i> x <i>S. spilurus niger</i>	32	13		4,21,22 4,21 4	Only females when <i>T. tholloni</i> female parent Only females when <i>T. tholloni</i> female parent Only males. Sex of parents not given
Paternal mouthbrooder x Substrate breeder	<i>T. tholloni</i> x <i>S. melanotheron</i> ^b				4,21	
Substrate breeder x Substrate breeder	<i>T. zillii</i> x <i>T. rendalli</i> ^c	30,31	1			Sex ratio 1:1

Sources: 1. Anon. 1962. 2. Avault and Shell 1967. 3. Bard 1960. 4. Bauer 1968. 5. Chen 1969. 6. Chen 1976. 7. Elder and Garrod 1961. 8. Elder et al. 1971. 9. Fishelson 1962. 10. Guerrero and Caguan 1979. 11. Hickling 1960. 12. Hsiao 1980. 13. Ibrahim 1975. 14. Jalabert et al. 1971. 15. Kuo 1969. 16. Lee 1979. 17. Lessent 1968. 18. Lovshin and Da Silva 1975. 19. Lowe (McConnell) 1958. 20. Mortimer 1960. 21. Peters 1963a. 22. Peters and Brestowsky 1961. 23. Pierce 1980. 24. Pintø 1982. 25. Pruginin 1967. 26. Pruginin et al. 1975. 27. Trewavas and Fryer 1965. 28. Van Schoor 1966. 29. Welcomme 1964. 30. Welcomme 1965. 31. Welcomme 1966. 32. Whitehead 1960. 33. Whitehead 1962.

^aOrder of species does not indicate sex of parents, either because original source failed to give it, or to save space when both reciprocals have been produced.

^b=*S. macrocephalus*

^c=*S. melanopleura*

Table 7. A list of interspecific tilapia hybrids from the literature, considered doubtful or insufficiently documented.

Source in literature	Hybrid ^a	Reason for suspecting existence of hybrid
Balarin and Hatton 1979	<i>S. mossambicus</i> x <i>S. macrochir</i> <i>S. andersonii</i> x <i>S. mossambicus</i> <i>S. andersonii</i> x <i>S. macrochir</i> <i>S. spilurus niger</i> x <i>S. mossambicus</i>	Only source—Jhingran and Gopalakrishnan (1974), which does not refer to original papers.
	<i>S. mossambicus</i> x <i>S. andersonii</i>	Stated that successfully bred in ponds in Israel, but <i>S. andersonii</i> not present in Israel.
	<i>S. hornorum</i> x <i>S. macrochir</i>	No reference to original paper.
Elder et al. 1971	<i>T. tholloni</i> x <i>S. spilurus niger</i>	Refers to Peters (1963b) but no such hybrid appears in that paper, or in Peters (1963a).
	<i>S. niloticus</i> x <i>S. galilaeus</i>	Refers to Yashouf and Chervinski (1959), but existence later doubted by authors—see footnote in Peters and Brestowsky (1961).

^aOrder of species does not indicate sex of parents, either because original source failed to give it, or to save space when both reciprocals have been produced.

Table 8. Documented unsuccessful attempts at tilapia hybridization.

Breeding type	Parents		Reason for failure of hybridization	Source
	Female	Male		
Maternal x paternal mouthbrooder	<i>S. mossambicus</i>	<i>S. melanotheron</i> ^a	no fry obtained	Bauer (1968) Peters (1963a)
Maternal mouthbrooder x substrate breeder	<i>S. niloticus</i>	<i>T. tholloni</i>	high fry mortality	Peters (1963a) Bauer (1968)
	<i>S. mossambicus</i>	<i>T. tholloni</i>	high fry mortality	Peters (1963a) Bauer (1968)
	<i>S. aureus</i>	<i>T. zillii</i>	no fry obtained	Van Schoor (1966); Hsiao 1980
	<i>T. zillii</i>	<i>S. aureus</i>	no fry obtained	Van Schoor (1966); Hsiao 1980
Paternal mouthbrooder x substrate breeder	<i>S. melanotheron</i> ^a	<i>T. tholloni</i>	high fry mortality	Peters (1963a) Bauer (1968)
Substrate breeder x substrate breeder	<i>T. sparrmanii</i>	<i>T. zillii</i>	no fry obtained	Van Schoor (1966)
	<i>T. zillii</i>	<i>T. sparrmanii</i>	no fry obtained	Van Schoor (1966)
Substrate breeder x biparental mouthbrooder	<i>T. zillii</i>	<i>S. galilaeus</i>	no fry obtained	Van Schoor (1966)

^a= *S. macrocephalus*

surplus of males occurring in most cases (Pruginin et al. 1975). A similar phenomenon has been observed in some interspecific hybrids of sunfish (Centrarchidae) (Hubbs and Hubbs 1933; Childers 1967, 1971).

The apparent ease of hybridization between different species of tilapias poses the question of how speciation has occurred in this group of fish. For a species to establish itself as a separate breeding group, a reproductive barrier from a hypothetical ancestral group or from other species is required.

Reproductive barriers may be physiological, behavioral or geographic. The existence of at least a partial physiological barrier to reproduction is shown by failure to obtain viable progeny in certain combinations, and by cases where hybrid progenies are fewer than those obtained from intraspecific spawning (Lovshin and Da Silva 1975). However, Hickling (1960) has shown that in his *S. mossambicus* x *S. homorum* crosses, the number of fry obtained was at least as large as that in intra-

specific spawns involving *S. mossambicus*.

