SESSION I: BIOLOGY

Chairman's Overview

R. H. LOWE-MCCONNELL

At the start of this first session of the Conference it is very important to stress the aims of the meeting, as set out in Roger Pullin's letter of invitation, namely, "the urgent need to bring tilapia biologists and culturists together to exchange views and information and to define approaches and priorities for future work". We need to keep this firmly in mind and aim to produce the most constructive guidelines for future research.

The two groups of people mentioned, the tilapia biologists who have been working mainly under field conditions or in laboratories (or both) and those with practical experience of aquaculture, have much to give one another of very different experiences that can help to solve one another's problems. This is a two-way process. As a field worker myself, I know only too well the complexity of working conditions in natural waters in the tropics, where so many species interact and where, for example, it is often so difficult to determine fish growth rates. We have to look to those who grow tilapias in ponds to solve many problems posed in the field, in particular, those concerning the switch from growth to reproduction (nanism, dwarfing) which is such a special feature of tilapia biology. I regard this as possibly the key problem for our attention. If we could really understand the mechanism which controls the switch from growth to reproduction, this would be one of the biggest steps towards improving tilapia culture.

This session is concerned mainly with field studies, and should provide a good background to our subsequent consideration of the physiology of tilapias from both field and laboratory work. For those who grow tilapia in ponds, we must stress the vast scale of the theatre for field studies. The equatorial Lake Victoria in East Africa is over 6.5 million ha and the Kafue floodplain, another site for much tilapia research, around 121,000 ha. Sampling such huge areas presents special problems, and errors arise in extrapolation of results. Catch statistics are of very variable reliability compared with emptying a pond and weighing all the fish. Furthermore, what is loosely referred to as 'fish production' from these vast areas is really the fish catch and only a very small percentage of the total biological production (unlike ponds from which most of the total production may be channelled into spawners).

In this session we have four papers.

Dr. Ethelwynn Trewavas first introduces the taxonomy and speciation of tilapias, and says why it is so important to know which species we are dealing with when making studies of any kind. We all owe a great debt of gratitude to Dr. Trewavas who has toiled away for very many years putting

together a definitive monograph on the tilapias. I see her herculean efforts at first hand—I share her habitat among the tilapia bottles at the Natural History Museum in London—and I have seen (and have benefited from) the ever-ready help she has given so unstintingly to numerous biologists from all over the world.

Second, we have the contribution on ecology and distribution prepared by Dr. J-Cl. Philippart with Professor J-Cl. Ruwet, who is unable to attend this meeting. They have selected certain areas of ecology, believing that aspects such as growth and production would be treated in other papers. They have considered the physico-chemical factors involved in tilapia distribution; feeding behavior, e.g., trophic spectra, variations in feeding regimes and the periodicity of feeding activity (subjects which lead onto our later discussions on physiological aspects of feeding); reproductive behavior, comments on practical implications and the choice of microhabitats and spatial segregation. They have then assessed the ecological consequences of introductions and transfers of tilapias in Africa and elsewhere.

Dr. D.L.G. Noakes then presents a paper that he and Dr. E. Balon, who is also unable to be here, have prepared on life histories of tilapias. This seems to be a rather theoretical paper but it leads up to a practical suggestion of culture methods which might help to produce the large fish with late onset of breeding and fast growth rates that we all desire.

Lastly, the paper which I was asked to prepare on tilapias in fish communities was originally aimed to look at the partitioning of resources among sympatric tilapias and at some of the factors controlling tilapia numbers in nature (with special attention to the switch from growth to reproduction in *Sarotherodon niloticus*). It became clear, however, that much of what I had written had considerable overlap with other manuscripts, so I have attempted, at very short notice, to fill in some gaps by collating information on tilapia growth rates, production and yields under natural conditions.

Tilapias: Taxonomy and Speciation

E. TREWAVAS

Fish Section
British Museum (Natural History)
Cromwell Road, South Kensington
London, S.W. 7, England

The tilapias are here grouped into two genera, *Tilapia* and *Sarotherodon*, characterized by both their feeding and their reproductive habits and structures. There is some overlap in feeding habits, some species of both genera feeding on detritus and periphyton, but substrate-spawning and mouthbrooding respectively characterize the two genera.

The mouthbrooding of the species of *Sarotherodon* is of two main types, biparental or parental in subgenus *Sarotherodon* (in the restricted sense) and maternal brooding with mating of a lek pattern in the rest. The maternal mouthbrooders have been divided into several (5 to 7) subgenera: *Oreochromis*, *Danakilia*, *Alcolapia*, *Nyasalapia* and *Neotilapia* are recognized here. Speciation, both allopatric and sympatric, of subgenus *Sarotherodon* has taken place in west Africa, and of the other subgenera mostly in east and central Africa. There is no doubt that the division between subgenus *Sarotherodon* and other subgenera is deeper than the divisions within the latter. For this reason some authors (Thys, Peters) prefer a generic grouping that goes no lower than *Tilapia*, but the mouthbrooding subgenera have so much in common that they must have descended from one or a few closely related substrate-spawning species, and grouping them all at the generic level seems to have both theoretical and practical justification.

An example is given of the importance of recognizing specific distinctions.

Biology and Taxonomy

All the tilapias, in the broad sense, have in common a mainly herbivorous diet, in distinction to the majority of fishes which feed predominantly on small invertebrates or on young or small-sized fishes. They are therefore only one step from the primary producers (plant life) and as they grow to a good size they are a valuable food source for man, the omnivore.

Structural adaptations to this diet are the long, coiled intestine, which may be up to fourteen times the body length, the bicuspid and tricuspid teeth of the jaws and the small, sharp pharyngeal teeth used to prepare the food by shredding the coarser materials and breaking some of the cell walls before passing it on to the stomach. Since the preferred diet of the

different species varies from coarse vegetation (grasses, young shoots and leaves of water weeds) to unicellular algae and even bacteria, the teeth also vary in the degree of coarseness and movability.

Tilapias all exhibit a high degree of parental care and in this function they are sharply divided into substrate-spawners and guarders of the brood on the one hand and mouthbrooders on the other (Lowe-McConnell 1959).

A division based on diet roughly coincides with one based on reproductive habits. I say 'roughly' partly because tilapias are flexible and opportunistic in their feeding habits, but also because of two species that fail to conform.

Tilapia mariae is a substrate-spawner, but its usual diet consists of epiphytic algal growths and its jaw teeth are fine, slender-shafted and movable. Its pharyngeal teeth are fine, on a bone whose anterior blade may be as long as the toothed area and its standard gill-raker count is 12-16: high for a *Tilapia*.

Sarotherodon niloticus niloticus is a maternal mouthbrooder, but its jaw teeth are nearly as stout as those of *Tilapia zillii* and its pharyngeal teeth are firm, on a triangular area whose length is often greater than the length of the blade. But the gill-rakers are more numerous than in *T. mariae*, the standard count being 18-26.

But this overlap is merely an inconvenience when we try to define the two groups and no one would doubt to which group each species is related.

The substrate-spawners constitute the genus *Tilapia* Smith (1840), the mouthbrooders *Sarotherodon* Rüppell (1852).

Tilapia was an effort by A. Smith, its author, to spell the Bushman word for 'fish', which began with a click, rendered 'Til'. *Sarotherodon* means 'brush-toothed'.

Examples of the two genera familiar to fish culturists are: *Tilapia sparrmanii* A. Smith, *T. rendalli* Boulenger, *T. zillii* (Gervais), *T. cabrae* Boulenger, *Sarotherodon melanotheron* Rüppell, *S. galilaeus* (Linnaeus), *S. niloticus* (Linnaeus), *S. aureus* (Steindachner), *S. mossambicus* (Peters), *S. niger* (Günther) and *S. macrochir* (Boulenger).

The four examples of *Tilapia* were named after persons who collected the originals or *(T. sparrmanii)* had explored their region of origin. The word *melanotheron* means 'black-hinged' or 'black-chinned', *galilaeus* and *niloticus* are self-explanatory, *'aureus'* refers to the golden-yellow color of the preserved fish (not the living) and *'macrochir'*, meaning 'big hand', refers to the long pectoral fin, the homolog of the forelimb (arm and hand) of man.

T. sparrmanii feeds on the coarser algae and grasses and also on the small animal life among them. It is sometimes described as omnivorous. It is valued for pond use in South Africa because its wide temperature tolerance enables it to withstand the winters of the High Veldt.

T. rendalli and *T. zillii* have strong cusped teeth in jaws and pharynx and are specialized feeders on vascular plants. Ruwet (1963a) has given a vivid description of the voracious attack by *T. rendalli* on the newly flooded grasses of the Mwadingusha dam on River Lufira, Zaïre.

These two species, which are not very easily distinguished at sight, have largely complementary areas of distribution. *T. zillii* is a Soudanian form, extending from west Africa through the Chad basin to the Nile, Lake Albert

and Lake Turkana into Israel and the Jordan Valley. *T. rendalli*, one of the forms formerly included in '*T. melanopleura*', has a wide distribution in the Upper Zaïre and Kasai, Lakes Tanganyika and Malawi, the Zambezi basin and the Limpopo. At Yangambi, near Kisangani, where the River Zaïre turns westwards, the natural distributions of the two species overlap. In west Africa *T. rendalli* is replaced by *T. dageti*, which appears to be less abundant than *T. zillii*.

At Yangambi *T. zillii* is in nature less abundant than *T. rendalli*. Gosse (1963), who administered the fishponds at Yangambi, did not at first realize that his *T. rendalli* ponds included an admixture of *T. zillii*, but after a while the more robust *T. zillii* dominated the pond populations. The same thing evidently happened in the ponds at Yaounde, Cameroon, to which Gosse had inadvertently sent a mixture of the two species.

In Lake Victoria *T. zillii* was introduced from Lake Albert and *T. rendalli* either from Shaba or Zambia. At first they were believed to have interbred, but later, when introductions were made into many farm dams in Uganda and Kenya, the *Tilapia* were named as *T. zillii*.

Gosse was emphatic that *T. rendalli* was by far superior as a food fish. It is therefore important for pisciculturists to know one from the other. The differences are:

Color. *T. zillii* usually has two horizontal dark stripes, one mid-lateral, the other nearer the dorsal outline. These are crossed by vertical bars and the strongest marks are blotches at the intersections. The caudal fin is usually covered by a grey network with pale interstices. The eggs are green.

T. rendalli usually shows dark vertical bars only and the scales have each a dark basal crescent. The caudal fin has a spotted upper half and a red or yellow lower half. This red or yellow pigment may also color the anal fin. The eggs are yellow.

Both species frequently have a carmine flush on the lower flanks, behind the pectoral fin, and this is not confined to one sex or to mature fishes.

General shape. *T. rendalli* is typically more deep-bodied than *T. zillii* but this is an average difference and not suitable for individual identification.

Meristic characters (counts). The number of gill-rakers is the same in both species: 8-10 below the joint of the first arch. This distinguishes them at once from *Sarotherodon*. The mean numbers of scales, vertebrae and dorsal fin-rays provide good distinctions and the modal numbers of dorsal spines are sufficiently well-marked to allow a quick field test on a number of specimens. *T. zillii* usually has 28 vertebrae, *T. rendalli* 29. In *T. zillii* the commonest number of dorsal spines is XV, in *T. rendalli* XVI (Table 1). For the whole dorsal fin, among 130 *T. rendalli* I found 26% with XVI 12, 66.9% with XVI 13; other combinations were found in only one or two fishes. Among 40 *T. zillii* 18 (45%) had XV 12 and 10 (25%) XV 13.

There are about 29 species of *Tilapia* and most of this speciation has taken place in the western rivers of Africa. The euryhaline *T. guineensis* is found in lagoons and estuaries along the coast from Angola to Senegal. Other species

are little known beyond their native rivers, although *T. tholloni* has been much used in laboratory studies.

Table 1. Frequency distribution of vertebrae and dorsal spines in *Tilapia zillii* and *T. rendalli*.

		T. zillii	T. rendalli
Vertebrae	27	5	
	28	33	1
	29	2	31
	30		1
Dorsal spines	XIII	2	
	XIV	60	
	XV	467	4
	XVI	63	124
	XVII		2

In the eastern rivers north of the Zambezi *Tilapia* was never reported before the widespread introductions of the last three decades. But the fish fauna of Mozambique and Tanzania was little known and we cannot now be sure that the presence of *T. rendalli* in the rivers of Tanzania is not natural. We do know, however, that Kenyan waters were devoid of this genus until the introduction of *T. zillii*.

The tilapias most cultivated are species of *Sarotherodon*, the mouthbrooders.

It is now well known that the details of the mouthbrooding habit are not the same in all mouthbrooding tilapias (Heinrich 1967; Peters and Berns 1978). The type-species of *Sarotherodon, S. melanotheron*, is, as it happens, the most atypical. In nature it lives in brackish water and it is a paternal mouthbrooder. Many studies of its behavior show that in comparison with *S. mossambicus* for example, it has retained vestiges of some of the reproductive habits and even structures of the substrate-spawners. So has its relative in fresh waters, *S. galilaeus*. When we subdivide the mouthbrooders, it is these two species *(S. melanotheron* and *S. galilaeus)* that typify *Sarotherodon* in the strict sense, that is, subgenus *Sarotherodon. S. mossambicus, S. niloticus, S. aureus* and other east and central African species have a reproductive schema that excludes the males from the care of the brood. They are in breeding time sexually dimorphic and the female takes the eggs as soon as they are fertilized to special nursery areas where she holds them in her mouth until the yolk is sufficiently reduced for them to swim freely. Even then, for several days she takes them back into her mouth at night or when danger threatens. The east African maternal brooders have received a second subgeneric name, the earlier available being *Oreochromis* (now raised to genus; see Addendum).

The meaning of *Oreochromis* is 'mountain cichlid'. (*Chromis* was an early name given to both cichlids and a marine genus and is now restricted to the latter). It was first given to *Oreochromis hunteri* Günther (1889), an inhabitant of a small rocky crater-lake on the slopes of Mount Kilimanjaro. Little is known about the habits of this species, but from its structure

and geographic situation it is believed to be a maternal mouthbrooder like its neighbors S. *pangani* and S. *mossambicus.*

It is commonly believed that systematic conclusions are based on anatomical considerations involving dissection and the use of the microscope. Such evidence is indeed most important, but there is no aspect of an organism's biology that a systematist can afford to ignore. In defining the subgenera *Sarotherodon* and *Oreochromis* the main evidence is behavioral, backed by geographical. The geographical evidence is well set out by Thys (1963). Many observers have contributed to the behavioral evidence briefly summarized above.

I do not know of any structural character that trenchantly separates the two subgenera. Some members of *Oreochromis,* including *S.(O.) hunteri* have four anal spines, either in all or in some individuals, but others have only three; all species of subgen. *Sarotherodon* have three. In no species of subgen. *Sarotherodon* are the jaws enlarged in sexually mature males. They are enlarged in several species of subgen. *Oreochromis* but not in all. The vertebral numbers range from 26 to 32 in subgen. *Sarotherodon,* 27 to 34 in *Oreochromis.* Parallel adaptations to various feeding regimes have developed in species of the two subgenera. If we do not know the breeding habits of a species we can place it in a subgenus only if its overall characters add up to a general resemblance to a geographically-close member of one or other of the subgenera.

The development of a tassel on the male genital papilla is a conspicuous feature that characterizes a number of related species *(S. macrochir,* the Malawi flock, etc.) and for these we may use a subgeneric name *Nyasalapia* Thys (1968).

In the case of S. *tanganicae,* of whose breeding habits little is known, the fact that its ventral scales are very small suggests relationship to *Oreochromis.* But it has very specialized teeth and as it has been given a subgeneric name of its own, I propose to use it and to call it *Sarotherodon (Neotilapia) tanganicae.*

Another peculiar species in the same kind of limbo is the little S. *franchettii* of Lake Afrera (= Giulietti) in Dancalia, eastern Ethiopia. Its outer teeth as well as the inner are tricuspid and it has only 27 vertebrae and 10-12 lower gill-rakers. It has been given its own subgeneric name by Thys (1968) and so I propose to leave it as *Sarotherodon (Danakilia) franchettii. (Danakilia* is now raised to genus; see Addendum).

For zoologists who are not systematists and for fish culturists there is no need to use subgeneric names, and for these all the mouthbrooding tilapias may be referred to by the generic name *Sarotherodon* followed by the specific name.

