ICLARM STUDIES AND REVIEWS 6

Applied Genetics of Tilapias

Giora W. Wohlfarth
and Gideon I. Hulata

INTERNATIONAL CENTER FOR LIVING AQUATIC RESOURCES MANAGEMENT

Applied Genetics of Tilapias

Giora W. Wohlfarth

and

Gideon I. Hulata

1981

ICLARM

INTERNATIONAL CENTER FOR LIVING AQUATIC RESOURCES MANAGEMENT
MANILA, PHILIPPINES

Applied Genetics of Tilapias

G. W. WOHLFARTH
AND G. I. HULATA

1981

Published by the International Center for Living Aquatic Resources Management
MCC P.O. Box 1501, Makati, Metro Manila, Philippines

Printed in Manila, Philippines

Wohlfarth, G.W. and G.I. Hulata. 1981. Applied Genetics of Tilapias.
ICLARM Studies and Reviews 6, 26 p. International Center for
Living Aquatic Resources Management, Manila.

ISSN 0115-4389

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

Preface

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

Contents

Applied Genetics of Tilapias

G. W. WOHLFARTH AND G. I. HULATA

Abstract

Wohlfarth, G.W. and G.I. Hulata. 1981. 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 intermuscular 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. hornorum* 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. hornorum* 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.