The possible roles in speciation of breeding and territorial behavior and breeding coloration of males are discussed by Elder et al. (1971) and Axelrod and Burgess (1976). The possible role of geographic separation in speciation is obvious. It seems virtually certain that one reason for the occurrence of "natural" hybrids is the breaking of the geographical reproductive barrier by artificial transfer of tilapias in African lakes (Fryer and Iles 1972). Lake Victoria, for example, has been separated from other aquatic systems since the Miocene period, and contains two endemic tilapia species, *S. esculentus* and *S. variabilis*. Since the 1930s, there have been frequent introductions of tilapias into this lake consisting of *S. spilurus niger*, *S. niloticus*, *S. leucostictus*, *S. mossambicus*, *T. rendalli* and *T. zillii*. The natural hybrid found in Lake Victoria is between the endemic species *S. variabilis* and the introduced *S. niloticus* (Welcomme 1964).

Sex Determination

The genetic mechanism of sex determination in tilapias is of both practical and theoretical interest, due to the production of all-male broods in some interspecific hybrids.

The first all-male brood was produced by crossing female *S. mossambicus* with male *S. homorum*. The reciprocal cross resulted in a segregation of one female to three males, while the different back crosses yielded 1:1 sex ratios (Hickling 1960). The all-male broods were apparently not due to the total mortality of females, since the mean number of progeny from hybrid crosses was not smaller than that obtained from intraspecific crosses.

Available data show that six interspecific crosses between female mouthbrooding tilapias can result in all-male hybrid (F_1) broods. In four of these combinations, the reciprocal cross yielded a sex ratio of 1:3 (Pruginin et al. 1975). The other two reciprocals have not been tested. All-female broods have been obtained in three crosses between female mouthbrooding species and species belonging to different breeding types. Details of crosses resulting in monosex broods and their reciprocals are shown in Table 9.

Hickling (1960) attempted to explain his results by adopting the chromosomal sex-determining mechanism of the platyfish *Xiphophorus maculatus* (Gordon 1947). According to this analogy, a dual system of sex-determining chromosomes exists in different species of mouthbrooding tilapias (Figure 1).

Two further genetic investigations were carried out to test this hypothesis. Chen (1969) continued with *S.*

mossambicus and *S. homorum*, while Jalabert et al. (1971) worked with two different species, *S. niloticus* and *S. macrochir*. In both studies, some of the crosses resulted in the predicted sex ratios, but other results could not be explained in this way. According to a further model of sex determination in *Sarotherodon* (Avtalion and Hammerman 1978), two non-homologous pairs of chromosomes carry the sex-determining factors, one pair being termed sex chromosomes and the other autosomes. The model is based on a re-examination of Chen's (1969) results. Since two non-linked loci are involved in this model, the predicted segregations include sex ratios such as 3:5 and 9:7 which cannot occur in simpler models. This model explains Chen's (ibid.) unexplained results, but not those of Jalabert et al. (1971). Hammerman and Avtalion (1979) stated that fitting their model to the results of Jalabert et al. (1971) requires assigning different values to the different chromosome strengths. Another attempt at designing a general model of sex determination in tilapias was based on one pair of sex chromosomes with one sex-determining locus consisting of a series of multiple alleles (Moav, unpublished).

All the models discussed imply, at least by inference, that the genus *Sarotherodon* can be divided into two groups of species, one with homogametic females and the other with homogametic males. This means that crosses between species of the same group will result in a 1:1 sex ratio, whereas crosses between species of different groups result in 0:1 or 1:3 ratios. According to this reasoning, *S. mossambicus*, *S. niloticus* and *S. spilurus*

Table 9. Interspecific crosses of tilapias, which resulted in monosex hybrid progenies (F = females, M = males).

Breeding type of parents	Parent species		Sex ratio of progeny (F:M)	Sex ratio of reciprocal (F:M)	Source
	Female	x Male			
Female mouthbrooder	<i>S. mossambicus</i>	<i>S. hornorum</i>	0:1	1:3	Hickling (1960); Chen (1969); McConnell (1966)
x	<i>S. niloticus</i>	<i>S. macrochir</i>	0:1	1:3	Lessent (1968); Jalabert et al. (1971)
Female mouthbrooder	<i>S. niloticus</i>	<i>S. aureus</i>	0:1	1:3	Fishelson (1962); Pruginin (1967); Hsiao (1980)
	<i>S. niloticus</i>	<i>S. hornorum</i>	0:1	1:3	Pruginin (1967)
	<i>S. niloticus</i>	<i>S. variabilis</i>	0:1	not attempted	Pruginin (1967)
	<i>S. spilurus niger</i>	<i>S. hornorum</i>	0:1	not attempted	Pruginin (1967)
Paternal x maternal mouthbrooder	<i>S. melanotheron</i> ^a	<i>S. mossambicus</i>	1:0	failed to spawn	Peters (1963a); Bauer (1968)
Substrate breeder x Female mouthbrooder	<i>T. tholloni</i>	<i>S. niloticus</i>	1:0	high mortality of embryos	Bauer (1968)
	<i>T. tholloni</i>	<i>S. mossambicus</i>	1:0	high mortality of embryos	Peters (1963a); Bauer (1968)