Peters (1979) and Thys (1968, 1971a, 1971b) would prefer to leave the tilapias undivided for the general and applied zoologist and to lump substrate-spawners and mouthbrooders alike in a broad genus *Tilapia.* If I interpret them rightly their reason for this is:

S. *melanotheron* and S. *galilaeus,* the two best known species of subgen. *Sarotherodon,* have breeding habits distinct not only from those of *Oreochromis* but also in some ways from each other. Specifically, S. *melanotheron* has large yellow eggs brooded normally by the father alone,

whereas *S. galilaeus* has small green eggs brooded by both parents. What further differences may exist among the species apparently related to these we do not know. Perhaps they even evolved from different species of *Tilapia* or from the same species at different times. Therefore we may eventually recognize different lines of evolution in these species and wish to call them by different generic names. Meanwhile let us be conservative and call them all *Tilapia*.

This is the position of Thys and Peters. My view (Trewavas 1973a, 1973b, 1980 and in press) is, however, that the mouthbrooding species showing affinity to *Tilapia* are sufficiently alike in their feeding adaptations and even in their breeding habits to show close interrelationship and that this justifies separating them from the substrate-spawning *Tilapia* under the one generic name. The substrate-spawners have themselves branched out into a number (about 29) of species and I find it difficult to lump all the mouthbrooders together with them as *Tilapia*. In the last few years I notice that fish culturists and others have followed my proposal to call the mouthbrooders *Sarotherodon*.

Speciation

The pattern of speciation in *Sarotherodon* and *Tilapia* leads to the conclusion that it has occurred in two ways: 1) by geographical isolation; allopatric and 2) by ecological diversification in one area; sympatric (see Figures 1 and 2).

1. Examples of allopatric speciation are:

a. *Tilapia zillii* and *T. rendalli*, described above. Their coming together at Yangambi is probably secondary. A number of allopatric and geographically more restricted species related to these are present in west Africa.

b. *Sarotherodon melanotheron* and its subspecies in areas along the coast, separated by steeper shores. (These have been ranked as species by Thys (1971b), a matter of policy).

c. The tasselled tilapias surrounding the Rift Valley: *S. variabilis, S. upembae* and its related form in the Malagarasi, *S. rukwaensis, S. macrochir* and the Malawi flock considered as a unit.

d. *S. mossambicus* and related forms in the eastern rivers.

2. Examples of sympatric speciation are:

a. The species of the Malawi flock, *S. squamipinnis, S. saka, S. lidole* and *S. karongae*, whose ecological differences are described by Lowe (1952, 1953).

b. The two species of the Malagarasi swamps, *S. karomo* and the other species related to *S. upembae*. The highly specialized jaws and teeth of *S. karomo* must indicate a specialization in feeding on the epiphytic growths.

c. The species of the small lake Barombi Mbo in Cameroon, especially evident in *S. linnellii* and *S. caroli* (Trewavas et al. 1972).

When two species occur together but each has its nearest relatives elsewhere, this is regarded as allopatric speciation in two lines that have come together geographically, and not, of course, as sympatric speciation. Such are *S. esculentus* and *S. variabilis* in Lake Victoria related respectively to *S. niloticus* and the tasselled tilapias. Other examples are *S. shiranus* (related to *S. mossambicus*) and the *S. squamipinnis* group considered as a

unit (related to the tasselled group) all inhabiting Lake Malawi; *S. andersonii* and *S. macrochir* in the upper Zambezi, Kafue and Okovango basins related respectively to *S. mossambicus* and the tasselled group.

That the sarotherodons have not formed such huge species flocks as have the haplochromine and other cichlids of the Great Lakes I put down to the fact that as colonizers they were already highly specialized for feeding on minute epiphytic and planktonic algae and had few or no rivals in that field. That they diversified at all within these limits is a matter for wonder.
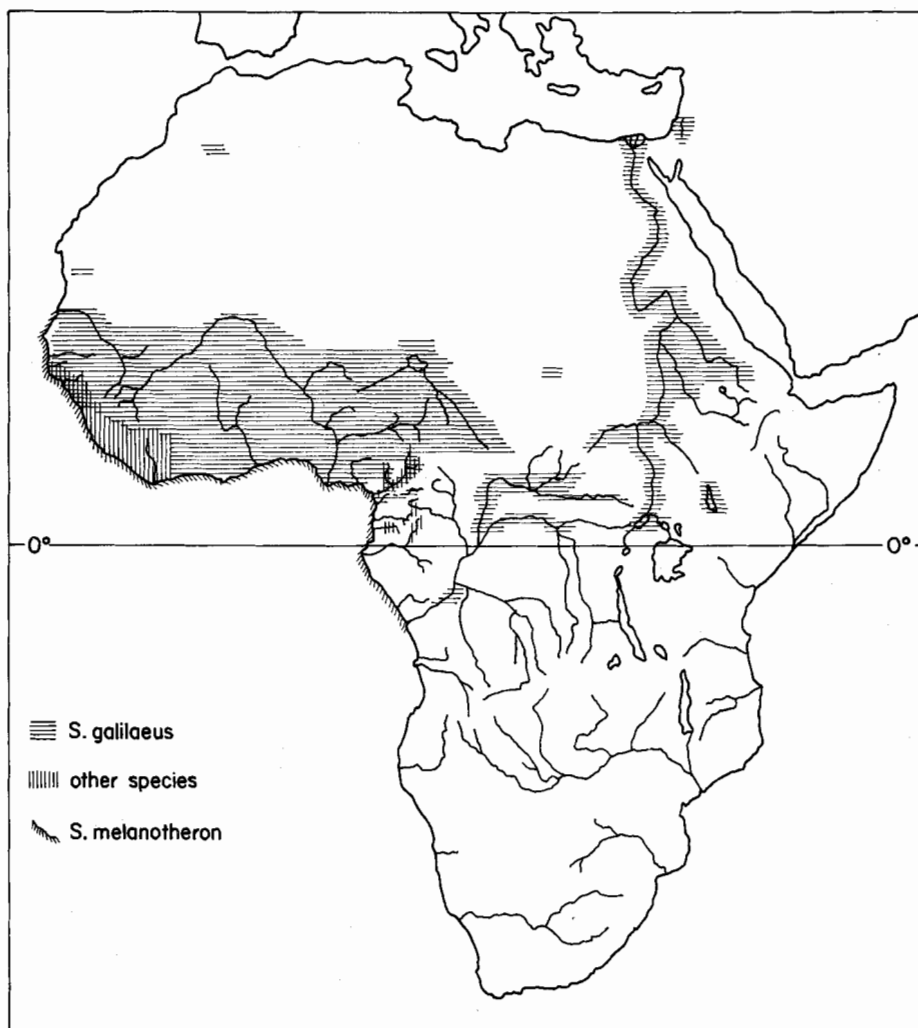

Figure 1. Natural distribution of the subgenus *Sarotherodon* of genus *Sarotherodon*. ≡ *S. galilaeus*, ‖‖‖ other species except ᵐᵐ the brackish water *S. melanotheron*. (Trewavas, in press)
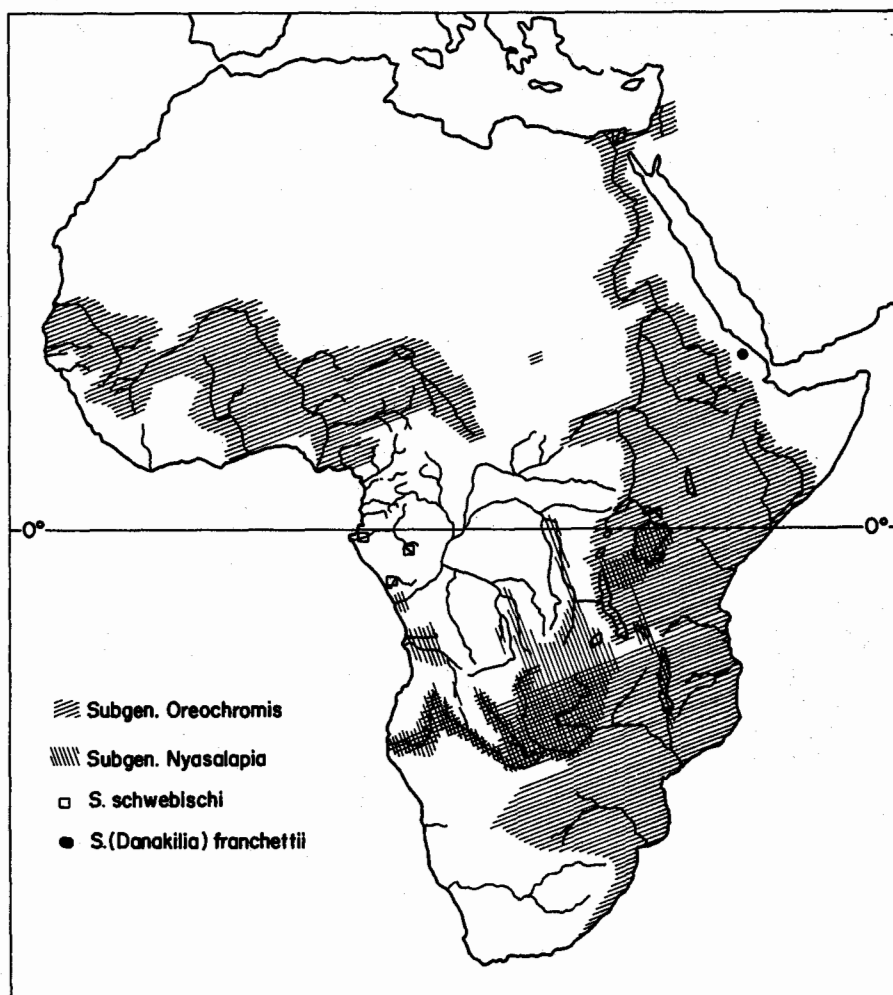
Figure 2. Natural distribution of the subgenera *Oreochromis* (////) and *Nyasalapia* (\\\\\). □ *S. schwebischi* (Sauvage), of uncertain subgeneric affinity and ● *S. (Danakilia) franchettii* (Vinciguerra). (Trewavas, in press).

Sarotherodon Species and Fish Culture

S. galilaeus is the only species of subgenus *Sarotherodon* that has been used for fish culture. It has not been favored for ponds, mainly, I think, because of its slower growth, but it is (or was) so used in Cameroon, the stock being mainly from the Chad basin, but also from R. Sanaga, the latter perhaps a distinct subspecies. Moreover *S. galilaeus* has done well in man-made lakes and reservoirs in open water.

The other well-known cultured species are members of subgen. *Oreochromis* and the tasselled species, *Nyasalapia*. The familiar names are *S. niloticus* with seven subspecies, of which three have been cultured experimentally by Pruginin et al. (1975); *S. aureus*, which accompanies *S.n. niloticus* through

much of its area of distribution; *S. mossambicus* and *S. hornorum* well known for their hybridization and its effect on sex ratio (Chen 1969; Hickling 1960); *S.s. spilurus* and *S.s. niger*, which were studied in Kenya by Van Someren (1962) and Van Someren and Whitehead (1959a, 1959b, 1960a, 1960b, 1961a, 1961b, 1961c); *S. macrochir*, which was studied in Zambia and Shaba and transported to Ivory Coast where it was experimentally interbred with *S. niloticus* (Jalabert et al. 1971; Lessent 1968); and *S. andersonii* studied in Zambian ponds by Mortimer (1960) and in the Kafue floodplains by Dudley (1979) and Kapetsky (1974).

The taxonomy of the species of *Sarotherodon* is dealt with fully in a new work (Trewavas, in press).

Although the practical fish farmer cannot be expected to go into the niceties of specific distinctions, I suggest that key suppliers of stock should know what species they are using and whether these are pure. It is only necessary to recall that the sex-ratio may be affected by mixing the species, many of which interbreed easily. There is also the possibility that one species, and not necessarily the most desired, may oust the other as *T. zillii* did *T. rendalli* at Yangambi (Gosse 1963).

Further I suggest that in Africa itself fisheries officers should look carefully at the native species before importing stock from other regions. If on due consideration they decide to import stock they should keep a careful record of it.

Addendum: Alternative and Preferred Classification

Since writing the above, I have had discussions with fish culturists in Kenya. They are using a brood tank whose design is based on the breeding habits of members of subgenera *Oreochromis* and *Nyasalapia*, namely the 'lek' system with migration of the brooding mother to a 'nursery' area. They refer to this as the system characteristic of *Sarotherodon*. It is not, however, the system practiced by species of *Sarotherodon sensu stricto*, exemplified by *S. galilaeus*, and I have advised them to refer to it as the Oreochromis system of breeding. This and other considerations now lead me to believe that we should place more emphasis on the gap between *Sarotherodon* and the other subgenera by placing the latter in a separate genus, the earliest available name for which is *Oreochromis. Danakilia* is also generically distinct.

The mouthbrooding tilapias used for fish culture accordingly would be grouped in two genera, *Sarotherodon* and *Oreochromis* the latter comprising four subgenera as shown in the accompanying table.

Genus	Subgenus	Type species	Other examples
Tilapia A. Smith	(three to six)	*T. sparrmanii* A. Smith	*T. rendalli* Boulenger *T. zillii* Gervais
Sarotherodon Rüppell		*S. melanotheron* Rüppell	*S. galilaeus* (Linn.) *S. linnellii* (Lönnberg)
Oreochromis Günther		*O. hunteri* Günther	
	Oreochromis Günther	*O. hunteri* Günther	*O. (O.) niloticus* (Linn.) *O. (O.) mossambicus* (Peters) *O. (O.) aureus* (Steindachner) *O. (O.) spilurus* (Günther)
	Nyasalapia Thys	*O. (N.) squamipinnis* (Günther)	*O. (N.) macrochir* (Boulenger) *O. (N.) variabilis* (Boulenger) *O. (N.) angolensis* (Trewavas)
	Alcolapia Thys	*O. (A.) grahami* (Boulenger) = *O. alcalicus grahami*	*O. (A.) alcalicus alcalicus* (Hilgendorf)
	Neotilapia Regan	*O. (N.) tanganicae* (Boulenger)	None
Danakilia Thys		*O. (D.) franchetti* (Vinciguerra)	None

Discussion

GUERRERO: Is it difficult to inter-breed *Tilapia* species or *Sarotherodon* species with *Tilapia* species such as *T. zillii?*

TREWAVAS: Have you ever tried to interbreed them?

GUERRERO: No, but the literature suggests incompatibility between *Sarotherodon* and *Tilapia.* One is a mouthbrooder and the other a bottom spawner. I was wondering if it is difficult to interbreed them. Do you think this is possible or that *Tilapia* species will hybridize?

TREWAVAS: *T. zillii* and *T. rendalli* do hybridize or they are believed to hybridize in Lake Victoria where they have both been introduced.

GUERRERO: We have not tried it, but I want to find out if it is possible because of the differences between the two groups. *Tilapia* species seem more difficult to interbreed as opposed to *Sarotherodon* species.

TREWAVAS: The two genera have never been known to interbreed in nature, nor freely if they are placed together in one tank, but hybrids have been obtained by artificial fertilization at Tübingen. Some attempted crosses were unsuccessful, but in one case hybrids structurally intermediate have been reared to adult size. They were all females.

AVTALION: We have been testing immunological techniques in my laboratory for the different species of *Sarotherodon.* All of them are crossreacting antigenically. We could

not find any antigenic differences with these species. In mammalians we know there is no antigenic crossreactivity between different species. Now, to what extent the species should be called subspecies, I do not know, but several tilapias cannot be termed different species *per se* if we refer to immunological criteria. In this respect, we found some differences between *T. zillii* and *Sarotherodon* species, but no differences between *S. galilaeus, S. aureus,* and *S. niloticus.* However, this matter needs to be studied in more detail.

LOWE-McCONNELL: So the particular question is, do you think that the latter are truly separate species as you have been unable to find any immunological differences?

ROBERTS: I think we will have to distinguish between antigenic characteristics (which means tissue matching) and serum and muscle enzymes, because there are certainly differences between all of the *Sarotherodon* species in terms of the numbers of enzyme loci.

HEPHER: But you can also find such differences between sexes.

ROBERTS: Yes, this has been reported, but not to anything like the same degree as the differences between species.

HEPHER: But there are differences.

ROBERTS: We did not find differences between sexes. I think the important point is that, while someone like Dr. Trewavas has devoted so much time to distinguishing morphologically between these different species, Dr. Avtalion, from his antigenic and immunological studies, finds that there is no difference. I think we have to be very careful with our definition of a species and recognize a problem here.

LOWE-McCONNELL: This is a particular subject for people who are interested in speciation.

PULLIN: Dr. Avtalion, you said that you found a large difference between *T. zillii* and *Sarotherodon* species which tends to support the generic split.

AVTALION: Yes, there is quite a significant difference.

TREWAVAS: It is interesting that you bracket both kinds of *Sarotherodon*, that is, *S. (Sarotherodon) galilaeus* together with *S. (Oreochromis) niloticus* and *aureus.*

HEPHER: We have noticed that it is very easy to hybridize *S. niloticus* and *S. aureus,* but it is very difficult to cross *S. galilaeus* with *S. aureus* or *S. niloticus.* Maybe this has some significance.