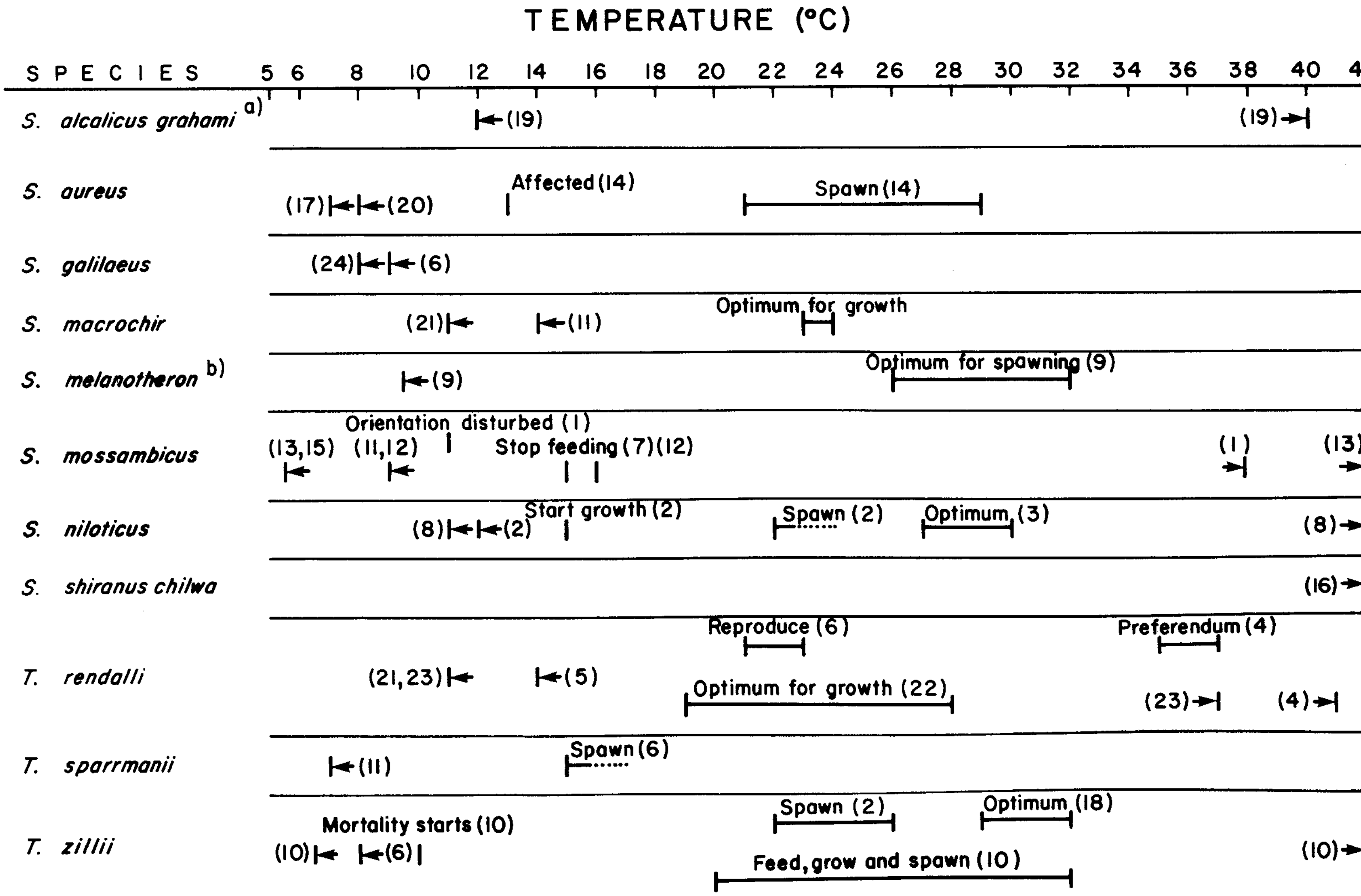
Species	Natural distribution	Distribution by man	Sources
T. rendalli[a]	West Africa (Senegal and Niger River systems), Central Africa (Congo River system), and Eastern South Africa (Zambesi River system as far as Natal	Sudan, Malagasy Republic, Southern U.S.A., Mexico, Puerto Rico, Brazil, Colombia, Pakistan, Thailand and Malaysia	Balarin and Hatton 1979; Chimits 1955, 1957; Jubb 1967; Ruwet et al. 1975
T. sparrmanii	Africa, south of the Equator (Zambesi River, down to the Orange River system	Tanzania, Japan	Balarin and Hatton 1979; Chimits 1957; Ibrahim 1975; Jubb 1967; Sterba 1962
T. tholloni	Tropical West Africa, from Cameroon to the south of Congo		Ruwet et al. 1975; Sterba 1962
T. zillii	Africa, north of the Equator (Nile River system and Western Africa up to Morroco), 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
S. andersonii	Upper Zambesi River system	Congo, Zambia, South Africa	Hickling 1967; Jubb 1967
S. aureus	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
S. esculentus	East Africa (Lake Victoria)	Tanzania, Malagasy Republic	Lowe (McConnell) 1956
S. galilaeus	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
S. hornorum	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
S. leucostictus	East Africa (Lakes Albert, Edward and George)		Elder et al. 1971
S. macrochir	Southern part of Central Africa (Upper Zambesi River system)	Congo, French Equatorial Africa, Ivory Coast, Liberia, Malagasy Republic	Balarin 1979; Chimits 1955; Jubb 1967; Vincke 1979
S. melanotheron[b]	West Africa (coastal districts from Senegal to Congo)	U.S.A. (Florida)	Balarin and Hatton 1979; Pauly 1976; Sterba 1962
S. mossambicus	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)	Balarin 1979; Chimits 1955; Jubb 1967; Sterba 1962
S. spilurus niger	East Africa (Lake Rudolf)	Mozambique, Malagasy Republic, Zambia	Balarin and Hatton 1979; Elder et al. 1971
S. niloticus[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
S. variabilis	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 Zambesi 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 transplantation from Egypt. *S. niloticus* was first imported to Alabama (U.S.A.) from Brazil in the early 1970's and not in the 1950's as mistakenly reported (Tave and Smitherman 1980).