^a=*S. macrocephalus*

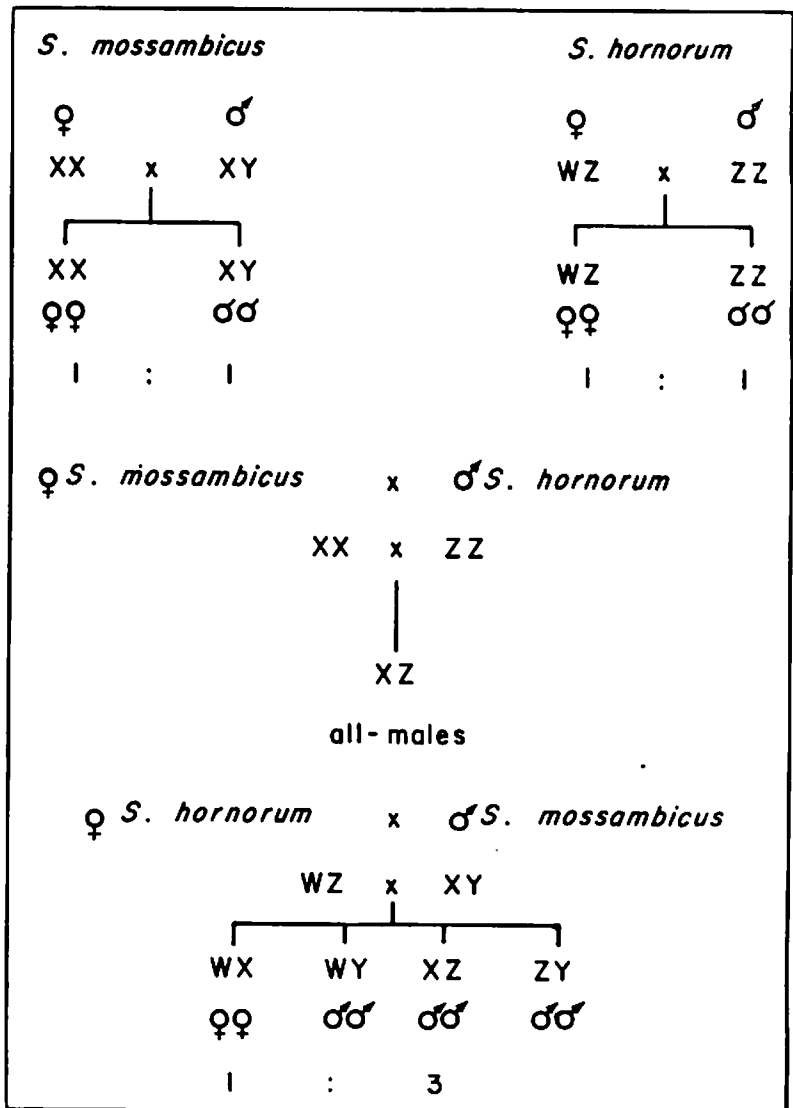


Figure 1. A suggested chromosomal mechanism of sex determination in tilapias (after Chen 1969).

niger belong to the female homogametic group, since their hybrids with *S. hornorum* males are all-male. Similarly, *S. hornorum* and *S. aureus* should belong to the female heterogametic group, since their hybrids with *S. niloticus* females are all-male. However, neither the hybrid between *S. niloticus* and *S. spilurus niger*, nor the one between *S. hornorum* and *S. aureus*, show the expected 1:1 sex ratio (Pruginin et al. 1975; Lee 1979).

In more general terms, the only sex segregations predictable from any mendelian system are mendelian ratios. Results of interspecific crosses, however, frequently resulted in non-mendelian sex ratios (Pruginin et al. 1975), which cannot be explained in these terms. From the above it is clear that none of the proposed models gives satisfactory explanations of all the known sex segregations in tilapia hybrids, or permits predicting results of new crosses. There is no evidence for the existence of a "strong," i.e., chromosomal mechanism of sex determination in tilapias, as indicated more generally in fresh water teleosts (Ohno 1970).

The difficulties of investigating sex determination in the tilapias are partially due to the complete lack of known visual sex-linked markers. It was with the aid of such markers that sex determination in the platyfish was worked out (Kallman 1973). Use of electrophoretic sex-linked markers could be a promising method to continue these studies. Avtalion et al. (1975) found an electrophoretic band present in males, but not females, of *S. galilaeus*, *S. vulcani* and *S. aureus*. However it has not been demonstrated that these electrophoretic markers are sex-linked and not merely sex-limited.

The number of chromosomes has been investigated in a number of tilapia species (Table 10), and in most cases the diploid content is $2n=44$. Not a single case of a heteromorphic pair of chromosomes, which might be

Table 10. Known chromosome numbers in tilapias.