LOWE-McCONNELL: I think the important thing here is that there are "tilapias," there are "sarotherodons" and there is a group in west Africa that are more difficult to define. We do not know much about these.

TREWAVAS: Yes, I think that *S. galilaeus* is the only species that fish culturists have had anything to do with from that group.

Ecology and Distribution of Tilapias

J-CL. PHILIPPART AND J-CL. RUWET

Service d'ethologie animale
Institut Ed. van Beneden
Université de Liège
Quai van Beneden, 22
B-4020 Liège
Belgium

This paper reviews three aspects of the ecology of tilapias: i) their geo-
graphical distribution, ii) the physical (current velocity, depth, temperature)
and chemical (salinity, alkalinity, pH, oxygen and other dissolved gases)
factors which influence this and iii) aspects of their behavioral ecology
namely feeding behavior, reproductive behavior, selection of microhabitat,
schooling behavior and movement. Maps are given showing the natural
distribution of the principal substrate-spawning genus *Tilapia* and the mouth-
brooding genus *Sarotherodon* and the history of their transfers in Africa
and introductions to other continents are tabulated.

The natural distribution of the tilapia species depends upon: i) historico-
geological factors which led to geographical isolation and speciation, ii)
ecological factors which demonstrate the requirements and preferences of the
species mainly with regard to temperature and salinity and iii) behavioral
mechanisms relating to feeding and reproductive strategies. Data on the
natural distribution, ecological amplitude and eco-ethological characteristics
could help in the selection of species for culture and introductions for fish-
eries and in the prevention of unfortunate consequences, such as unwanted
hybridization, competition for food or spawning grounds, and contamination
of pure wild strains or failure of the introduced stocks (e.g., due to unsuitable
temperature conditions, overpopulation and nanism, etc.). The dangers of
introductions made without sufficient knowledge of the biology of the
species and recipient ecosystems and the necessity for better control of fish
transfers and future research on the basic and applied ecology of tilapias are
all stressed.

Introduction

In their recent review Balarin and Hatton (1979) concentrated on the
biology of tilapias in relation to their uses in aquaculture. However, apart
from their considerable economic importance for aquaculture and fisheries,
tilapias are important elements of biocenoses, involved in the workings of
tropical aquatic ecosystems. As such they raise a multitude of problems in
basic ecology, the study of which could have, if it had been done in advance,

prevented the large number of unsuccessful attempts to culture or to introduce tilapias.

This paper is written from a broad ecological perspective, although practical applications are shown whenever these arise. Five aspects of tilapia ecology are discussed:

1. Geographical distributions, with special emphasis on assessing the success of introductions and transfers.
2. Analysis of physical and chemical factors which influence the natural distribution of tilapias and characterize their ecological range.
3. Feeding behavior.
4. Reproductive behavior.
5. Selection of microhabitats and dynamics of spatial separation.

Zoogeography and Distribution

ORIGINAL DISTRIBUTIONS OF TILAPIAS

The family Cichlidae is widely distributed in Africa (including Madagascar) and Palestine, in South and Central America, in southern India and in Sri Lanka (Lagler et al. 1977). The tilapias, however, originated exclusively from the African continent (excluding Madagascar) and from Palestine (Jordan Valley and coastal rivers). In Africa they are absent only from the Northern Atlas and from south west Africa. This is an old pan-African group with a slow or average rate of speciation, primarily riverine, secondarily lacustrine. About seventy species are nowadays distinguished as two genera: *Tilapia* (macrophagous, substrate-spawners) and *Sarotherodon* (microphagous mouthbrooders). Their original distributions are given in Figures 1a, b and 2a, b, c and in Table 1. The data used for this review stem from Thys (1963, 1964, 1968, 1971a, 1971b), Trewavas (1966), Fryer and Iles (1972), Ruwet and Voss (1974), Ruwet et al. (1975) and Balarin and Hatton (1979), which relate specifically to tilapias, and from other works on African ichthyology, Günther (1889), Pellegrin (1921), Poll (1957, 1973), Ruwet (1961, 1962), Greenwood (1965, 1966, 1974, 1976), Jubb and Farquaharson (1965), Bell-Cross (1968, 1972, 1973), Daget (1968), Gee (1968b), Petr (1968, 1969, 1975), Lowe-McConnell (1969, 1975, 1979), Jubb and Gaigher (1971), Gaigher (1973), Green et al. (1973, 1978), Trewavas (1973a, 1973b), Johnson (1974), Eccles (1975), Ottobo (1976), Landau (1979), and other studies cited below.

The natural distributions of the species reflect two types of factors:

1. those historico-geological factors which led to geographical isolation and to speciation (endemic species in lakes or stretches of rivers): a knowledge of the past geology and hydrography of Africa is necessary to understand the species distributions, while, conversely, a knowledge of the species distributions helps in confirming hypotheses concerning the evolution of hydrographic basins and their former connections.
2. those ecological factors which demonstrate the requirements and preferences of the species with regard to temperature, salinity, the chemical composition of the water, and the behavioral mechanisms which reflect feeding and reproductive strategies.

Dealing first with the historical factors: for those affecting distribution,

our ideas are based essentially on the synthesis by Thys (1963) on the tilapias of Zaïre and adjacent regions, and on Beadle (1974) for the paleo-geography. The maps (Figures 1 and 2) show that:

a. The genus *Tilapia* has a very wide distribution except for the eastern slope of the eastern Rift valley and river basins facing the Indian Ocean. They are abundant in west and central Africa. Speciation is slow; they are 'stable', river-dwelling, close to the original stock. The species are separated not by geographical or hydrographic barriers, but rather by ecological or behavioral barriers.

b. The genus *Sarotherodon* is rare in west Africa, absent from the Zaïre basin, but abundant, diversified and specialized in small local populations in the Rift lakes. The subgenus *Oreochromis (S. mossambicus, S. mortimeri, S. andersonii* and *S. spilurus niger)* occurs in the basins facing the Indian Ocean. The various *Sarotherodon* species are segregated by geographical and hydrographical barriers and generally have a small range of distribution, except for *S. galilaeus, S. niloticus* and *S. mossambicus.*

The examples discussed below show the relationship between past geological-hydrological events and the natural distribution of tilapias.

DISTRIBUTION OF *T. ZILLII, S. GALILAEUS* AND *S. NILOTICUS*

These three 'soudanian' species have a very wide common range (Senegal, Niger, Chad, Nile, Jordan, Lake Turkana (Rudolf), Lake Albert) resulting from former interconnections of the Chad and Nile basins.

S. niloticus, originating from the upper Nile in Uganda evidently moved southwards, colonizing all the western Rift lakes down to Lake Tanganyika. It also colonized central and western Africa, via the Chad and Niger basins. Its expansion is still taking place; it has not yet reached some of the tributaries of the upper Niger and it is rare in the coastal rivers of western Africa. Conversely, *T. zillii* and *S. galilaeus* have spread eastwards towards the Nile and the first Rift lakes.

It seems likely that the Chad-Nile connection came into existence later than the southward push of *S. niloticus* along the Rift lakes, and later than the separation of Lake Albert from Lake Edward, which could explain why *S. niloticus* occurs in the latter lake though *T. zillii* and *S. galilaeus* did not reach it. *T. zillii* and *S. galilaeus* were present in the Ubangi and Uele Rivers, now tributaries of the Zaïre river, before these two rivers were captured by the Zaïre. This capture must have taken place before the Chad-Nile connection since *S. niloticus* is absent from the Ubangi-Uele system. The Ituri River (Zaïre, central Africa) is a particular case: *T. zillii* evidently colonized it in an eastward direction, but not *S. galilaeus*, which found itself competing against *S. niloticus* already established. Before its integration with the Zaïre basin, the Ituri was linked with Lake Albert, which was populated with *S. niloticus*. In the great Zaïre basin, the expansion of *T. zillii* was prevented by the presence of *T. tholloni*.

The *S. galilaeus* coming from the north did not manage to invade the Zaïre basin, which seems to be an environment hostile to microphagous cichlids,

though *S. galilaeus* reached, and was able to establish itself in the Malebo (Stanley) Pool upriver from Kinshasa.
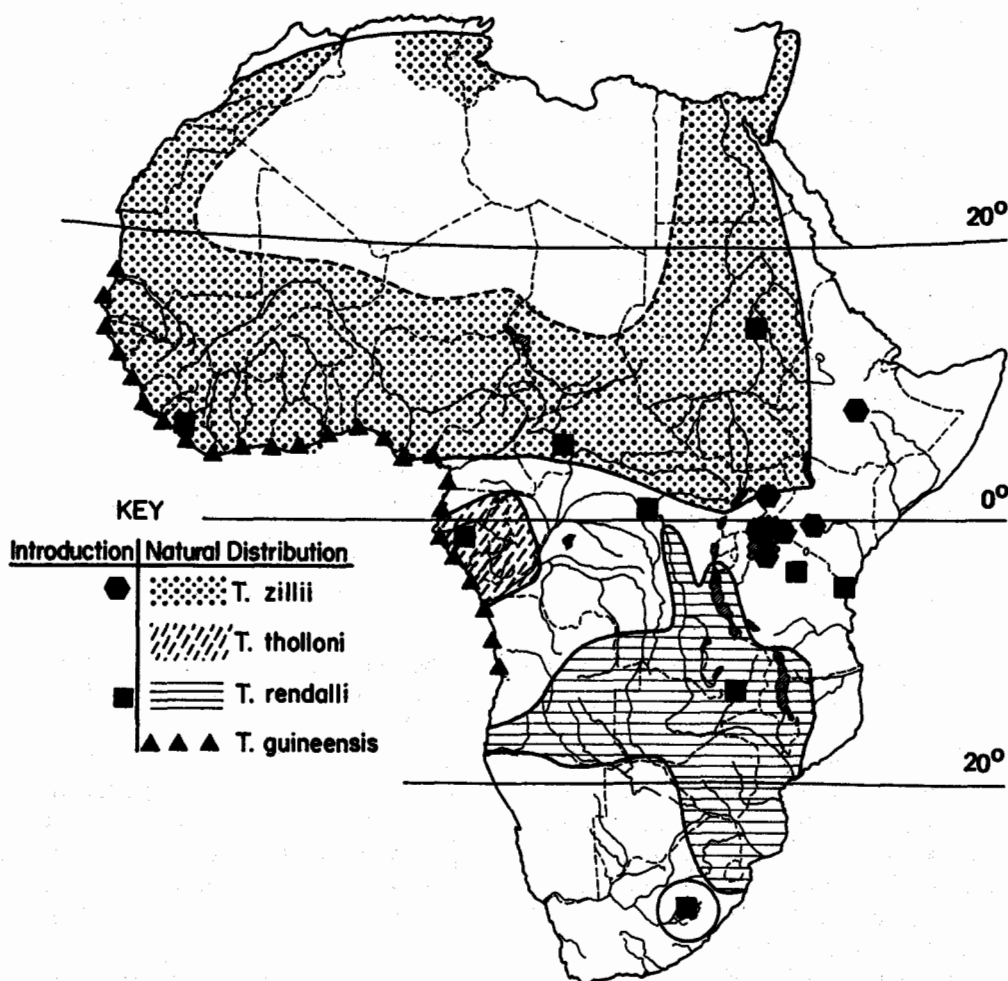
Figure 1a. Substrate-breeding tilapias (genus *Tilapia*): natural distribution and introductions of *T. zillii, T. tholloni, T. rendalli* and *T. guineensis*. The many transfers of *T. rendalli* in South Africa are not recorded precisely but only suggested.

DISTRIBUTION OF *S. MACROCHIR* AND *S. ANDERSONII*

These two species are sympatric in part of their range. *S. macrochir* lives in the rivers and lakes of the Upper Zaïre: Bangweulu-Luapula-Mweru, Luvua, Lufira and Upper Lualaba, which were part of the Zambezi basin prior to their capture by the Zaïre. It also occurs in the upper Zambezi and in the Kafue. The absence of *S. andersonii* from the system now belonging to the Zaïre river north of the present Zaïre/Zambezi divide is evidence that its arrival in the upper Zambezi occurred after this divide was established. Below the Victoria Falls on the Zambezi, below the Kafue Gorges and the Luangwa Falls, *S. andersonii* is replaced by *S. mortimeri*. But since the

construction of the Kariba and Cabora Bassa dams, *S. andersonii* has been recorded in the Middle Zambezi (Balon 1974; Jackson and Rogers 1976).
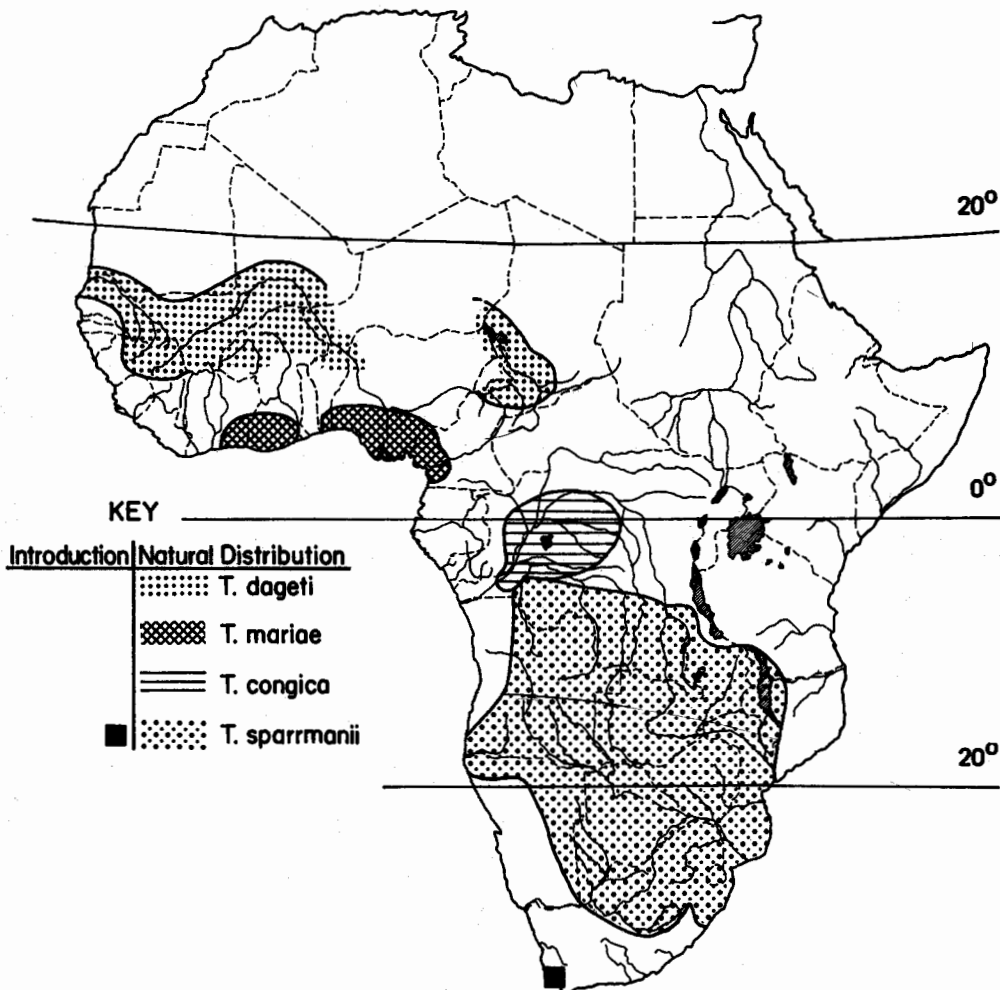
Figure 1b. Substrate-breeding tilapias: natural distribution and introductions of *T. dageti, T. mariae, T. congica* and *T. sparrmanii.*

DISTRIBUTION OF *T. RENDALLI* AND *T. SPARRMANII*

The distribution of these species is quite similar and quite 'Zambezian'. The presence of *T. rendalli* and *T. sparrmanii* in the Zaïre basin can be explained by the capture of a number of rivers in the Zambezi system by the Zaïre river and its tributaries in Shaba and Kasai. But while *T. sparrmanii* could not colonize the Lualaba below the Kongolo (probably because of the high temperatures), *T. rendalli* has colonized the Lualaba to the limits of its basin. Also it has colonized the Tanganyika basin and its tributaries, via the Likuga. *T. rendalli* possibly came into Lake Tanganyika after the penetration by *S. niloticus*, which came from Lake Kivu after the latter was captured by the Ruzizi.