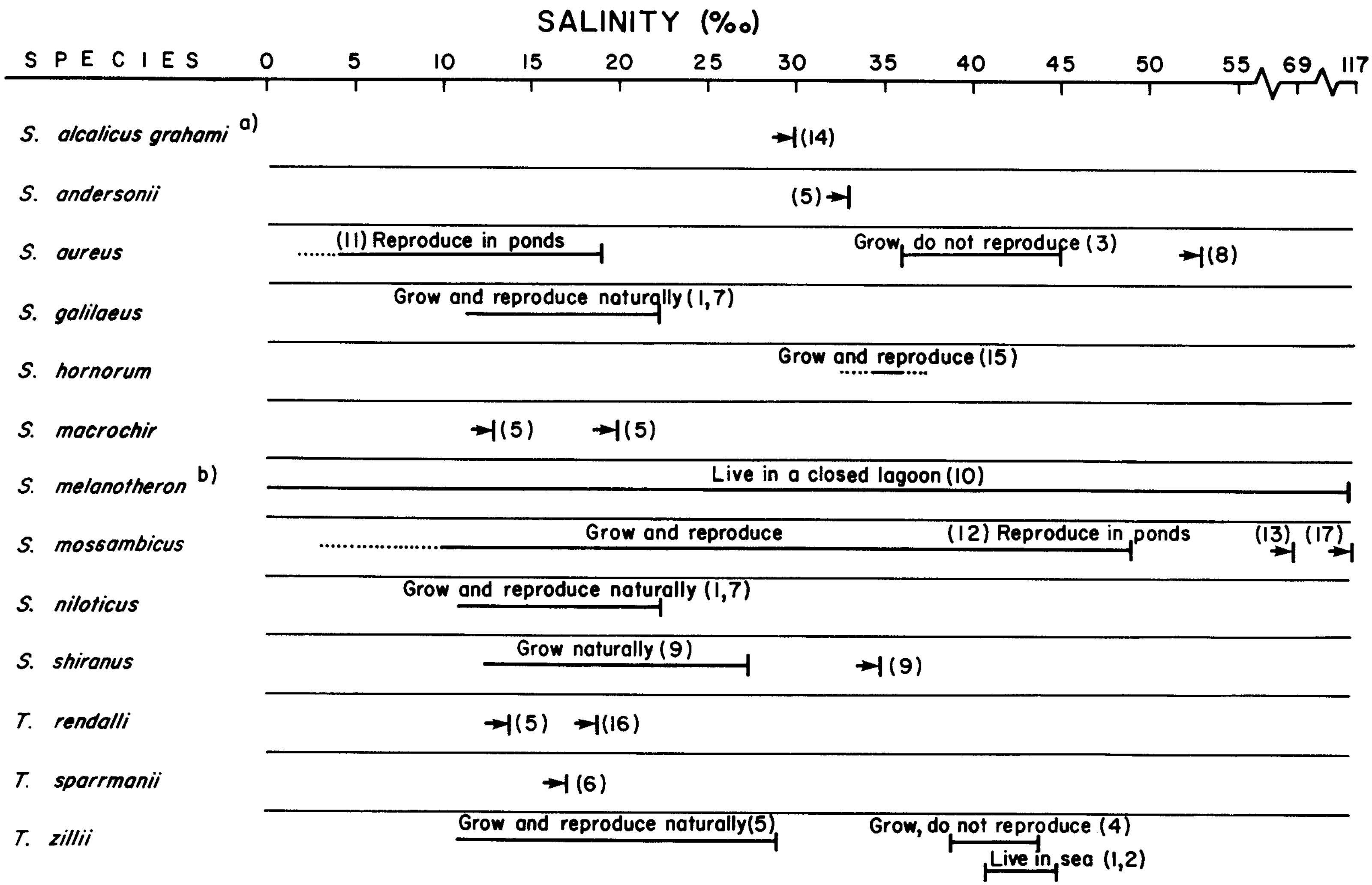
Table 2. Temperature ranges of tilapias (partially after Balarin and Hatton 1979). (|← and →| are symbols for the extreme temperatures tolerated. Figures in parentheses refer to list of sources below).



Sources : 1. Allanson et al. 1971. 2. Bardach et al. 1972. 3. Beamish 1970. 4. Caulton 1975. 5. Caulton 1976. 6. Chimits 1957. 7. Dendy et al. 1967. 8. Denzer 1967. 9. Finucane and Rickney 1965. 10. Hauser 1977. 11. Hofstede 1955. 12. Kelly 1956. 13. Kirk 1972. 14. McBay 1961. 15. Mironova 1969. 16. Morgan 1972. 17. Perry and Avault 1972. 18. Platt and Hauser 1978. 19. Reite et al. 1974. 20. Sarig 1969. 21. Sklower 1951. 22. Spass 1960. 23. Whitefield and Blaber 1976. 24. Yashouv 1958b.