Species	No. chromosomes (2n)	Source
<i>S. alcalicus grahami</i> ^a	48	Denton (1973), Park (1974)
<i>S. aureus</i>	44	Kornfield et al. (1979), Thomson (1981)
<i>S. galilaeus</i>	44	Badr and El Dib (1976), Kornfield et al. (1979)
<i>S. mossambicus</i>	44	Denton (1973), Natarajan and Subrahmanyam (1968), Thompson (1976, 1981)
<i>S. niloticus</i>	40	Badr and El Dib (1976)
<i>S. niloticus</i> x <i>S. aureus</i>	44	Avtalion (pers. comm.)
<i>T. rendalli</i>	44	Michele and Takahashi (1977)
<i>T. zillii</i>	38	Badr and El Dib (1976)
	44	Kornfield et al. (1979)
<i>T. sparmanii</i>	42	Thompson (1981)
<i>T. mariae</i>	42	Thompson (1981)

^a=*S. grahami*

regarded as sex chromosomes, has been described in tilapias. This is the typical situation in freshwater fishes (Ebeling and Chen 1970), in which heteromorphic pairs of chromosomes are the exception, rather than the rule. Even in the platyfish, the evidence for a chromosomal mechanism of sex determination is genetic and not cytological. Kallman (1973) demonstrated in the platyfish that autosomal sex-determining effects are superimposed on the previously established sex-chromosome mechanism. Evolutionary processes, including a change from female to male heterogamety, or vice versa, through an intermediate phase of polygenic sex determination, have been explored by Bull and Charnov (1977).

Variation Within Species

Existence of genetic variation of traits of economic importance within a species or population, is a prerequisite for selective breeding. The heritability of a given trait, a measure of the proportion of the total variance attributable to the additive genetic variance, is the major genetic determinant of the response to selection (Falconer 1960).

Little effort has been made to investigate and analyze variances within tilapia populations. This is largely because breeding work to date has concentrated on attempts to produce mono-sex progeny.

The heritability of growth and weight has been estimated in *S. mossambicus* and *S. niloticus*. A population of *S. mossambicus* was subjected to bi-directional

mass selection (Tkhien 1971). The weight deviations of the up and down selected parents from their median control was compared to the deviations of their five-month old progenies from the progeny of the median control. The estimates of realized heritability were higher for down selection (23.9% and 13.9% for females and males, respectively) than for up selection (0.9% and 8.3% for females and males, respectively). In *S. niloticus* heritability estimates for weight and length at 45 and 90 days were obtained from the analysis of the variance components in a full and half sib study (Tave 1979; Tave and Smitherman 1980). The estimates of sire heritability did not differ significantly from zero, while the dam heritability estimates decreased from day

45 to day 90. The only significant estimate obtained was for the dam heritability of length at 45 days (54%), which decreased to zero at 90 days.

The effect of selectively fishing the larger individuals has been studied from the catch data of *S. niloticus* in Lake George (Gwahaba 1973). The mean size of fish declined from 900 g to 400 g in the period 1950 to 1970 and they matured at smaller size. The effect of periodically removing the larger individuals from a population of *S. mossambicus*, during three to four generations, on the growth of their progenies was studied in the laboratory (Silliman 1975). The control consisted of a similar population from which random samples were periodically removed. In the progeny of the test population, males grew at a slower rate than the male progeny of the control population. There was little difference in growth between the females, progenies of these two populations. It appears to be easier to bring about a genetic deterioration in tilapia populations by negative selection, i.e., preferential use of the smaller fish as progenitors of further generations, than to improve growth by mass selection of the larger individuals.

The effect of negative selection, by removing the larger individuals, was the subject of two studies. Gwahaba (1973) investigated a natural population of *S. niloticus* which had been overfished for 20 years. In Silliman's (1975) experimental study, the growth of the progeny

of a selectively fished population was compared to that of a randomly fished population. In both cases, the populations responded to this selective fishing by decreased growth. These studies suggest the existence of additive genetic variation for growth rate in the investigated populations.

A recent study indicated variation in fecundity between different stocks of *S. niloticus* when hybridized with *S. hornorum*. The number of hybrid fry obtained from the Ghana stock was 3-4 times higher than that obtained from the Ivory Coast stock of *S. niloticus* (Hulata, Rothbard and Wohlfarth, unpublished results).

Breeding efforts aimed at producing monosex hybrids have revealed genetic variation for sex determining factors. Pruginin et al. (1975) examined the progeny of several pairs of *S. niloticus* x *S. aureus*. Some pairs yielded all-male progeny, while others produced varying proportions of males, between 51 and 99%. A breeding program aimed at isolating reliable brood stock, under way at Dor (Israel), consists of progeny-testing single pair reciprocal crosses between different species of *Sarotherodon* (Hulata et al. 1980).

Genetic variation in body coloration was found in *S. mossambicus* (Fitzgerald 1979) and *S. niloticus* (Radan 1979). The mode of inheritance of the red body coloration requires investigation.

Population Control

Uncontrolled reproduction of tilapias leads to stunted populations. In polyculture, it may also have a deleterious effect on the growth of other fishes. Attempted techniques for controlling reproduction may be classified as genetic and non-genetic.

NON-GENETIC METHODS OF POPULATION CONTROL

a. Use of Predators

Bardach et al. (1972) recommended the use of predators to consume young tilapia. This method has met with varying degrees of success (Lovshin and Da Silva 1975). When effective, it may result in marketable tilapias at harvest plus small extra yield of the predator. However, the predator effect may be inadequate or too strong (Huet 1972). This technique is practiced in Africa (Shehadeh 1976) and has been demonstrated in El Salvador (Dunseth and Bayne 1978).

b. Monosex Culture

The most effective and widely used technique for population control is monosex culture (Mires 1977). It can be accomplished by sorting the sexes and stocking one sex only, or eliminating one sex from the population

by sex reversal or hybridization (a genetic method to be mentioned below). Monosex culture of male tilapias is practiced due to the superior growth rate of males. Sorting tilapias for monosex stocking is time-consuming, wasteful (Pruginin et al. 1975) and demands some skill.