Distributions of *T. sparrmanii* and *T. rendalli* overlap markedly, but the former is more southern, while the latter reaches north to the edges of the equatorial basin.
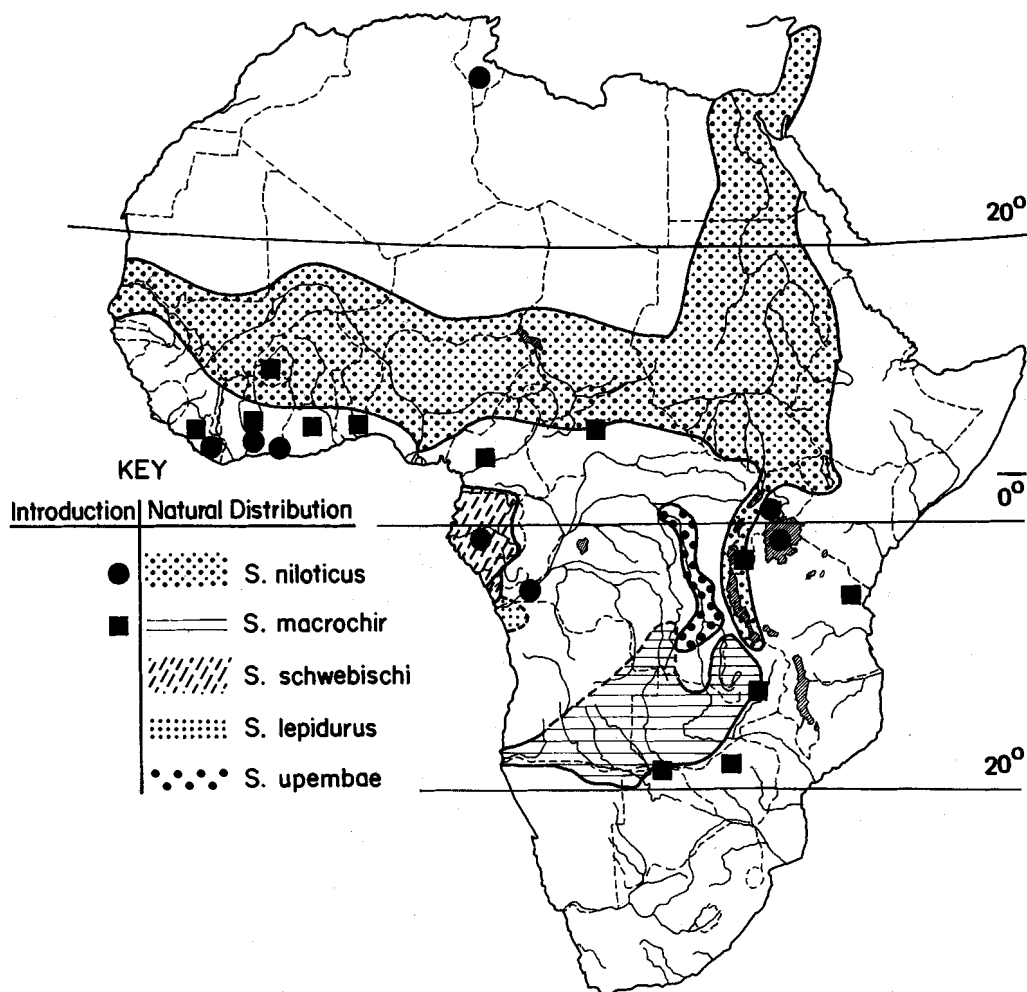
Figure 2a. Mouthbrooding tilapias: natural distribution and introductions of *S. niloticus* (genus *Sarotherodon*), *S. macrochir, S. schwebischi, S. lepidurus* and *S. upembae.*

DISTRIBUTION OF *T. GUINEENSIS, S. MELANOTHERON* AND *S. MOSSAMBICUS*

These very euryhaline species have a wide distribution, the first two on the western (e.g., Baron 1974), the third on the eastern coast. They can move from one estuary to the next, especially during floods.

It is particularly noteworthy that the macrophagous substrate-spawning

tilapias of the *Coptodon* subgenus (*T. zillii, T. rendalli, T. tholloni, T. congica, T. guineensis*) all have a wide distribution and exclude each other geographically.

Species of the *Sarotherodon* group—with the exception of *S. galilaeus, S. niloticus* and *S. mossambicus*—are specialized and more localized; many species overlap (*S. esculentus* and *S. variabilis* in Lake Victoria; *S. leucostictus* and *S. niloticus* in Lakes Edward and George; *S. macrochir* and *S. andersonii* in the Zambezi; *S. galilaeus* and *S. niloticus* in the Nile; *S. niloticus, S. aureus* and *S. galilaeus* from Senegal to Chad; several species in Lake Malawi). This overlapping suggests particular preferences and requirements which guarantee ecological isolation. From this, it follows that a knowledge of the natural geographical distribution is necessary to understand the origin of the present situation by explaining it in relation to the geological-hydrobiological history of the continent, select intelligently the species to be cultured, and deduce certain ecological requirements and preferences.
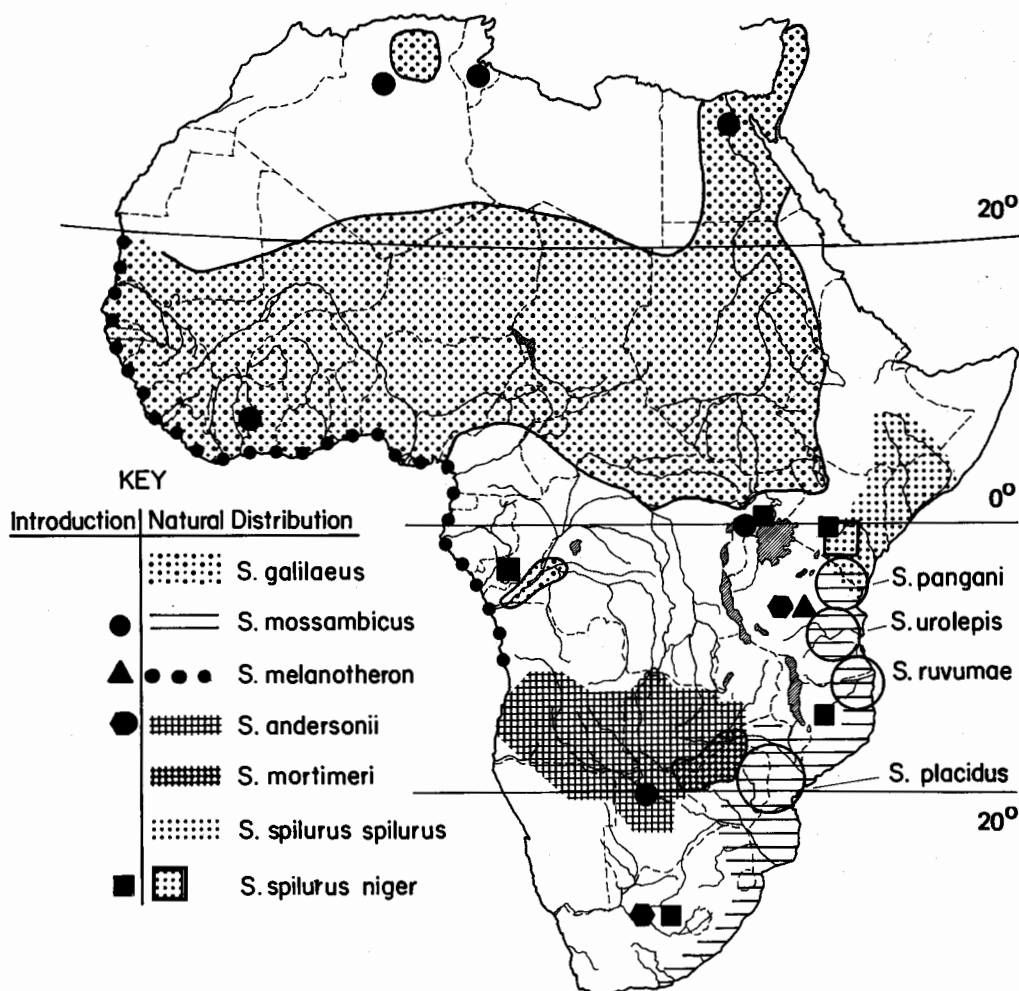

Figure 2b. Natural distribution and introductions of *S. galilaeus, S. mossambicus, S. melanotheron, S. andersonii, S. mortimeri, S. spilurus spilurus, S. spilurus niger, S. pangani, S. urolepis, S. ruvumae, S. placidus.*
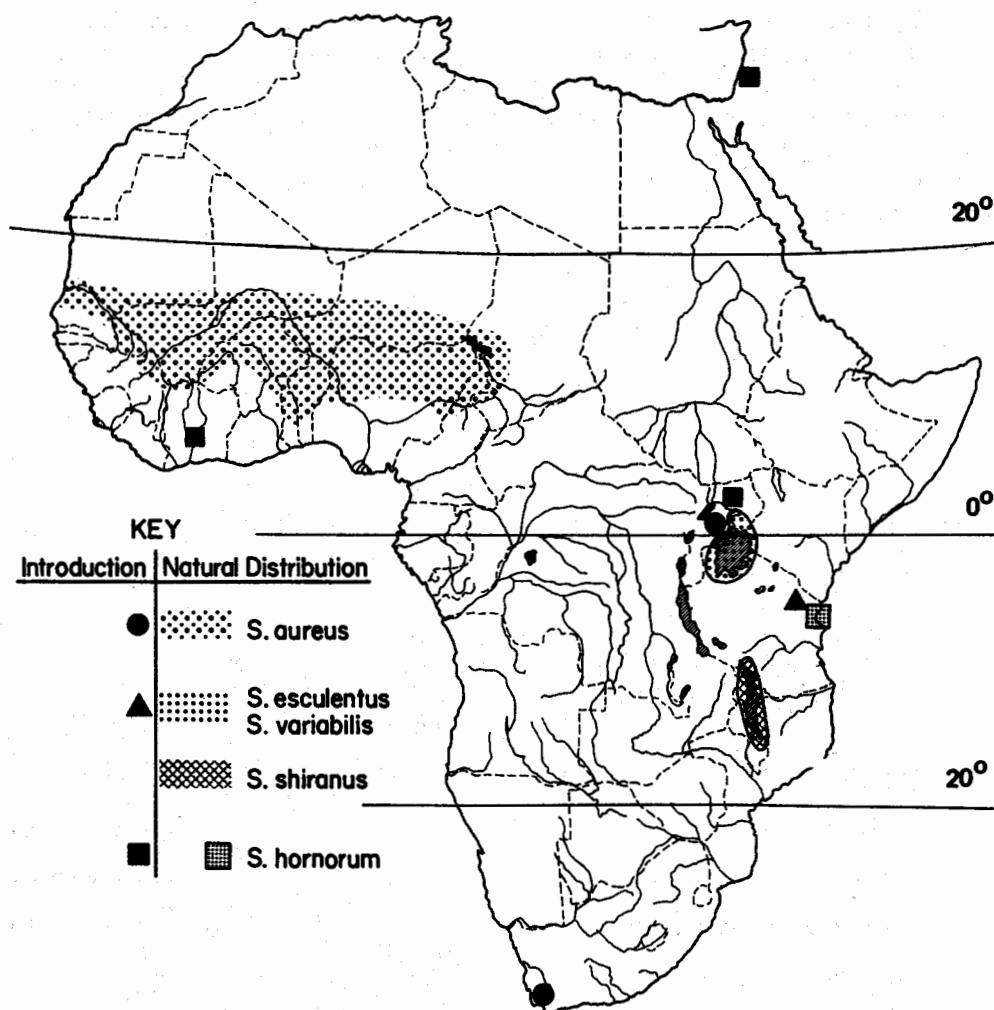
Figure 2c. Natural distribution and introductions of *S. aureus, S. esculentus, S. variabilis, S. shiranus* and *S. hornorum*.

Table 1. Tilapia species with a relatively restricted or endemic geographical distribution (species not included in the maps of Figures 1 and 2).

A. Lakes of eastern Africa

S. leucostictus	L. Albert and Edward/George (Zaïre, Uganda)
S. esculentus, S. variabilis	L. Victoria, Kyoga, Nabugabo (Uganda, Kenya, Tanzania)
S. alcalicus alcalicus	L. Natron (Tanzania)
S. alcalicus grahami	L. Magadi (Kenya)
S. amphimelas	L. Manyara, L. Kitangiri (Tanzania)
S. karomo	Malagarasi swamps (Tanzania)
S. lidole, S. saka, S. squamipinnis, S. karongae	L. Malawi (Malawi)
S. shiranus shiranus	L. Malawi, upper R. Shire (Malawi)
S. shiranus chilwae	L. Chilwa and L. Chiuta (Malawi/Moz.)
S. rukwaensis	L. Rukwa (Tanzania)
S. tanganicae	L. Tanganika
S. hunteri	L. Chala (Kenya)
S. jipe, S. girigan	L. Jipe (Kenya)

B. Other lakes

T. guinasana	L. Guinas (S.W. Africa)
T. gefuensis	L. Gefu (Angola)
T. multiradiata (= T. zillii)	L. Chad (Chad)
T. bemini	L. Bemin (Cameroon)
T. dekerti	L. Ejagham (Cameroon)
T. kottae	L. Barombi ba Kotto (Cameroon)
T. discolor, T. bosumana, S. galilaeus multifasciatus	L. Bosumtwi (Ghana)
S. linnellii, S. lohbergeri, S. caroli, S. steinbachi	L. Barombi Mbo (Cameroon)

C. Rivers of the eastern coast

S. urolepis	R. Rufigi, Kingani, Mbemkuru (Tanzania)
S. ruvumae	R. Ruvuma (Mozambique-Tanzania)
S. pangani, S. korogwe	R. Pangani (Tanzania)

D. Rivers of the Guinea-Ghana coast

T. brevimanus, T. walteri, T. louka, T. coffea, T. joka, T. rheophila, S. caudomarginatus, S. tournieri

E. Rivers of the Cameroon-Congo-Angola coast

T. camerunensis	R. Meme (Cameroon)
T. ogowensis	R. Ogooué (Cameroon)
S. mvogoi, T. margaritacea	R. Nyong (Cameroon)
T. cabrae	Rs. Ogooué, Chiloango, Kwilu, Bengo, Quanza (lower)
S. angolensis	R. Quanza, Bengo (Angola)
S. sanagaensis	R. Sanaga (Cameroon)
T. cameronensis	R. Sanaga (Cameroon)

The original distribution of the African tilapias has been modified by the deliberate or unplanned introduction of several species outside their distribution area (within the same basin, or from one basin to the next). Figures 1 and 2 summarize the main data from the literature (Bardach et al. 1972; Fryer and Iles 1972; Beadle 1974; Lowe-McConnell 1975; George 1975; Vincke 1979; Coche 1978; Balarin and Hatton 1979; Moreau 1979a, 1979b), while Table 2 presents a synthesis of the best known examples of introductions into natural habitats and into reservoirs.

These transfers had different objectives:

i. Stocking natural lakes in which no tilapias occurred *(S. alcalicus grahami* into Lake Nakuru, *S. spilurus niger* and *T. zillii* into Lake Naivasha, *S. spilurus niger, S. esculentus* and *S. niloticus* into many lakes in Uganda and Ruwanda; *S. macrochir* and *T. rendalli* into Lake Lusiwashi).

ii. Introduction into a natural habitat to fill an ecological niche not occupied by any of the tilapias present *(T. zillii* and *S. niloticus* into Lake Victoria and Lake Kyoga) in the hope of increasing fishery yields.

iii. Introduction into artificial water bodies to develop new fisheries based on the introduced tilapias *(S. mossambicus* and *S. niloticus* into the reservoir of a southern Tunisian oasis), or to utilize the plankton production of reservoirs *(S. macrochir* into Lakes Kariba and McIlwaine; *S. placidus* into Lake Kyle; *S. mossambicus* and *S. mortimeri* into the lakes of the Zimbabwe eastern highlands).

iv. Biological control of aquatic vegetation *(T. rendalli* into Sudanese irrigation channels and some artificial lakes of Shaba), or for the control of mosquitos *(S. niloticus*, see George 1975).

v. Fish culture in rice fields (Vincke 1979; Khoo and Tan 1980), in floating cages, and especially in ponds (Bardach et al. 1972; Coche 1978). Although at first confined to these aquaculture systems, the tilapias have inevitably escaped into natural waters (during draining of ponds, break-up of dykes, floods). For example, *T. rendalli* escaped into the Pangani River in Tanzania (Trewavas 1966) and *S. mossambicus* into the middle Zambezi basin (Jubb 1974).

vi. Involuntary introductions occurring during the deliberate introduction of another species *(S. leucostictus* into Lake Naivasha, *T. rendalli* into Lakes Victoria and Kyoga), or because of the confusion between sympatric species which have hardly begun to differentiate *(S. niloticus* and *S. aureus; S. mossambicus* and *S. placidus; S. mossambicus* and *S. mortimeri*, and the *Sarotherodon* species of the east coast rivers in general).