[a]= *S. grahami*
[b]= *S. macrocephalus*

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. Fryer and Iles 1972. 6. Fukusho 1969. 7. Kirk 1972. 8. Lotan 1960. 9. Morgan 1972. 10. Pauly 1976. 11. Perry and Avault 1972. 12. Popper and Lichatowich 1975. 13. Potts et al. 1967. 14. Reite et al. 1974. 15. Talbot and Newell 1957. 16. Whitefield and Blaber 1976. 17. 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: Phytoplankton Blue-greens	Natural food: Phytoplankton Diatoms	Natural food: Microphytes	Macrophytes	Detritus	Benthos	Artificial food: Oil cakes mill wastes	Artificial food: Plants	Artificial food: Protein-rich pellets
S. alcalicus grahami[a]			11								
S. andersonii	3					3		3			
S. aureus	16	25						24			1,5
S. esculentus				3,9,10,12				3			
S. galilaeus				12,14			14				
S. leucostictus				12,22			12				
S. macrochir				3							3
S. melanotheron[b]				8		23	7,8,19,23	7,20	23	23	
S. mossambicus	15,17	19		19,11	19,26	3,19	3	3	3,17	3	
S. niloticus	12		18	11,22			11,12,22	13	6,27		1
S. shiranus							11				
S. s. niger.	4			11	4			4,11			
S. variabilis							10,12				
T. rendalli		19				2,11,19	11	19	3,23	3,23	
T. sparrmanii						4					
T. zillii					12	12				21	

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. Johnson 1974. 15. Man and Hodgkiss 1977. 16. McBay 1961. 17. Mironova 1969. 18. Moriarty 1973. 19. Munro 1967. 20. Pauly 1976. 21. Payne 1071. 22. Semakula and Makoro 1967. 23. Sivalingam 1975. 24. Spataru 1976. 25. Spataru and Zorn 1978. 26. Swingle 1960. 27. 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 (egss/female)	Cultured in[a]	Sources
S. andersonii	200-250	1.8 kg	12-15	300-700/year	Central East Africa	8
S. aureus	2-3 g/day	31.5 cm	6	2,900-4,000/year	Israel[b]	3-14
S. esculentus		37.5 cm	5	up to 700/spawn	Tanzania	5,7
S. galilaeus		0.8 kg		5,000/year	Africa	3
S. leucostictus			6 (7.5 cm)	up to 400/spawn	Kenya and Uganda	7,12
S. macrochir	150-250	2.0 kg		up to 800/spawn	Africa	2,7,8,12
S. melanotheron[c]		0.3 kg			Africa	13
S. mossambicus	150-350	39 cm	2-3	up to 800/spawn (6-11 spawns)	Southern Africa, South East Asia	3,8
S. spilurus niger		1 kg	4		East Africa	6
S. niloticus	2-3 g/day	2.5 kg	4-5	700-2,000/spawn	Africa, Israel[b], South East Asia, Latin America[d]	6,7
S. shiranus		39 cm			Malawi	3,10,11
S. variabilis		0.5 kg		up to 300/spawn	East Africa	7
S. vulcani	2-3 g/day		6	2,000-2,100/year	Africa, South East Asia	14
				7,000-8,000/year		7,8
T. rendalli	150-200	1.3 kg			Colombia	2
T. sparrmanii		0.15 kg		up to 3,300/spawn		1,6
T. tholloni		0.15 kg			Cameroons	6
T. zillii		0.8 kg	5	300-12,000/year	Africa, South East Asia	4,5,12