Sex reversal, a technique developed at Auburn University for producing monosex tilapia populations, was recently reviewed by Shelton et al. (1978). The potential of this technique (Guerrero 1975, 1979) was demonstrated under experimental conditions. Application of this technique on a commercial scale is being investigated in Israel.

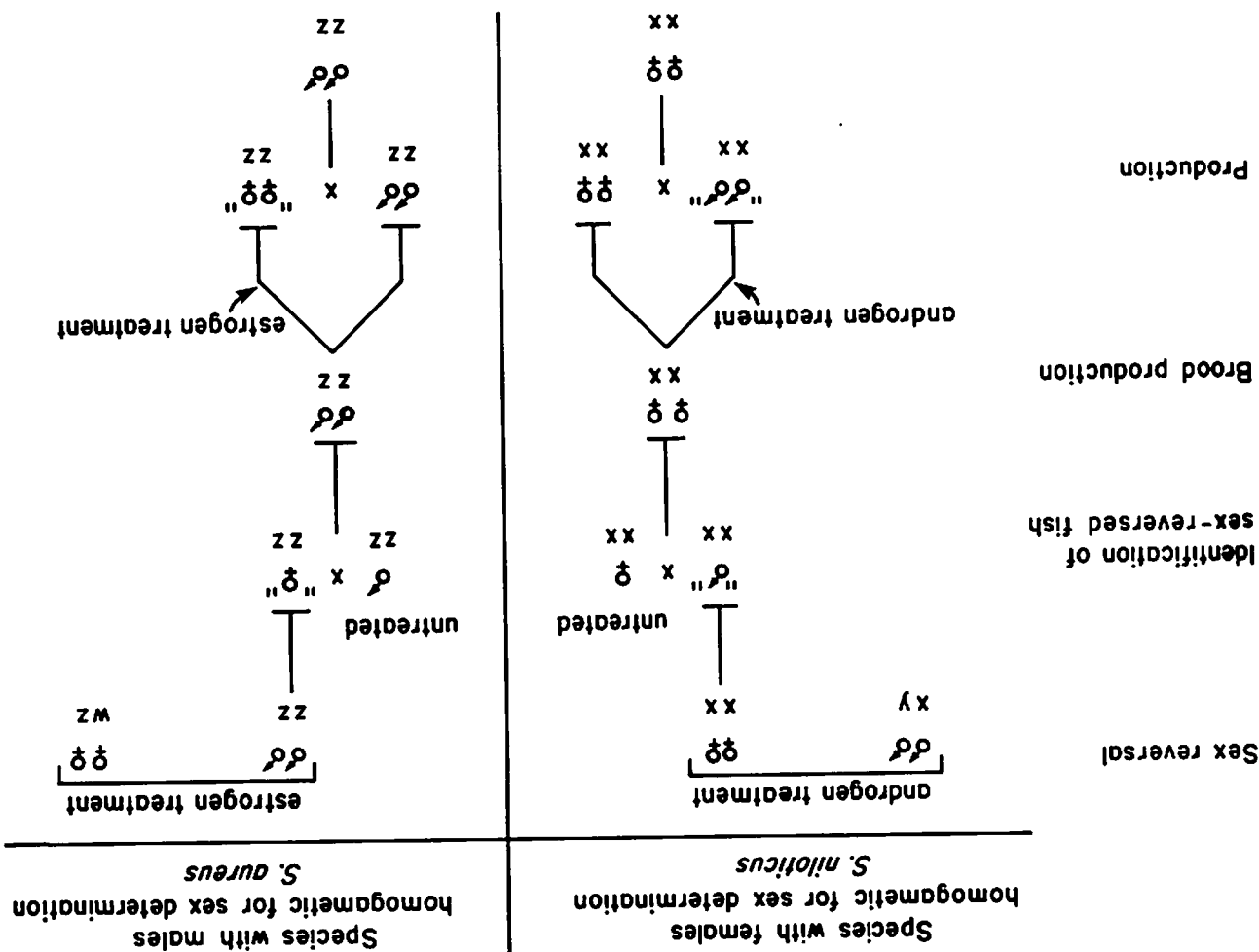
c. Reproductive Sterilization

Preventing unwanted reproduction of tilapias through sterilization (e.g., Al-Daham 1970; Katz et al. 1976; Nelson et al. 1976) did not yield practical results. Use of hormonal repression of female gonads (Dadzie 1974; Chiba et al. 1978; Lanzing 1978) is also controversial.

d. Cage Culture

Reproduction of tilapias may be controlled by growing them in cages (Pagan-Font 1975; Rifai 1980). This method appears to be of limited commercial value.

Figure 2. Simplified scheme of *Sarotherodon* brood production by hormone sex-reversal. Progeny of phenotypically sex-reversed individuals only are illustrated (from Shelton et al. 1978).



Alternative, homogametic sex-reversed individuals may be spawned with normal homogametic individuals to yield monosex progeny (Shelton et al. 1978), as shown in Figure 2. The production of all-male *S. aureus* populations through breeding requires estrogen sex reversal for producing hormone-induced phenotypic females (genotypic males). These females require identification from normal females by progeny-testing. The same approach may be applied to *S. niloticus*, for producing all-female populations (Figure 2) by androgen treatment to sex-reverse homogametic females into phenotypic males.