The reasons for the success, or lack of it, in these introductions, their effects on the various ecosystems and the aquacultural aspects will be discussed in a later section in the light of information on the ecology of the various species. On the strictly biogeographical level, the older, unrecorded introductions, or those made in a doubtful manner (lacking present-day

taxonomic and hydrographic knowledge) all represent small catastrophes. In several cases it is indeed impossible to know if the presence of a given species is a natural occurrence (which could have far-reaching consequences in biogeographical and paleographical terms) or simply the results of human activities.

The following examples may be cited:

i. Natural occurrence or old introduction: *S. hornorum* in Zanzibar; *S. hunteri* in Lake Chala, Kenya (Trewavas 1966).

ii. Endemicity of *S. girigan* and *S. jipe* in Lake Jipe (these two species were introduced into the Pangani River and now occur in the whole basin, Trewavas 1966).

iii. The biogeographical relevance of the presence of *S. mossambicus* in the Thalamakane River, Botswana (Jubb and Gaigher 1971), in small water bodies in the Namib desert (Dixon and Blom 1974), and in two tributaries of the middle Zambezi (Jubb 1974) where this species was considered to be absent. Another similar case is the presence of *S. macrochir* in the middle course of the Buzi River, Mozambique (Bell-Cross 1973), completely outside the rest of its range.

To add to the confusion, during the fifties many aquaculturists called any macrophagous substrate-spawning tilapia 'melanopleura', whatever its geographical origin. Thus *T. zillii*, *T. rendalli*, *T. tholloni* and *T. guineensis* have often been spread around in Africa confused under the name *"melanopleura"*.

INTRODUCTIONS OUTSIDE AFRICA

The first, probably accidental, introduction of a tilapia outside Africa was that of *S. mossambicus* prior to 1939 in Java where a few individuals were caught in the Serang River (Atz 1954; Riedel 1965). From then on, *S. mossambicus* was introduced into various countries (see Riedel 1965). Then the practice spread to other species, and now tilapias occur in natural waters throughout the tropics, even in Australia (Queensland). Figure 3, drawn from data in Balarin and Hatton (1979), Welcomme (1979a, 1979b), Rosenthal (1976), Courtenay and Robins (1973), Bardach et al. (1972), FAO (1977c) and some other authors, shows the worldwide pattern of introductions of the species of major importance: *S. mossambicus*, *S. niloticus*, *S. aureus*, *S. hornorum*, *T. rendalli* and *T. zillii*. Other species introduced outside Africa are dealt with in Table 3.

The objectives of these introductions were, as in the case of Africa, pond culture (see Bardach et al. 1972; Coche 1978; Vincke 1979), the stocking of natural habitats, of man-made lakes and water storage reservoirs, of mining pits, and the control of aquatic vegetation. For twenty years there have also been introductions to stock cooling waters and geothermally heated waters in temperate regions, in Japan, the USA and in Europe (e.g. TVA 1978; Kuroda 1977; Mélard and Philippart 1980).

Table 2. Tilapia introductions in natural waters of Africa.

Lake Victoria (Lake Kyoga) (Uganda-Kenya-Tanzania)

— two indigenous endemic species: *S. esculentus* and *S. variabilis*
— four introduced species: *S. leucostictus, S. niloticus, T. zillii* and *T. rendalli* (accidentally with *zillii*) between 1951 and 1954.
— good acclimatization of introduced species favored by the existence of empty ecological niches, notably the niche for a macrophage herbivorous tilapia: *T. zillii* underwent a large development and became almost as abundant as *S. variabilis* which was one of the main exploited species (Welcomme 1967a).
— but negative effects (see Fryer and Iles 1972; Fryer 1961a; Welcomme 1964, 1967a):
  i. in the first stages of its growth, *T. zillii* shared the same niche as the alevins of *S. variabilis*, then competed with them and supplanted them due to more rapid growth and greater aggression.
  ii. *T. zillii* competed with and also supplanted *S. variabilis* for the occupation of breeding grounds.
  iii. *S. niloticus* competed with *S. esculentus* and hybridized with *S. variabilis*.
  iv. *T. zillii* hybridized with *T. rendalli*, naturally allopatric.

Koki lakes (Uganda)

— no indigenous tilapias
— complete failure with the introduction of *S. spilurus niger* and *S. esculentus* but satisfactory success with *S. niloticus* (see Lowe (McConnell) 1958)

Lake Bunyoni-Lake Nkugute (Uganda)

— no indigenous tilapias
— complete failure of *S. spilurus niger* introduction (Lake Bunyoni) and *S. esculentus* (Lake Nkugute) (Lowe (McConnell) 1958) and success of *S. niloticus* in the two lakes
— but hybridization *S. niloticus* x *S. spilurus niger* and *S. niloticus* x *S. esculentus*; excessive development of *S. niloticus* populations with, in consequence, retarded growth, nanism, infestation by parasites and finally a very poor result from the fishery point of view (Beadle 1974, p. 83).

Lake Naivasha (Kenya)

— no indigenous tilapias
— introduction of *S. spilurus niger* in 1925 and of *T. zillii* and *S. leucostictus* (accidental) in 1956
— good initial acclimation in *S. spilurus niger* which formed the mainstay of the fishery during the years 1950-60; in 1961 appearance of hybrids of *S. spilurus niger* x *S. leucostictus;* increase in their number (57% of catches in 1962) followed by their regression particularly marked after 1971, date of the total disappearance of *S. spilurus niger;* after this date, great development of *S. leucostictus* which became the dominant species in the lake and of *T. zillii* (Elder et al. 1971; Siddiqui 1979b)

Lake Lusiwashi (Zambia)

— no indigenous tilapias
— introduction of *S. macrochir* (1949) and *T. rendalli* (1959) successful (catches: 80 t, Fryer and Iles 1972) because ecologically complementary species (microphagous and macrophagous) transplanted close to their original area of distribution in a milieu offering vacant niches.

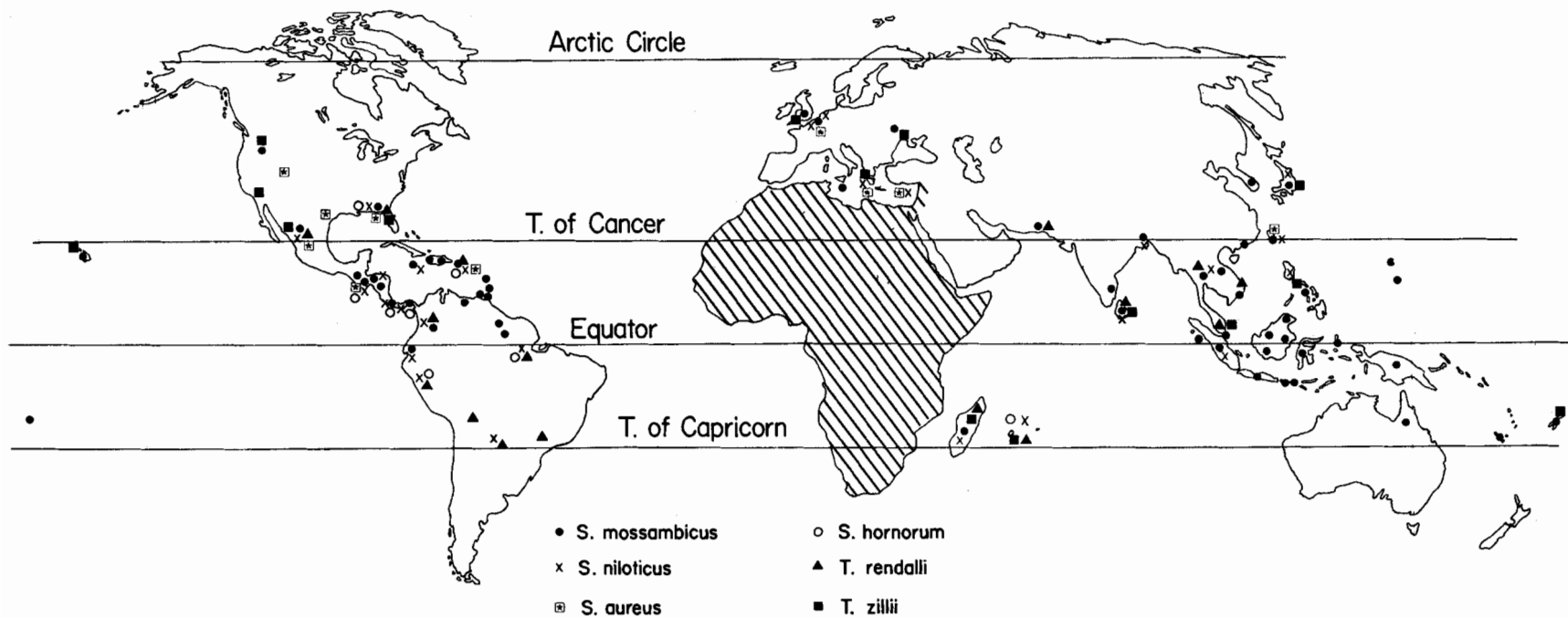Figure 3. Introductions of tilapias (six principal species) outside Africa (see also Table 3).

Legend:
- ● S. mossambicus
- ○ S. hornorum
- × S. niloticus
- ▲ T. rendalli
- ⊞ S. aureus
- ■ T. zillii

Map labels: Arctic Circle, T. of Cancer, Equator, T. of Capricorn

Table 3. Results of introductions of tilapias outside the African continent.

	S. mossambicus	
Africa	Madagascar	established in numerous waters of the country (Lamarque et al. 1975)
SE Asia	Java, Malaysia, Sri Lanka	established in natural waters (Atz 1954)
	Indonesia	established in natural water but often forming very dense, slowly-growing populations (Welcomme 1979b)
	New Guinea	established in natural waters at same time as 21 exotic species (Glucksman et al. 1976; West and Glucksman 1976)
	Philippines	established in brackish water but considered a pest in the *Chanos* ponds (Pillai 1972; Rabanal and Hosillos 1957, cited by Rosenthal 1976)
	Thailand, Bangladesh	initially well-established in natural waters then regressed spontaneously (Welcomme 1979b)
	Hong Kong	established in Plover Cove Reservoir (Man and Hodgkiss 1977a, 1977b)
	Taiwan	established throughout the country (rice fields) but problems due to too low winter temperatures, overpopulation and nanism (Chen 1976)
	North Vietnam	acclimatized (Le et al. 1961)
	China	established in brackish and marine coastal waters and in the rivers of the central and southern provinces, e.g., Fukien (Borgstrom 1978)
	Japan	cultivated in ponds but transferred in winter into hot springs (Fukusho 1968)
America	Haiti, Jamaica, St. Lucia, Grenada, Puerto Rico	established in natural waters (Atz 1954)
	Nicaragua	established, at least in Lake Moyua (Riedel 1965)
	Mexico, El Salvador	introduced for fish culture (FAO 1977c) and probably established in nature
	Ecuador	reared in fish culture with satisfactory results up to altitudes of 2,400 m (!) (FAO 1977c)
	Colombia	establishment in natural waters of certain regions (lower than 1,000 m) but dissemination in the country from there interrupted until they have better knowledge of the risks of competition with the indigenous species (FAO 1977c)
	U.S.A.	introduced into Florida by aquariophiles and considered a pest (Courtenay and Robins 1973); reared commercially in geothermal water in Idaho (Ray 1978); Hawaii (Neil 1966)
	S. niloticus	
Africa	Madagascar	established in numerous lakes (e.g., Lake Itasy, 1,200 m altitude) and rivers (Lamarque et al. 1975)

Table 3 (cont'd)

SE Asia	Indonesia	established in natural waters where found to be economically very interesting (Welcomme 1979b)
	Bangladesh, Thailand	established in natural waters but the populations declined some years after the introduction (Welcomme 1979b)
	Japan	principal species of tilapia raised in industrial warm water (Kuroda 1977)
America	Mexico	cultivated in numerous fish stations and established in numerous artificial lakes in the center and south of the country (FAO 1977c)
Europe	Cyprus	established (?) in a reservoir (Welcomme 1979b)
	Belgium	cultivated intensively in warm water of a nuclear power plant with possibility of surviving in the cooling stream in summer (Mélard and Philippart 1980)

S. aureus

SE Asia	Philippines, Taiwan	introduced for hybridization
America	El Salvador	introduced for rearing in ponds and in cages with risks of escapes
	Puerto Rico	established in quarry lakes used for rearing in cages (Pagan-Font 1977)
	U.S.A.	introduced with a view to biological control of the vegetation in lakes of central Florida in 1961 and actually established in at least 20 counties where it is the object of commercial exploitation (Langford et al. 1978) but catches are small and it is responsible for the destruction of the vegetation and native species of fish in the waters colonized (Courtenay and Robins 1973); probably established in certain lakes in south Texas but maintained artificially in cooling water of electric power stations (Stickney and Hesby 1978); surviving in a natural lake in Alabama only when the winter is exceptionally warm (Habel 1975); reared in geothermal water in Colorado (Lauenstein 1978)
Europe	Cyprus	established (?) in a reservoir (Welcomme 1979b)

S. macrochir

Africa	Madagascar	established all over the country in certain mangrove swamps (e.g., Nemakia) (Lamarque et al. 1975)

S. melanotheron

America	U.S.A.	reproducing in natural waters in Florida but does not seem destructive (Courtenay and Robins 1973; Welcomme 1979b)

S. spilurus niger

Africa	Madagascar	failed introduction because temperature too low at altitude (in Balarin and Hatton 1979)

Table 3 (cont'd)

S. shiranus chilwae

Africa	Madagascar	only cultured experimentally (George 1976)

S. hornorum

America	Puerto Rico, Brazil, U.S.A	introduced for hybridization in numerous experimental fishery and fish culture stations

S. galilaeus

Europe	Germany	experiments for rearing in industrial thermal effluents (in Balarin and Hatton 1979)

T. rendalli

Africa	Madagascar	established in numerous lakes and rivers but has seriously perturbed the ecology of Lake Kinkony (Lamarque et al. 1975)
	Mauritius	introduced for fish culture in 1956, it escaped into rivers and reservoirs where it occasionally has serious effects on the indigenous flora and fauna (George 1976)
Asia	Sri Lanka	well-established in natural waters where a vacant ecological niche existed (Welcomme 1979b)
	Thailand	at first well-established in natural waters then progressively regressing and disappearing, probably due to competition from local species (Welcomme 1979b)
America	Brazil	reared intensively in the northeast and the central-south of the country and established in natural waters, notably Lake Pinheiro in Brazilia and in numerous hydroelectric reservoirs in Sao Paulo State; but many reports of overpopulation and destruction of the vegetation (Nomura 1976, 1977)
	Colombia	cultivated in ponds and established in natural waters in the Valle del Cauca between 1,000 m and 1,400 m; but the dissemination into other regions is forbidden until more is known of the effects on the ecosystems and the native species (Norena 1977)
	Peru	cultivated in ponds and established in certain lakes (FAO 1977c)
	Bolivia, Paraguay	only cultivated in ponds (FAO 1977c)
	Mexico	cultivated in ponds up to an altitude of 1,500 m in the center and south of the country (FAO 1977c)

T. zillii

Africa	Madagascar	established in numerous ponds, lakes and rivers (Lamarque et al. 1975)
SE Asia	Malacca, Fiji	introduced but established (?)
	Taiwan	little appreciated by fish culturists because of its aggressiveness (Chen 1976)
America	U.S.A.	introduced to Hawaii (?); established in natural waters in Florida; reared commercially in

Table 3 (cont'd)

		geothermal water in Idaho (Ray 1978; TVA 1978); experiments on biological control of vegetation in California but progressively abandoned because of mortalities and slow feeding activity due to low temperature (Hauser 1977; Platt and Hauser 1978)
Europe	Great Britain	introduced accidentally and considered acclimatized in a canal receiving thermal effluents from an electricity station (Wheeler and Maitland 1973)
	T. mariae	
America	U.S.A.	established in natural waters in Florida (Hogg 1976)
	T. guineensis	
Europe	Belgium	experiments (abandoned) for rearing in industrial thermal effluents (Mélard and Philippart 1980)
	T. sparrmanii	
Asia	Japan	experiments for rearing in industrial effluents

Physical and Chemical Factors Affecting
Tilapia Distribution

HABITAT DIVERSITY

Within their original areas of distribution, the tilapias have colonized widely different habitats: permanent and temporary rivers, rivers with rapids, large equatorial rivers (Zaïre), tropical and subtropical rivers (Senegal, Niger, Nile, Zambezi, Limpopo), deep lakes (Albert, Kivu, Tanganyika, Malawi), swampy lakes (Bangweulu, Mweru, Victoria, Kyoga, Rukwa, Chad), highly alkaline and saline lakes (Magadi, Natron, Manyara, Mweru Wantipa, Chilwa, Chiuta, Turkana, Tana), other saline lakes (Lake Quarun), hot springs (for example in Lake Magadi), volcanic crater lakes (Lakes Chala, Barombi Mbo, Barombi ba Kotto) or meteoritic crater lakes (Lakes Bosumtwi), lakes with low mineral content (Lake Bangweulu, Lake Nabugabo), sometimes very acidic waters (Lake Tumba), permanent water bodies in the Sahara (Pellegrin 1921 in Beadle 1974) and in the Namib desert (Dixon and Blom 1974), open or closed estuaries, lagoons and coastal brackish lakes that often become hypersaline, marine habitats with normal salinity of Atlantic water and hypersaline in the Red Sea (Gulf of Suez).