[a]According to Jhingran and Gopalakrishnan (1974).
[b]Mainly as female *S. niloticus* x male *S. aureus* hybrid.
[c]= *S. macrocephalus*
[d]Mainly 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 1975. 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. Differences 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 breds, 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 in nature	Deliberate crosses carried out in ponds or tanks	Deliberate crosses carried out under lab. conditions	Sex of hybrid progeny in deliberate crosses
Maternal mouthbrooder	*S. niloticus* x *S. spilirus niger*	17	21		Surplus of males
x	*S. niloticus* x *S. macrochir*		3,12,15		Only males when *S. niloticus* female parent.
Maternal mouthbrooder	*S. niloticus* x *S. aureus*		9,14,21,22,30		Occasionally males only when *S. niloticus* female parent
	S. niloticus x *S. variabilis*	25,26	21		Only males when *S. niloticus* female parent
	S. niloticus x *S. leucostictus*		21		Surplus of males
	S. niloticus x *S. hornorum*		14,16,21		Only males when *S. niloticus* female parent
	S. niloticus x *S. mossambicus*		6,13,24,30		Surplus of males
	S. mossambicus x *S. hornorum*		5,10		Only males when *S. mossambicus* female parent
	S. mossambicus x *S. andersonii*	18			
	S. mossambicus x *S. spilurus niger*		29		Surplus of males
	S. mossambicus x *S. aureus*		2,30,31		Surplus of males (*S. aureus* misidentified as *S. niloticus*)
	S. vulcani x *S. hornorum*		21		Large surplus of males
	S. spilurus niger x *S. hornorum*		21		Only males when *S. spilurus niger* female parent
	S. spilurus niger x *S. leucostictus*	7,8	21		Surplus of males
	S. amipheles x *S. esculentus*	23			
	S. vulcani x *S. aureus*		22		Large surplus of males
	S. hornorum x *S. aureus*		14,21		Surplus of males
Maternal mouthbrooder	*S. melanotheron*[b] x *S. mossambicus*			4,19	Only females when *S. melanotheron* female parent
x					
Paternal mouthbrooder	*S. melanotheron*[b] x *S. niloticus*			4,19	
Maternal mouthbrooder	*T. tholloni* x *S. mossambicus*			4,19,20	Only females when *T. tholloni* female parent
x	*T. tholloni* x *S. niloticus*			4,19	Only females when *T. tholloni* female parent
Substrate breeder	*T. zillii* x *S. mossambicus*			4	
	T. zillii x *S. spilurus niger*	28	11		Only males. Sex of parents not given
Paternal mouthbrooder	*T. tholloni* x *S. melanotheron*[b]			4,19	
x					
Substrate breeder					
Substrate breeder	*T. zillii* x *T. rendalli*[c]	26,27	1		Sex ratio 1:1
x					
Substrate breeder					

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

[a]Order 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	*S. mossambicus* x *S. macrochir* *S. andersonii* x *S. mossambicus* *S. andersonii* x *S. macrochir* *S. spilurus niger* x *S. mossambicus*	Only source–Jhingran and Gopalakrishnan (1974), which does not refer to original papers.
	S. mossambicus x *S. andersonii*	Stated that successfully bred in ponds in Israel, but *S. andersonii* not present in Israel.
	S. hornorum x *S. macrochir*	No reference to original paper.
Elder et al. 1971	*T. tholloni* x *S. spilurus niger*	Refers to Peters (1963b) but no such hybrid appears in that paper, or in Peters (1963a).
	S. niloticus x *S. galilaeus*	Refers to Yashouv and Chervinski (1959), but existence later doubted by authors–see footnote in Peters and Brestowsky (1961).

[a]Order 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 Female	 Male	Reason for failure of hybridization	Source
Maternal x paternal mouthbrooder	*S. mossambicus*	*S. melanotheron*[a]	no fry obtained	Bauer (1968) Peters (1963a)
Maternal mouthbrooder x substrate breeder	*S. niloticus*	*T. tholloni*	high fry mortality	Peters (1963a) Bauer (1968)
	S. mossambicus	*T. tholloni*	high fry mortality	Peters (1963a) Bauer (1968)
	S. aureus	*T. zillii*	no fry obtained	Van Schoor (1966); Hsiao 1980
	T. zillii	*S. aureus*	no fry obtained	Van Schoor (1966); Hsiao 1980
Paternal mouthbrooder x substrate breeder	*S. melanotheron*[a]	*T. tholloni*	high fry mortality	Peters (1963a) Bauer (1968)
Substrate breeder x substrate breeder	*T. sparrmanii*	*T. zillii*	no fry obtained	Van Schoor (1966)
	T. zillii	*T. sparrmanii*	no fry obtained	Van Schoor (1966)
Substrate breeder x biparental mouthbrooder	*T. zillii*	*S. galilaeus*	no fry obtained	Van Schoor (1966)

[a]= *S. macrocephalus*