If such sex-reversed broodstocks are obtained, there is, in practice no real difference between this method and interspecific hybridization. In both cases different parental stocks need to be kept separate and free of contamination, in order to ensure the production of monosex populations. This method requires testing on a commercial scale.

The large-scale culture of all-male sex-reversed populations seems, at present, to be an unreliable and impractical.

b. Use of Sex-Reversed Individuals as Brood Stock

Production of all-male populations by interspecific hybridization has been discussed above. The practical aspects of this approach were described by Mires (1977). A plan for a commercial set up for tilapia hybridization in Panama (Central America) was recently described by Pretto Malca (1979).

a. Interspecific Hybridization

GENETIC METHODS OF POPULATION CONTROL

Control of reproduction by high density stocking rates has been suggested by Allison et al. (1979). The small size of fish at harvest may be a disadvantage of this method.

e. High Density Stocking Rates

Use of Electrophoretic Markers

Genetic markers are widely used in genetic and breeding investigations and in studies of genetic variation in natural populations. Electrophoretic markers are used mainly when visual markers are not available, since their identification is more cumbersome and time consuming than visual inspection. The major advantage in the use of electrophoretic markers is the ability to identify heterozygotes from homozygotes since, as a rule, electrophoretic alleles are co-dominant. The technique has been used for investigating the genetic structure of fish populations, as reviewed by Kirpichnikov (1973), Utter et al. (1974) and Allendorf and Utter (1979).

Methods of application of electrophoretic markers to selective breeding of fish include strain identification and maintenance of line purity, more efficient designs for genetic tests, construction of complex familial structures for genetic analysis of production traits, and family selection programs (Moav et al. 1976).

The electrophoretic techniques have been applied to tilapias for solving taxonomic problems and identifying species (Iles and Howlett 1967; Chen and Tsuyuki 1970; Hines and Yashouv 1970; Hines et al. 1971; Basasibwaki 1975; Herzberg 1978; Kornfield et al. 1979). Diagnostic differences, facilitating species recognition, have been found in haemoglobins, muscle myoglobulins,

liver and eyes several serum enzymes (e.g., esterases, transferrins, LDH) and tissue specific LDH. Intraspecific polymorphism in these markers was found by Chen and Tsuyuki (1970), Hines et al. (1971) and McAndrew and Majumdar (1983).

Avtalion et al. (1975, 1976) attempted to identify *S. niloticus*, *S. aureus* and their hybrid by electrophoretic species-specific markers in order to facilitate the production and maintenance of stocks consistently yielding all-male hybrids. Since the electrophoretic patterns overlap in these species, it was attempted to select for different patterns in each species. Brood stocks identifiable as species have been produced in this way. This process appears to have been accompanied by an increase in the proportion of males in interspecific crosses. It has not led to the production of 100% all-male progeny (Mires, pers. comm.).

A male-specific electrophoretic marker was discovered by Avtalion et al. (1975) in adult *S. aureus*, *S. galilaeus* and *S. vulcani*. A similar marker was found by Hardin (1976) in *S. aureus*, but only in ripe males. It seems likely, therefore, that this male-specific marker is hormonally induced and cannot be used to distinguish between natural and sex-reversed individuals.

Future Breeding Research

The large discrepancy between actual and potential tilapia production is, in part, due to present lack of knowledge in many aspects of their culture, research and breeding methods. Some methodological and breeding research projects, which may contribute to the improvement of tilapias, are discussed below.

METHODOLOGY FOR COMPARATIVE PERFORMANCE TESTS

Reliable methods for comparing different genetic groups are required for any trait under investigation. For traits such as tolerance to low temperatures or high salinity, the methodology appears simpler than for growth rate. Pruginin et al. (1975) compared the growth and sex-ratio of different groups of tilapias (species and hybrids) by stocking each group separately into a number of replicated ponds. This is an inefficient method, enabling only few groups to be compared in a given test.

A more efficient method, enabling comparison of a larger number of groups in a given number of ponds, has

been developed for the common carp (*Cyprinus carpio*). It consists of stocking all the groups into the same (communal) pond in a replicated test. This method requires means of identifying the different groups, with the aid of either natural markers or by artificial marking. It also requires a method of correcting for differences in weight gain between the groups, caused by chance differences in initial weights (Wohlfarth and Moav 1972). Results of growth tests carried out in such communal ponds require evaluation by comparing them with results obtained in separate ponds (Moav and Wohlfarth 1974). This system of growth testing, though found suitable for the common carp, has yet to be evaluated with different groups of tilapia.

CHOICE OF SPECIES

A genetic survey of the existing population should be one of the first steps in any breeding program. In tilapias, surveying implies choice of species, followed by choice of stocks from the chosen species. A full survey is an impractical task due to the large number of tilapia

species. A reasonable beginning may be a comparison between species presently cultured and species which, according to available knowledge, show good production and the likelihood of acclimatization in a given location.

Choice of species does not necessarily mean choice of a single species. A tilapia polyculture system, utilizing differences in feeding habits between different species (Table 4), may be more rational than the culture of a single species. This has been attempted in Uganda by co-stocking *S. niloticus* with the macrophyte feeder *T. zillii* (Semakula and Makoro 1967).