All these different habitats represent (both in terms of absolute amplitude and in terms of the speed at which fluctuations take place) an extraordinary varied range of physical parameters (depth, current velocity, turbidity), of temperature and of chemical composition, especially salinity, pH, dissolved oxygen (DO) and other gases.

Balarin and Hatton (1979) have collated the extensive literature concerning

tolerance limits and the preferences of tilapias for the physico-chemical properties of their habitats. Here we shall recall some of these data and complement them with more recent results (post-1976), dealing mainly with data pertaining to ecological conditions actually encountered in the natural habitats and some semi-natural habitats (fish ponds). Data obtained under laboratory conditions are discussed only when this is necessary to define better the ecological amplitude of certain species.

CURRENT VELOCITY AND DEPTH

Several tilapias are perfectly adapted to fast-flowing rivers with rapids, for example, *T. rheophila* endemic to the Konkoure river, Liberia (Thys 1969) and *T. busumana* of Lake Bosumtwi, Ghana and the rivers flowing into it, especially the Ebo river where *T. busumana* occurs in places where the slope ranges from 13 to 60‰ (Lelek 1968). *S. andersonii* and *T. sparrmanii* may be found in the upper and middle reaches of the Kalomo river (a tributary of the Zambezi) where the slope has an average of 2.21‰ (min. 0.9‰, max. 10‰) and 5.73‰ (min. 3‰, max. 19‰) respectively, but not in the lower reaches where the slope is very steep (average 6.63‰) (Balon 1974, p. 459). Even for such species well adapted to river life, rapids and falls are hostile zones which often represent ecological barriers (mechanical obstacles, excessive current velocities, oxygen and nitrogen supersaturations) which prevent the mixing of neighboring but different ichthyofaunas.

Quite a number of tilapias, especially those with a wide area of distribution, may be encountered in both rivers and lakes where they tend to remain in shallow inshore waters (for reproduction and feeding) and in the pelagic epilimnion (for their nutrition in the case of plankton-feeders). This depth limitation of tilapia distribution (see Table 4) can be found even in the majority of species that are endemic in the African Great Lakes.

According to Caulton and Hill (1973) for *S. mossambicus*, and Caulton (1975a, 1975b) for *T. rendalli* and *T. sparrmanii*, tilapias should be physiologically unable to adapt to the increased pressure that goes with increasing depth. However, the depth distribution of lake-dwelling tilapias is also influenced by temperature and oxygen gradients, as well as by concentration of dissolved toxic gases such as CO_2, and especially H_2S and NH_3. The temporal dynamics of distributions with regard to habitats are examined below because it is obvious that these are the result of several factors, some of which are interacting, for example, the influence of temperature on the DO and other dissolved gases, on the toxicity of NH_3 and H_2S, on the innate abilities to compensate and on the speed of adaptation to depth/pressure; in *S. mossambicus* the maximum adaptation depth is 20 m at 30°C but only 7 m at 15°C (Caulton and Hill 1975).

Whether a tilapia is rheophilic (current loving), limnophilic, or indifferent to current velocity, may be readily appreciated from the results of introductions (deliberate or not) of typically riverine species into lakes, of typically lacustrine species into rivers, and from the evolution of tilapia populations after the transformation of habitats with a fast flow to ones with a slow flow

(e.g. man-made lakes). This transformation, however, affects not only current velocity but also the depth *per se*, the thermal regime, various physical and chemical factors and the structure of the whole ecosystem (see Balon 1974, for Lake Kariba on the Zambezi).

Table 4. Data on depth distribution of tilapias.

S. variabilis and *S. esculentus*	maximum 35 to 40 m in Lake Victoria from bottom trawling (Bergstrand and Cordone 1970, in Fryer and Iles 1972).
S. variabilis	present to 13 m in Lake Victoria (Gee 1968, in Fryer and Iles 1972).
S. esculentus	present to 30 m but most abundant at less than 13 m in Lake Victoria (Gee 1968, in Fryer and Iles 1972).
S. tanganicae	common in Lake Tanganyika but rarely captured at less than 10 m (Poll 1956).
S. mossambicus	adults absent in less than 12 m but juveniles (max. 15 m) and alevins capable of descending to a greater depth in Lake Sibaya, S. Africa (Bruton and Boltt 1975).
S. macrochir	observed by diving to 12-14 m in Lake McIlwaine, Zimbabwe and other lakes in that area (Caulton, pers. comm.).
S. niloticus, S. galilaeus and *T. zillii*	captured in gillnets to 7 m in Lake Kainji, Nigeria (Ita 1978).
S. multifasciatus, T. discolor and *T. busumana*	maximum 30 m, 10 m and 7 m respectively in Lake Bosumtwi, Ghana (Whyte 1975).
T. sparrmanii	observed in diving to 30 m in Lake Sibaya, S. Africa (Bruton and Boltt 1975) (but maximum depth compensation of 15 m at 22°C as experimentally determined by Caulton (1975b).
T. rendalli	maximum 7.5 m in Lake Kariba (in Caulton 1975a, 1975b)

TEMPERATURE

Tilapias are thermophilic fishes, and their geographical distributions are closely determined by temperature, particularly by low temperatures. Thus a natural population will be able to maintain itself if:
   a. there is, during part of the year, a temperature high enough to allow for reproduction and for sufficient growth;
   b. the temperature at no time drops below values that are lethal for all individuals.

Figure 4 summarizes the main published data on the temperature ranges to which tilapias are exposed in nature and their thermal tolerance limits. It should be noted, however, that the latter are influenced by acclimation (thermal history) and were not determined under uniform conditions (see also Chervinski, this volume).

The most northerly natural occurrence of tilapias is in Lake Huleh, Israel, in which the *T. zillii* population has to withstand temperatures of 6 to 7°C during the coldest nights (Kirk 1972). Observations reported by Hauser (1977) in California suggest that *T. zillii* can survive for two weeks at 13°C, but some began to die at 11.2°C. Their lower tolerance limit was 6.5°C,

which corresponds well to the naturally occurring minimum in Lake Huleh. Hauser (1977) also reports a minimum temperature for reproduction of 20°C in *T. zillii*. *S. aureus*, *S. niloticus* (introduced) and *S. galilaeus*, which occur with *T. zillii* in Lake Huleh and Lake Kinneret, Israel, are almost as resistant to low temperatures as this latter species. In ponds *S. niloticus* and *S. galilaeus* tolerate winter temperatures of 8°C for several hours each night (Yashouv 1958), while *S. aureus* died at 8-9°C during experiments (Sarig 1969). It may be mentioned, however, that Chervinski and Lahav (1976) reported an improved low temperature resistance of the local Israeli *S. aureus* over that of *S. niloticus* imported from Africa.

The southernmost natural occurrences of tilapia include *S. mossambicus* in coastal waters near Port Elizabeth (33°42'S). This has been attributed by Jubb (1967, in Beadle 1974) to the fact that the southeastern coast of Africa is swept by a warm current (the Agulhas) which maintains subtropical conditions at a latitude at which tilapias would not normally occur (cf. their absence at the same latitude on the west coast). In Africa *T. sparrmanii* is the species which occurs at the lowest latitude naturally, tolerating winter temperatures of 7°C and needing a minimum of 16°C for reproduction (Chimits 1957). As a result of introductions, *T. sparrmanii* and *S. aureus* have been established in the Cape region (Caulton pers. comm.).

Table 5 lists the tilapias which occur naturally, or after having been introduced, in lakes of Africa and Madagascar at altitudes higher than 1,000 m. In natural environments 2,000 m seems to represent the limiting altitude. The species which tolerate best the climates occurring at 1,500 to 2,000 m are *S. niloticus*, *S. leucostictus* and *T. zillii*. In ponds *T. zillii* has been reported from an altitude of 2,500 m in Uganda (Chimits 1957), *T. rendalli* from up to 1,400 to 1,500 m in Mexico and Colombia (FAO 1977c) and *S. mossambicus* from up to 2,400 m in Ecuador (FAO 1977c). For similar altitudes rivers tend to have minimum temperatures during the cold season that are lower than those in lakes, which explains why few tilapias occur in rivers above an altitude of 1,300 m. Studies by Gaigher (1973) have shown that *T. sparrmanii* occurs in rivers above 1,220 m in the upper reaches of the rivers of the Limpopo basin, but that *T. rendalli* and *S. mossambicus* are limited to warmer rivers, below 1,220 m.

In addition to their temperature tolerance, the distributions of tilapias can be related to their maximum swimming performance, which occurs at 24°C in *T. sparrmanii*, 28°C in *T. zillii* and *S. macrochir*, 28 to 32°C in *S. niloticus* and 32°C in *S. mossambicus* and *S. galilaeus* (Fukusho 1968).

A few tilapias have colonized hot springs. *S. spilurus percivali* occurs in the hot springs of the northern Uaso Nyiro system where the temperature reaches 42.4°C (Trewavas 1966). *S. alcalicus grahami* is endemic in Lake Magadi where it can live close to the hot springs (35 to 40°C), tolerating short periods at 40 to 44°C (Coe 1966, 1967; Reite et al. 1974), and *S. shiranus chilwae*, endemic to Lake Chilwa (Malawi) can tolerate 40 to 42°C for short periods (Morgan 1972). It may be mentioned for comparison that North American species such as *Notropis lutrensis* and *Barbus callensis* occur in hot springs of 40°C (Castenholz and Wickstrom 1975) and that species of desert pupfish (Cyprinodontidae) may be found at temperatures of 42°C (Brown 1971).
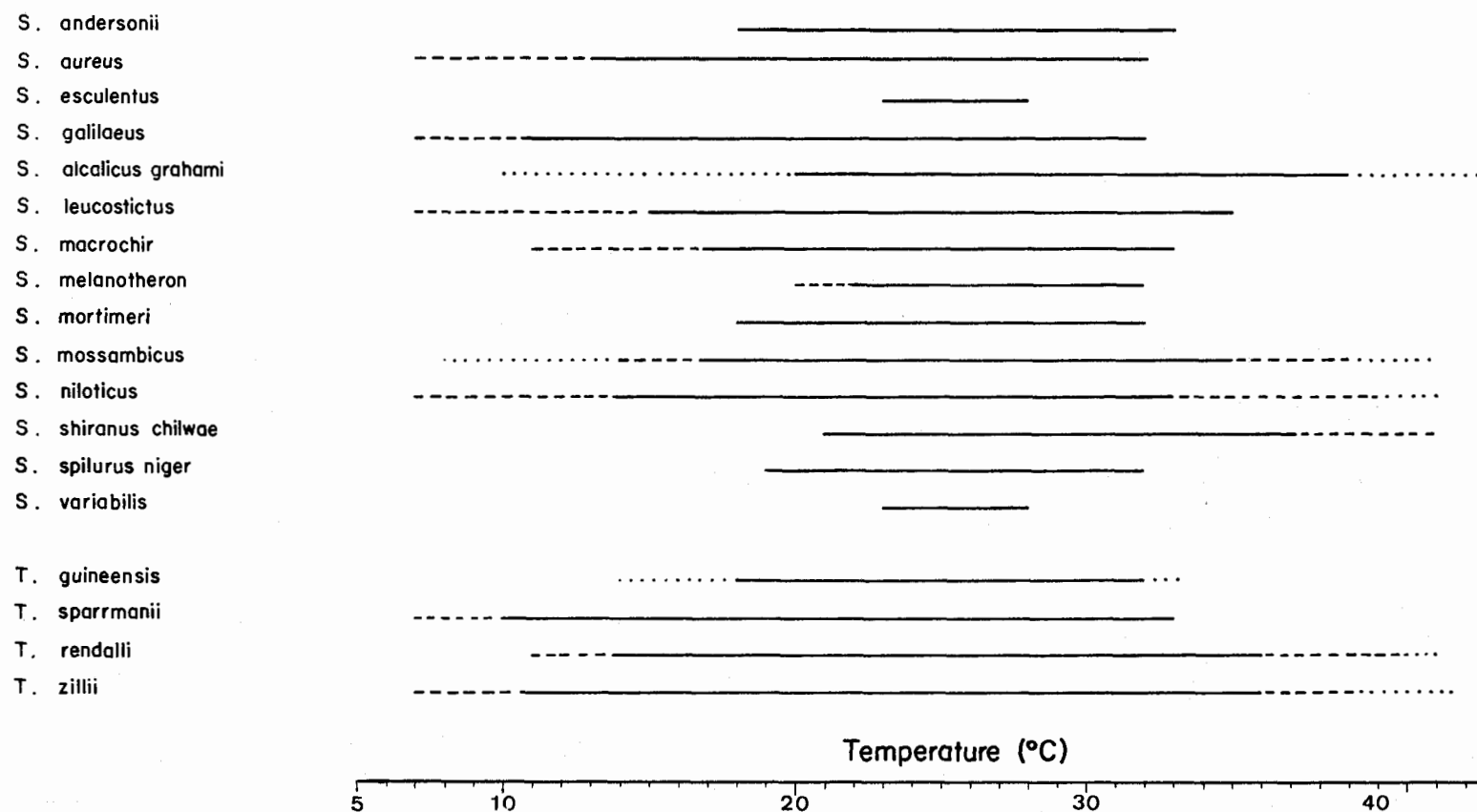
Figure 4. Thermal tolerance ranges of tilapias (*Sarotherodon* and *Tilapia*). —— normal range of temperature variation in natural habitats (after Welcomme 1972); ——— extreme temperatures tolerated in some natural habitats and in culture ponds (after Balarin and Hatton 1979); • • • • physiological limits of tolerance as shown by laboratory experiments (after Balarin and Hatton 1979).

Table 5. Tilapias indigenous or introduced with success in high altitude lakes in Africa (C_{20} = conductivity at 20°C in μS/cm; * signifies an introduction which failed).

Lake	Country	Latitude	Altitude (m)	Temperature (°C)	C_{20}	
Bunyoni	Uganda	1°16′ S	1973	21-22	99-262	*S. niloticus* (S. spilurus niger*, S. esculentus*)
Naivasha	Kenya	0°46′ S	1890	—	318-400	*S. leucostictus*, T. zillii* (S. spilurus niger*)
Tana	Ethiopia	12°00′ N	1829	—	—	*S. niloticus*
Mutanda	Uganda	1°12′ S	1790	—	200-230	*S. niloticus*
Kivu	Zaïre-Rwanda	1°30′-2°30′ S	1463	24-25	1240-4000	*S. niloticus*
Mohasi	Rwanda		1450	—	—	*S. niloticus*
Itasy	Madagascar		1200	18-29	—	*T. rendalli*, S. niloticus*
Bangweulu	Zambia	10°15′-12°304 N	1160	18-26	14-152	*S. macrochir, T. rendalli, T. sparrmanii*
Victoria	Kenya, Uganda, Tanzania	0°20′N-3°0′ S	1136	23-28	91-98	*S. esculentus, S. variabilis, S. niloticus*, S. leucostictus*, T. zillii*
Kyoga	Uganda	0°36′-2°0′ N	1100	28	245-365	idem Lake Victoria
Bosumtwi	Ghana	6°30′ N	1070	27-28	—	*S. multifasciata, T. discolor*
Manyara	Tanzania	3°25′-3°90′ S	1045	—	94	*S. amphimelas*
Upemba	Zaïre	8°25′-9°0′ S	1000	23-33	145-255	*S. niloticus, T. rendalli, T. sparrmanii*

Experimental studies, aquacultural and field observations (Balarin and Hatton 1979) demonstrate that many tilapias which are not especially adapted to warm waters can tolerate temporary temperatures of 35 to 42°C. For *T. zillii*, mortality begins when the temperature exceeds 39.5°C and the upper lethal temperature is 42.5°C (Hauser 1977). For *T. rendalli*, there is a sublethal zone of tolerance between 37 and 40°C (Caulton 1977) and an upper tolerance limit of 40.6 to 41.9°C after adaptation at 24°C (Morgan 1972). For *S. niloticus*, there is an upper tolerance limit of 42°C (Denzer 1968 cited by Aston and Brown 1978). *S. niloticus* also tolerates 36°C for 6 hours (with peaks of 40°C during brief periods) in industrial cooling waters in Belgium (Mélard and Philippart 1980). Lowe (McConnell) (1958) reports the capture of an *S. niloticus* individual from a hot spring of the Turkwel River, Kenya (40°C).

On the basis of their thermal preferences and their tolerances (both determined experimentally and from their geographical distributions), three categories of tilapias emerge:

1. Eurythermal species which tolerate a wide range of temperatures—
   T. zillii (6.5 to 42.5°C), *S. mossambicus* and *S. niloticus* (8 to 42°C), and also probably *S. aureus* and *S. galilaeus*.
2. Species that are eurythermal but seem less tolerant than 1. to high temperatures—*T. sparrmanii* (7°C to ?)—or to low temperatures, *S. spilurus niger* (8 to 10°C to ?), *T. rendalli* (11 to 41°C), *S. macrochir* (11°C to ?) and *S. alcalicus grahami* (10 to 41°C).
3. More stenothermal species such as *T. guineensis* (14 to 33°C, Mélard, pers. comm.) and *S. melanotheron* which lives in a temperature range of 18 to 33°C in West African lagoons (Fagade 1974; Pauly 1975, 1976) and is reported to die at 20°C in aquaria (Sterba 1967, in Balarin and Hatton 1979).

Within a species, the temperature preferences and tolerances depend on size, the young fish generally being more tolerant to higher, and often to lower temperatures than the adults. Thus Bruton and Boltt (1975) reported 16.5 to 39°C as the tolerated range, and 19 to 35°C as preferred range for fingerlings (less than 15 cm) compared to 19 to 32 and 22 to 30°C respectively, for adult *S. mossambicus* in Lake Sibaya, South Africa. These intraspecific variations in thermal tolerance have a physiological basis (see Whitfield and Blaber 1976 for *T. rendalli*) and play an important role in the spatial and dynamic aspects of the fish's distribution.

Because of their adaptations to specific environmental conditions, different populations of the same species may display different characteristics with regard to temperature which can be used when selecting strains for aquaculture or introductions.

Finally, the relationships between the thermal resistance of tilapias and other ecological factors, especially salinity, must be discussed. Thus *S. mossambicus* (Allanson et al. 1971) and *S. aureus* (Chervinski and Lahav 1976) tolerate low temperatures in saline water (5% seawater) better than in freshwater. This phenomenon helps to explain how the limit of the range of *S. mossambicus* can be so far south (to the estuary of the Kongie River, Port Alfred, South Africa) where, in spite of the influence of the sea, the winter temperature drops to 12°C (Allanson et al. 1971).

Several tilapias are euryhaline, able to live and reproduce at salinities higher than 30‰. These occur naturally in estuaries and coastal lagoons along the coast of west Africa (*T. guineensis, S. melanotheron*) or along the east coast of Africa (*S. mossambicus* and the related *S. hornorum* and *S. placidus*). Tilapias also occur in hypersaline habitats such as the Bay of Suez (42 to 43‰) in the Red Sea where *T. zillii* is now established (Bayoumi 1969, in Balarin and Hatton 1979), and in the Bardawil Lagoon in Israel (41 to 45‰) where *T. zillii* and *S. aureus* occur (Chervinski and Yashouv 1971; Chervinski and Hering 1973). The high salinity of certain lakes is also tolerated: Lake Magadi and Lake Natron (salinity 30 to 40‰) have endemic species *S. alcalicus grahami* and *S.a. alcalicus* (Coe 1966, 1967), and Lake Manyara, Tanzania (58‰), the endemic species *S. amphimelas*.

Several species, though less euryhaline, are capable of maintaining populations in habitats where the salinity reaches 30‰: *S. niloticus* and *S. galilaeus* in the Bitter Lakes of Egypt (13 to 29‰) (Kirk 1972), *S. niloticus*, *S. aureus* and *T. zillii* in Lake Qarun, Egypt (11 to 29‰) (Fryer and Iles 1972) and *S. shiranus chilwae* in Lake Chilwa (12 to 29‰). The last species, however, leaves the lake when the salinity becomes too high: conductivity at $20°C$ (C_{20}) = 5,000 $\mu S/cm$ (Morgan and Kalk 1970, in Beadle 1974).

Other species are less euryhaline and do not tolerate salinities above 20‰, such as *T. sparrmanii, S. andersonii, S. macrochir* and *T. rendalli*. These species occur essentially in freshwater, although some populations prosper in saline habitats, notably *S. macrochir* which (as the result of an introduction) occurs in the Nemakia mangrove swamp in Madagascar, in places where the conductivity reaches 350 to 10,000 $\mu S/cm$ (Lamarque et al. 1975), as well as in Lake Mweru Wantipa, Zambia (a natural population) where the salinity sometimes reaches 7‰ and the electrical conductivity 60,000 $\mu S/cm$ (Fryer and Iles 1972). However, *S. macrochir* occurs in the lake during only part of the year, when the salinity is lower than the extreme value given above. During high salinity periods, the populations take refuge in the rivers flowing into the lakes (Fryer and Iles 1972, in Beadle 1974).

A similar phenomenon may be observed in Lake Chilwa, Malawi, where salinity fluctuations occur (0.3 to 16.7‰ for the 1966 to 1970 period according to Morgan and Kalk 1970, cited by Beadle 1974). *S. shiranus chilwae* leaves the lake and takes refuge in the rivers and coastal pools when the salinity increases above 5‰ (C_{20} = 5,000 $\mu S/cm$), at salinities which were unfortunately not recorded precisely.

Also, it is well established that *T. rendalli* has colonized certain brackish habitats, Lake Poelela, Mozambique among others, where the salinity reaches 8‰ (Whitfield and Blaber 1976). These authors have demonstrated experimentally that *T. rendalli* (isosmotic at 10‰), can tolerate a maximum of 19‰, the salinity tolerance being maximal at 20 to $28°C$. Temperature and salinity are considered to be the determining factors for the distribution of this species. It is interesting, in this context, that *T. rendalli* has been introduced successfully into rivers and reservoirs south of the Pongolo River, South Africa (> $29°S$), which marks the southern limit of the natural distribution of this species. Whitfield and Blaber (1976) suggested that it is

because of its inability to tolerate salinities above 19‰ that *T. rendalli* never succeeded in colonizing, by way of estuaries, coastal lagoons and the sea, the more southern rivers where the temperature regime is still sufficient for its survival and reproduction. In this *T. rendalli* differs from *S. mossambicus* (Jubb and Jubb 1967, in Beadle 1974).

Other extreme situations with regard to salinity are represented by the rivers and lakes containing very low mineral contents in which tilapias occur: *S. macrochir*, *T. sparrmanii* and *T. rendalli* in Lake Mweru (salinity, 0.023‰; C_{20} = 14 to 35 μS/cm; Beadle 1974), *S. variabilis*, *S. esculentus*, *T. zillii* and *S. niloticus* (the latter two species introduced) in Lake Nabugabo near Lake Victoria, Uganda (salinity, 0.015‰; C_{20} = 25 μS/cm) and *T. congica* in Lake Tumba, Zaire (salinity = 0.016‰; C_{20}= 24 to 32 μS/cm) Dubois (1959).

Several species can adapt to a wide range of salinities: *T. zillii* (0.16 to 44‰), *S. mossambicus* (0 to 120‰) (Whitfield and Blaber 1979), and *S. amphimelas*, endemic in the hypersaline Lake Manyara (salinity 58‰; C_{20} = 94,000 μS/cm) and in Lake Kitangiri, Tanzania where a normal C_{20} = 185 μS/cm (Fryer and Iles 1972; Beadle 1974).

The different ranges of tolerance with regard to salinity of different tilapias often show when natural or man-made changes occur in certain habitats. Thus the construction of a dam across coastal rivers has isolated freshwater populations from species which normally prefer brackishwaters: *T. guineensis* in Lake Ayeme on the Bia River (Ghana/Ivory Coast border), and in Lake Mount Coffee on the St. Paul River (Liberia) (Thys 1971a).

The gradual increase of salinity in Lake Qarun (near Cairo, Egypt) (11‰ in 1920 and 22‰ in 1932) had led to the gradual disappearance of species that were abundant *(S. niloticus, S. aureus)* and their replacement by *T. zillii* which is much more euryhaline (Fryer and Iles 1972).

In the closed lagoons, lakes and coastal lagoons along the southeast coast of Africa, the irregular connections with the sea lead to a sequence of high and low salinities (Whitfield and Blaber 1979). The populations of *S. mossambicus* occurring in these habitats have thus to tolerate very wide ranges of salinity (0 to 120‰ in St Lucia Lake), the gradual character of which, however, allows the populations to adapt. This adaptation may be accompanied by a reduction of the biomass (*S. mossambicus* formed 12.3% of the catch when the salinity was 10‰ but only 1.2% when the salinity was 80%) or by a migration towards the upper parts of the estuaries where the salinity remains lower (Whitfield and Blaber 1979).

Studies by these authors demonstrate the absence of *S. mossambicus* from most of the estuaries that are permanently open to the sea and which are characterized by rapid variations in salinity because of the tides. *S. mossambicus* thus seems incapable of tolerating rapid changes of salinity, but tolerates seawater and/or slow changes in salinity very well. However, the absence of *S. mossambicus* from the estuarine systems studied by Whitfield and Blaber (1979) may not be caused by rapidly changing salinities, but could be linked to other negative factors also operating in these systems: rapid currents, bad conditions for nest construction, competition with marine fishes, predation by piscivorous fishes, etc.

S. alcalicus grahami in Lake Magadi tolerates a pH of 10.5 and an alkalinity of 80 g $CaCO_3$/l (Coe 1969; Reite et al. 1973). *S.a. alcalicus* of Lake Natron tolerates alkalinities that are even higher: up to 161 g $CaCO_3$/l (Morgan 1972). Reite et al. (1974) have shown experimentally that *S.a. grahami* can withstand a pH range of 5 to 11 for at least 24 h, but dies after 2 to 6 hours at pH's < 3.5 and >12. Morgan (1972) reported mortalities at alkalinities of 1.1 to 6.2 g $CaCO_3$/l (at a pH of 9.0 to 9.9 and 22.5°C) in *S. shiranus chilwae*, and at 3.5 to 4.9 g $CaCO_3$/l in *T. rendalli*. In the Sudan, *S. niloticus* tolerates pH's of 8 to 11 in ponds (George 1975). In Lake Tumba (Zaïre), where *T. congica* lives, the pH is as low as 4.5 to 5.0 (Dubois 1959).

OXYGEN AND OTHER DISSOLVED GASES

The available observations in nature and in ponds, cages and tanks suggest that tilapias are very resistant to low levels of dissolved oxygen (DO) (see Balarin and Hatton 1979). DO's as low as 0.1 ppm are tolerated by *S. mossambicus* (Maruyama 1958) and *S. niloticus* (Magid and Babiker 1975; Mélard and Philippart 1980). This enables some tilapias to live and reproduce in swamps and shallow lakes where strong deoxygenations occur from time to time which are fatal to other fishes. The physiological basis for this tolerance to low oxygen may be one of several types: (1) using haemoglobins which bind oxygen at very low tensions, 0.1 ppm in *S. macrochir* (Dussart 1963) and 0.17 ppm at 24°C in *S. esculentus* (Fish 1956); (2) breathing just below the water surface, flushing the gills with oxygen-rich water (Dussart 1963) and (3) withstanding anaerobiosis (Kutty 1972; Magid and Babiker 1975).

Tilapias can withstand not only low DO's, but also very high levels of CO_2, with maximum tolerance levels of 72.6 ppm in *S. macrochir* (Dussart 1963), and 50 ppm in *S. esculentus* (Fish 1956). Other gases (NH_3, H_2S) which originate from the decomposition of organic matter are also well tolerated. A recent experimental study by Redner and Stickney (1979) demonstrated that *S. aureus* can tolerate 2.4 ppm of un-ionized NH_3 (LD_{50}, 48 hr).

Massive fish kills involving tilapias do occur, however, in deep lakes in cases where the seasonal turnover of water brings the deoxygenated deep water to the surface, and in shallow lakes where violent storms mix the well-oxygenated surface waters with deoxygenated bottom waters, and stir up anoxic and toxic bottom mud (containing H_2S, NH_3 and CO_2). Such phenomena have affected the *T. rendalli* populations in Lake Chilwa (Morgan 1972) in the Nampongue River, Zambia (Tait 1965), and have been reported from Lake George, Uganda (with mortalities of 1.3 million fish, predominantly *S. niloticus*, in a few hours in 1957, Beadle 1974) and also from Tanganyika and Lake Victoria, near Entebbe in July, 1963 (Fryer and Iles 1972).

Finally it should be mentioned that life in lakes characterized by high phytoplankton production presumes a marked tolerance of conditions of

oxygen supersaturation (up to 400% in Lake Chilwa, Morgan 1972). Super-saturation of dissolved gases (oxygen and also nitrogen) often poses problems in the intensive rearing of tilapias in industrial heated effluents (Mélard and Philippart 1980).

OTHER FACTORS

Tilapias tolerate high turbidities and are rather resistant to pollution by toxic substances, whether organic or inorganic, natural or artificial (e.g., pesticides, see Balarin and Hatton 1979).

Feeding Behavior

FOOD COMPONENTS

Tilapias of the genus *Tilapia*, especially *T. rendalli*, *T. zillii*, *T. sparrmanii* and *T. tholloni* are macrophyte-feeders in which the adults feed preferentially on filamentous algae, aquatic macrophytes and vegetable matter of terrestrial origin (leaves, plants, etc.); but this specialization does not exclude certain stages of development (alevins) at certain times of year (winter), and in certain waters poor in aquatic vegetation, taking animal food (here including the alevins) as shown by Spataru (1978) for *T. zillii* in Lake Kinneret (Israel). In this lake, *T. zillii* also eats blue-green algae.

In the genus *Sarotherodon*, certain species (often endemic lacustrine species) seem very specialized feeders, notably *S. variabilis* of Lake Victoria (fine benthic sediments, Fryer and Iles 1972), *S. alcalicus grahami* of Lake Magadi (epilithic blue-green algae), *S. esculentus* (phytoplankton) and *S. macrochir* (phytoplankton and epilithic algae). But many species have a much more diversified feeding regime with a dominant vegetable component (epilithic, epiphytic and filamentous algae, phytoplankton, vegetable debris and fine sediments rich in diatoms and bacteria) and an animal component (zooplankton and benthic organisms such as insect larvae, crustaceans, molluscs). *S. aureus* (Spataru and Zorn 1978), *S. galilaeus* (Lauzanne and Iltis 1975) and *S. niloticus* (Moriarty 1973) eat blue-green algae. Moriarty and Moriarty (1973a) have demonstrated that *S. niloticus* can assimilate 70 to 80% of the carbon ingested in this form *(Microcystis, Anabaena* and *Nitzchia)*. *S. aureus* (Spataru and Zorn 1978), *S. shiranus chilwae* (Bourn 1974) and *S. mossambicus* (Bruton and Boltt 1975; Man and Hodgkiss 1977b) are equally able to eat vegetable debris and macrophytes. In certain waters *S. mossambicus* even catches terrestrial insects floating on the water surface and fish (Lake Sibaya, Bruton and Boltt 1975).

S. andersonii, *S. aureus*, *S. mossambicus* and *S. niloticus* appear to be omnivorous compared to *S. galilaeus* and *S. macrochir* which have a much more limited food spectrum. Studies made in Lake Kinneret, Israel (Spataru 1976; Spataru and Zorn 1978) show that feeding is much more selective in *S. galilaeus* (Pyrrophytes, *Peridinium* sp.) than in *S. aureus* (zooplankton, while this is abundant; phytoplankton and vegetable debris, when the zooplankton is less abundant).

In general a comparison of feeding in the same species of tilapia in a large range of water bodies reveals a very great variability of feeding regime. This is an element of the remarkable plasticity and ecological adaptability of tilapias. The general qualitative characteristics of the feeding regime depend on the following: 1) the type of organisms present, which depends on the limnological, physicochemical characteristics of the water body; 2) the accessibility of the food organisms according to their localization (for example, in certain lakes or reservoirs, some abundant types of food are situated too deep and are inaccessible to tilapias which are not able to descend to these depths (see Caulton and Hill 1973 for *S. mossambicus*) and 3) tne presence of competing species (tilapias or others) which forces each species to restrict its food spectrum and to exploit its specializations, e.g., in many tropical waters where competition for food is intense, *T. zillii* is strictly a macrophyte-feeder, whereas it eats plankton and benthos in Lake Kinneret, Israel (Sparatu 1978) and in Lake Qarun, Egypt (Alkholy and Abdel Malek 1972) where the competition is less.