At least two species are needed when the aim is production of all-male interspecific hybrids. Several pairs of species have shown promising results (Table 9) and, in choosing between these pairs, the characteristics of the species should be taken into account. Since performance of hybrids cannot be fully predicted from performance of the parental species, comparative testing of different hybrids is required for proportion of males and for other production traits. If a comparison between a given hybrid and its parental species shows that the feeding spectrum of the hybrid approaches that of both parental species, hybrid monoculture could be equivalent to polyculturing the two parent species.

POPULATION CONTROL

As mentioned above, the genetic methods attempted so far for population control consist of interspecific hybridization and use of sex-reversed fish for brood stock. Both of these methods require an understanding of the mechanism of sex determination. The two empirical studies investigating this mechanism by classical Mendelian methods of crosses, back crosses, etc., (Chen 1969; Jalabert et al. 1971) did not result in a conclusive model. It seems likely that further studies using the same method, without sex-linked markers, would meet the same fate. No sex-linked markers, visual or biochemical, have yet been discovered in tilapias, and a genetic survey for them appears a promising approach.

Our investigations aimed at producing all-male broods (Hulata et al. 1981, 1983) consist of a program of selection by progeny testing. Single-pair interspecific hybrids are produced reciprocally, and the individual parents of each cross are selected or discarded according to the sex-ratio of their hybrid progeny. Figure 3 exemplifies that in the *S. niloticus* x *S. aureus* crosses parental pairs whose progenies consist of males only (e.g., pairs no. 1 and 3) are selected. Parental pairs whose progenies consist of both males and females (e.g., pair no. 2) are discarded. Similarly, in the *S. aureus* x *S. niloticus* crosses, only pairs whose progenies segregate into 1 female:3 males

are selected. These selected fish are used for brood stock production.

Other genetic methods considered for population control include gynogenesis and polyploidy.

Gynogenesis consists of stimulating the development of unfertilized eggs by use of inactivated sperm, and restoring diploidy using cold shock treatments (e.g., Purdom 1976). The resulting gynogenetic individuals thus inherit all their chromosomes from their mothers. This method has been suggested as a means of population control in grass carp, since gynogenetic progeny of homogametic females are expected to be all-female (Stanley 1976). Gynogenesis has not been demonstrated in tilapias.

Polyploidy has been induced in *S. aureus* by cold shock treatment to developing eggs (Valenti 1975). If fertile tetraploids could be produced by this method, crossing them to normal diploid individuals may result in sterile triploid progeny (Refstie 1979).

Another method of reducing the problem of uncontrolled reproduction is by selecting either for a fewer eggs per female or for delayed sexual maturity. This selection may be carried out either between or within species. The potential benefit of reduced fecundity depends on the age of fish stocked, length of growth period and required market weight.

Reduced egg number is more likely to cause an increase in cost of fry production than late sexual maturity. Reducing fecundity by choice of species could probably be attained by substituting mouthbrooding species for substrate breeders, since the latter are more fecund (Fryer and Iles 1972). In mouthbrooding tilapias, it appears that *S. mossambicus*, the most widely used species, is also one of the most fecund. Substitution of less fecund species for *S. mossambicus* should reduce the amount of uncontrolled spawning.

Selection for late sexual maturity may also be an indirect method of increasing growth rate, since incubation of eggs and care of fry presumably interfere with parental feeding activity. A reduction in growth rate was accompanied by endocrinological changes at onset of sexual maturity in *Xiphophorus maculatus* (Kallman and Borkoski 1978).

GENETIC INVESTIGATIONS

Construction of rational breeding plans requires some knowledge of the inheritance of economically important characteristics. In most farmed livestock, heritabilities have been estimated for some traits, but in tilapias, as in most other fishes, very little is known. Some of the

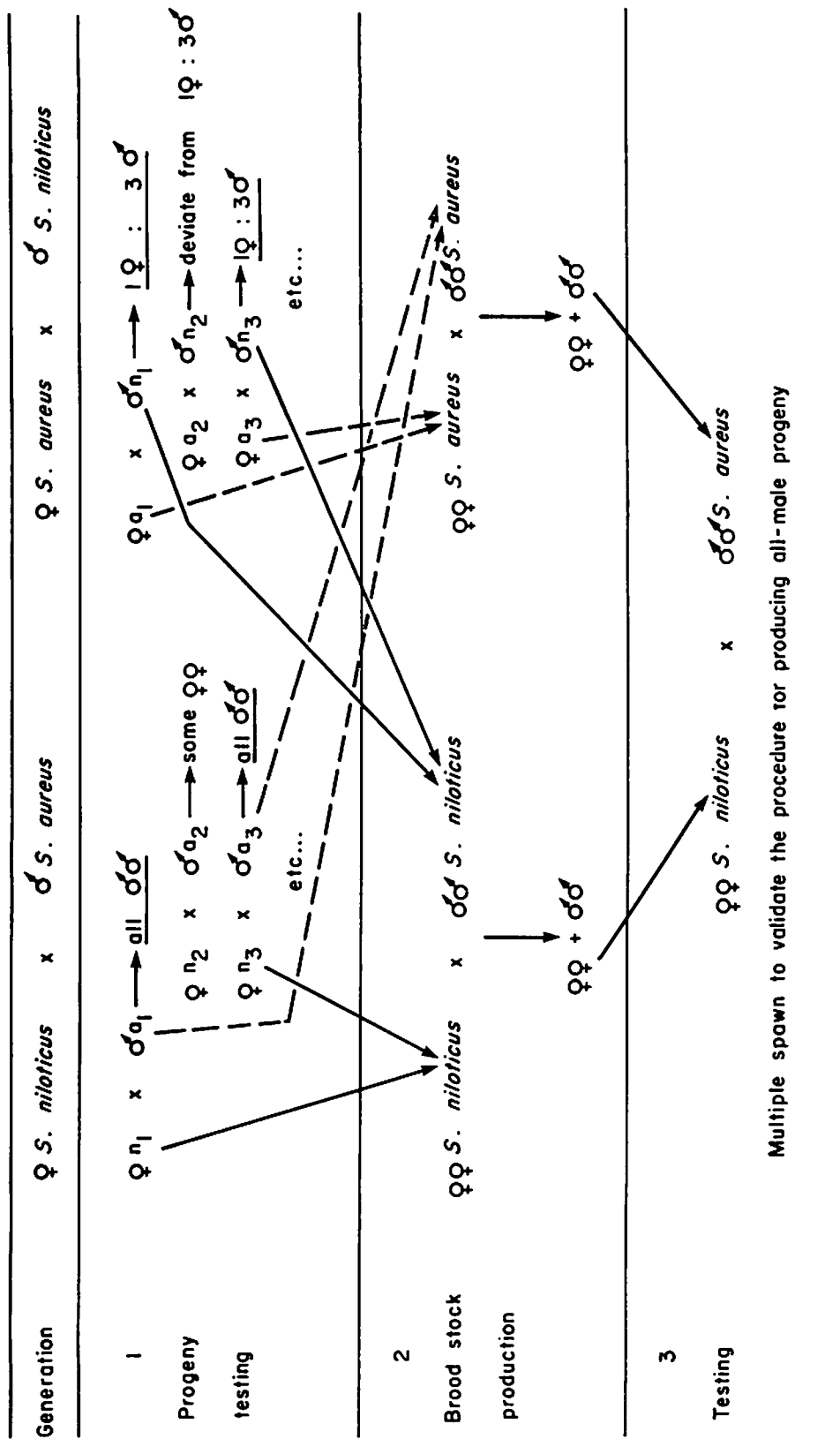


Figure 3. Procedure for progeny-testing *Sarotherodon* brood stocks, producing all-male interspecific hybrid broods (from Hulata et al. 1980).

genetic investigations required for tilapias are described below.

a. Estimating Heritabilities

The reported studies in tilapias yielded low estimates of heritabilities of weight and length. This implies that in the populations under investigation, individual selection for growth rate is not expected to be effective. In other populations, genetic response to selectively removing the larger individuals indicated the existence of genetic variation for growth rate (Gwahaba 1973; Silliman 1975). Further estimates of heritabilities are required, for several traits and in different species, in order to predict the suitability of individual selection for genetic improvement of tilapias.

b. Genetic Correlations

When selection is carried out on one trait, changes may occur in other traits. These "correlated responses" (Falconer 1960) are due to genetic correlations between different traits. Similarly, when selection is carried out simultaneously on two or more traits, the response in each trait may be slower than if a single trait is under selection. Estimates of genetic correlations are therefore required as criteria for choosing traits to be selected and to avoid undesirable correlated responses.

c. Effects of Inbreeding and Crossbreeding

Breeding programs often lead to a reduction in genetic variability, causing inbreeding, which may result

in a reduction in fertility and production. These negative effects of inbreeding, termed "inbreeding depression," have not been estimated in tilapias. Conversely, some of the most spectacular successes in plant and animal breeding are due to crossbreeding unrelated stocks. Heterosis, the phenomenon of the crossbred's performance exceeding that of either parent, also requires demonstration in tilapias (see discussion in Pruginin et al. 1975). An extra benefit of interspecific hybridization lies in the avoidance of any possible inbreeding depression, though this benefit may also be attained by crossing two unrelated stocks of the same species.

d. Inheritance of Genetic Markers

A knowledge of the heredity of morphological (e.g., red body coloration) and biochemical genetic markers may enable their utilization in experimental work (Moav et al. 1976).

APPLICATION OF RESEARCH RESULTS

The implementation of a successful breeding program is the production of improved broodstock. Genetic "contamination" from outside sources must be avoided. This is difficult when two different groups of fish are used for crossbreeding. As a rule, production of improved broodstocks should be carried out by professional fish breeders. When the fry to be produced are crossbreds between two stocks, or hybrids between two species, the farms should then be supplied with females of one stock or species and males of the other. Alternatively, the fry could be produced at central hatcheries for distribution to fish farms.

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- Philippine municipal fisheries: a review of resources, technology and socioeconomics. By I.R. Smith, M.Y. Puzon and C.N. Vidal-Libunao. 1980. ICLARM Studies and Reviews 4, 87 p.

Provides evidence of a trend towards overfishing in Philippine coastal waters, and of a willingness of fishermen to consider alternative livelihoods. The implications of the authors' findings to fisheries management and research are discussed. Published jointly with the Philippine Fishery Industry Development Council, Philippine Heart Center for Asia, East Ave., Quezon City, Philippines.

- Food potential of aquatic macrophytes. By P. Edwards. 1980. ICLARM Studies and Reviews 5, 51 p.

Reviews present uses of freshwater "weeds" in food production, as fertilizer, fish feed and for direct human consumption. Identifies the most promising areas of research for using the untapped potential of these resources.