VARIATIONS IN FEEDING REGIME WITHIN POPULATIONS

Within a given water body, the feeding regime of a species is extremely variable, depending on size and age, the microhabitats occupied by the fish and the time of year.

The alevins (both of species which are strictly phytoplankton-feeders or macrophyte-feeders when adult) generally have a diversified feeding regime extracting small organic particles from the sediments, phytoplankton, diatoms, periphyton, zooplankton and benthic organisms (Bruton and Boltt 1975 for *S. mossambicus;* Gophen 1980 for *S. galilaeus* and Whyte 1975 for the Lake Bosumtwi tilapias).

In Lake Sibaya, S. Africa (Bruton and Boltt 1975), the *S. mossambicus* adults captured in the marginal vegetation zones feed on diatoms, vegetable debris and mud, but those fish captured in open water (limnetic zone) feed on aerial insects (Coleoptera and Hemiptera). In Lake Kinneret, Israel (Spataru 1978), *T. zillii* captures prey from the surface in open water and rarely from the bottom except when breeding and guarding the young (April-May-June) when they feed equally on benthic organisms (chironomid larvae, ostracods, nematodes and sponge gemmules).

The qualitative seasonal variations of feeding regime depend partly on the annual cycle of production and availability of prey, and partly on the degree of feeding selectivity of the species and their distribution in different habitats at different times of year.

Seasonal changes in feeding have been studied in *T. zillii*, *S. galilaeus* and *S. aureus* in Lake Kinneret (Spataru 1976, 1978; Spataru and Zorn 1978), and in *S. mossambicus* in Plover Cove Reservoir, Hong Kong (Man and Hodgkiss 1977b).

In spring, *S. aureus* in Lake Kinneret feeds intensively and more or less selectively on zooplankton which is very abundant. Beginning midsummer, the zooplankton production slows down and its availability diminishes due to competition from other species. *S. aureus* then feeds more on benthic

debris and phytoplankton, which seems on the whole to be ingested passively rather than sought actively. *S. galilaeus* feeds much more selectively (phytoplankton: Pyrrophytes, *Peridinium* sp.) and its feeding regime has a less great seasonal variation, in accordance with the availability of its food. *T. zillii* feeds mainly on Coleoptera and chironomid pupae plus green, brown and above all red algae (*Peridinium* sp.) in winter and spring and on zooplankton (Cladocera) in summer and autumn (Spataru 1978). While breeding, *T. zillii* modifies its feeding habits and captures benthic prey normally not eaten at other times of year.

In Plover Cove Reservoir, Hong Kong, *S. mossambicus* feeds almost exclusively on mud and vegetable debris (more than 80% by volume) throughout the year, without appearing to have any seasonal cycle.

FEEDING PERIODICITY

According to Man and Hodgkiss (1977b), in Plover Cove Reservoir, Hong Kong, *S. mossambicus* feeds during the day. The feeding intensity (measured by an index of stomach fullness) is maximal between 12:00 P.M. and 3:00 P.M. and then slows progressively so that stomachs are completely empty between 12:00 A.M. and 3:00 A.M. Diurnal feeding has also been observed in *S. shiranus chilwae* (Bourn 1974), *S. alcalicus grahami* (Coe 1966, 1967), *S. niloticus* in Lake George (Moriarty 1973) and *T. busumana* in Lake Bosumtwi (Whyte 1975), but several other species are nocturnal feeders, notably *T. discolor* and *S. multifasciatus* of Lake Bosumtwi (Whyte 1975).

Tilapia feeding activity varies seasonally according to various factors: temperature, reproduction, interspecific competition. In Plover Cove Reservoir, Hong Kong, the seasonal cycle of feeding activity follows the temperature cycle: minimum activity in January-February (16 to 17°C) and maximum in July-September (27 to 30°C). In Lake Kinneret, Israel (Spataru and Zorn 1978), the feeding activity of *S. aureus* (measured by index of stomach fullness) is maximal in summer and autumn (temperature maximal, 30°C) whereas that of *T. zillii* is maximal in spring and relatively constant at other seasons (Spataru 1978).

Feeding activity is not interrupted while guarding the young in substrate-spawners (for example *T. zillii*, Spataru 1978) but normally stops in mouthbrooding females, though not always, because food has been found in the stomach of a mouthbrooding female of *S. alcalicus grahami* (Coe 1966, in Fryer and Iles 1972, p. 124).

Reproductive Behavior

PUBLISHED INFORMATION

Numerous authors have studied tilapia breeding behavior in the laboratory, in culture systems and in the field. The following notable references are not an exhaustive list:
S. esculentus (Cridland 1961)

S. galilaeus (Fishelson and Heinrich 1963; Iles and Holden 1969)

S. karomo (Lowe (McConnell) 1956a)

S. leucostictus (Lowe (McConnell) 1957; Welcomme 1967a; Hyder 1970a, 1970b; Siddiqui 1977a, 1977b)

S. macrochir (De Bont 1950; Ruwet 1962, 1963b; Carey 1965; Marshall 1979a, 1979b; Voss and Ruwet 1966; Ruwet and Voss 1966)

S. melanotheron (Aronson 1949; Oppenheimer and Barlow 1968; Pauly 1976)

S. mossambicus (Baerends and Baerends-van Roon 1950; Neil 1966; Bruton and Boltt 1975; Russock and Schein 1977; Baerends and Blokzijul 1963)

S. niloticus (Lowe (McConnell) 1958; El-Zarka et al. 1970a; Babiker and Ibrahim 1979)

S. variabilis (Lowe (McConnell) 1956a; Fryer 1961a)

T. guineensis (Voss and Ruwet 1966; Voss 1969)

T. rendalli (De Bont 1950; Ruwet 1962, 1963a; Donnelly 1969; Kenmuir 1973; Monfort and Ruwet 1968)

T. sparrmanii (Voss 1972a, 1972b)

T. tholloni (Monfort-Braham and Voss 1969)

T. zillii (Daget 1952; El Zarka 1956; Voss 1969; Loiselle 1977; Siddiqui 1979a)

Papers concerning tilapias endemic to the African Great Lakes are synthesized in Fryer and Iles (1972) and more recently Balarin and Hatton (1979) have collated information in the literature up to 1976.

PERIODICITY OF REPRODUCTION

In order to breed, most tilapias need a water temperature of at least 20°C (Huet 1970; Bardach et al. 1972; Balarin and Hatton 1979), but certain species are able to reproduce at a much lower temperature (for example *T. sparrmanii* at 16°C, Chimits 1957). Other factors also seem to play a releasing role, notably photoperiodicity and light intensity (see Balarin and Hatton 1979, p. 29) as well as the rainy season, via water temperature (temperature linked with rains), water level (accessibility of certain spawning grounds) or other mechanisms. Table 6 presents some data on the periodicity of tilapia reproduction at different latitudes and altitudes.

In equatorial and tropical waters where the temperature is high throughout the year, one observes numerous cases of continuous reproduction (e.g., *S. leucostictus* and *T. zillii* in Lake Naivasha) but the intensity often varies seasonally (e.g., *S. variabilis* in Lake Victoria). The same occurs in waters relatively constant from the point of view of photoperiodicity and temperature, where certain species have a well-defined breeding season generally associated with the rainy season (e.g., *S. esculentus* of Lake Victoria and *S. squamipinnis* of Lake Malawi) or the hot season which precedes it (*S. saka* of Lake Malawi). In this case, the length of the breeding season and the number of spawnings per female are very variable. *S. lidole*, *S. saka* and *S. squamipinnis* of Lake Malawi represent an extreme case as they produce only one spawning a year (but see also Berns et al. 1978).

In certain tropical and subtropical regions, low temperature inhibits

reproduction during part of the year, the length of time depending on the latitude and altitude of the place: the duration of the breeding season then conditions the number of spawnings a year, and consequently the overall fecundity of the populations. The breeding seasons coincide with the hottest times of year (*T. zillii* of Lake Qarun, Egypt, *S. mossambicus* of Lake Sibaya) sometimes just before the rainy season (*S. mortimeri* in the Zambezi River and *S. macrochir* and *T. rendalli* in Shaba).

Table 6. Data on the periodicity of reproduction of some tilapia species in natural waters at different latitudes and altitudes.

Coastal Lake Sibaya (S. Africa) 27°25′S

The breeding season of *S. mossambicus* starts in September (20-26°C) and is prolonged until March (duration: 7 months) but the maximum activity is concentrated in September-December; a complete cycle of reproduction lasts about 7 weeks (20 to 22 days for incubation of embryos and guarding the young and about 14 days for the maturation of ovules); the same female should therefore theoretically reproduce 3 to 4 times per year (Bruton and Boltt 1975).

The man-made Lake McIlwaine (Zimbabwe) 18°S

The breeding season of *S. macrochir* (introduced) lasts principally from September to December, that is to say during the hottest months of the year, just before the rainy season; but a rise in lake level later in the year (January-March) is able to stimulate a second phase of reproduction (Marshall 1979b).

Middle Zambezi 15-18°S

The short breeding season (one or more spawnings) of *S. mortimeri* coincides with the rainy season (Fryer and Iles 1972).

The man-made Lake Lufira (Shaba, Zaïre) 11°S, 1,100 m

S. macrochir and *T. rendalli* reproduce throughout the year but there is a very slight slowing down of reproduction during the cold dry season (May-July) and an intense activity in the rainy season (Ruwet 1962); observations made in fish culture in the same region (De Bont 1950), showed that the duration of the rainy season determines the number of spawnings (3 to 4 per year at intervals of 7 weeks in *T. rendalli*).

Lake Malawi 9°30′-14°40′S, 471 m

S. saka, *S. squamipinnis* and *S. lidole* produce only one spawning a year; *S. saka* breeds during the hot season (August-November) before the rainy season, *S. squamipinnis* during the rainy season (December-April) and *S. lidole* in October-November, just before the rainy season (Lowe 1952; Fryer and Iles 1972). Apart from the rains, the temperature conditions and photoperiodicity vary relatively little through the year.

Lake Naivasha (Kenya) 0°46′S, 1,890 m

The photoperiod is practically constant (12 h) and the temperature favorable throughout the year. Reproduction of *S. leucostictus* (introduced) is continuous (nonseasonal) and one cannot observe any correlation between its intensity and the seasonal precipitations (Siddiqui 1977b). Previously another author (Hyder 1970a) had concluded that a seasonal reproduction was correlated with certain conditions of temperature and light intensity. The observations of Siddiqui (1979a) indicated that *T. zillii* (introduced) reproduced equally throughout the year, with little seasonal variation in the intensity of reproduction.

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Table 6 (cont'd)

Lake Victoria 03°00'S-0°20'N, 1,136 m

Fryer (1961a) indicated that the reproduction of *S. variabilis* is continuous but there are seasonal variations in intensity which are not clearly correlated with climatic conditions (rains and temperature); there are at least three spawnings in a period of eight months. In *S. esculentus,* there exists a correlation between the rainy season and the periodicity of reproduction (Garrod 1959, cited by Fryer and Iles 1972); Welcomme (1967b) reported two reproductions or more a year.

Lake Bosumtwi (Ghana) 06°30'N, 1,070 m

The endemic tilapias of this lake breed throughout the year but the reproductive activity is maximal at a determined period of year: October-February *(T. busumana),* November-April *(S. multifasciatus),* December-May *(T. discolor)* (Whyte 1975).

Lake Moyua (Nicaragua) 12°35'N, 420 m

S. mossambicus (introduced) reproduces during 5-6 months corresponding to the rainy season (Reidel 1965).

Plover Cove Reservoir (Hong Kong)

S. mossambicus (introduced) is here at the extreme northern limit of its range for reason of temperature conditions (less than 20°C and practically without growth during 3 to 4 winter months); the breeding season extends from May to October and the same female lays at least twice per year (Hodgkiss and Man 1978).

Lake Qarun (Egypt) 29°29'N, 45 m

The breeding season of *T. zillii* coincides with the hottest months, May-November (El-Zarka 1956, cited by Siddiqui 1979a).

CHOICE OF SPAWNING GROUNDS, TERRITORIALITY,
SPAWNING AND GUARDING THE YOUNG

In the substrate-spawners the mature males first billet themselves for nesting along the shores where each delimits and defends a territory on the bottom; the females join them and after a fairly long courtship of several hours to some days, the couples are formed. The two partners participate in preparing a nest by digging holes of varying depth some of which may shelter an adult (De Bont 1950; Daget 1952; Ruwet 1962). In the Lufira reservoir (Ruwet 1962) *T. rendalli* established its territories at a depth of 20 to 80 cm (especially 50 cm) preferentially on ground with a marked slope and near to the marginal fringe of vegetation; the territories, which attain one meter diameter, may be adjoining, giving the impression of true colonies. In Lake Kinneret, Israel, *T. zillii* prefers bottoms with pebbles or sand with abundant vegetation *(Phragmites);* the territories are smaller (2.0 to 2.5 m^2) in habitats with dense vegetation than in open water (5 to 6 m^2) (obstructing vision curbs aggression by restricting the sight of neighbors) (Fishelson 1966a, 1966b).

Oviposition and fertilization are long operations: males and females alternately apply the genital papilla to the bottom, at the side of a hole,

the one depositing a batch of eggs, the other covering them with milt, and the application forms a plaque of spawn composed of several thousand eggs stuck to the bottom.

Males and females then guard the eggs, and ventilate them with the aid of their fins. After hatching, they move the alevins frequently from one hole to another. As soon as they know how to swim, the alevins organize themselves into a cloud which stays in the immediate neighborhood of the nest and retreats into a hole in time of danger. They are constantly regrouped by the jolting movements, accentuated by contrasting colors, of one parent while the other mounts guard at the boundary of the territory (Voss and Ruwet 1966). After 2 to 3 weeks, the alevins leave the territory and the parents are able to recommence spawning.

In mouthbrooders, the males remain in the nesting zones. Each carrying a marked, often brilliant, color, delimits and defends a territory and makes a nest where he tries to attract and retain a female (Lowe-McConnell 1959). The organization of the breeding arenas varies. In Lake Victoria and the Malagarasi swamps the arenas of *S. variabilis* and *S. karomo* observed by Lowe-McConnell (1956a, 1959) were situated in open water, on a sandy bottom, at a depth of 0.15 to 1.0 m *(S. variabilis)* and 0.5 to 1.5 m *(S. karomo)*. In the Lufira reservoir (Ruwet 1962) *S. macrochir* nest at a depth of 0.8 m to 1.5 m (mode, 1.2 to 1.3 m) on a flat bottom, devoid of vegetable debris from the beaches, and on high alluvial banks situated towards the open water. In Lake McIlwaine, the areas of *S. macrochir* are established in shallow water but certain nests are made exceptionally up to 5 m deep (Marshall 1979b). Bruton and Boltt (1975) have studied in detail (mainly by diving) the distribution and the characteristics of *S. mossambicus* nests in Lake Sibaya, according to type of habitat, depth and vegetation. Most of the nests are established at the edge of the littoral terrace, just before the steep slope. The nests are situated at a depth of 0.4 to 8.5 m but with a maximum concentration between 0.5 and 5.0 m; the size of the nest increases with depth; they are associated with scattered vegetation of medium density, composed mainly of *Scirpus* sp. and *Potamogeton* sp.

The females make only brief visits onto the arenas. Passing from one territory to another, they are courted by several successive males, until the moment when, stopping in front of a nest basin, a female deposits a batch of eggs, the male fertilizes them immediately and the female takes them in her mouth to brood them. The operation is very brief (50 to 60 seconds) and may be repeated with the same male, or with another in a neighboring territory (successive polygyny and polyandry, Ruwet 1963b). Finally, the female leaves the arena, where the males stay billeted, and she carries several hundred eggs in her mouth (see Balarin and Hatton 1979) which she broods, staying in a zone sheltered with vegetation (brooding area) described by Bruton and Boltt (1975) for *S. mossambicus*. As soon as the yolk sac is resorbed (see Table 7) the female lets the alevins escape from her mouth. They form a cloud which orientates itself constantly in contact with the mother, following her slow movements and taking refuge in her mouth at the least sign of danger, warned by her movements (see Voss and Ruwet 1966). When the alevins reach a certain size (9 to 10 mm in *S. mossambicus*, Bruton and Boltt, 1975) the females leave the brooding areas and sometimes gather

in schools of several hundred individuals, notably in *S. variabilis* (Fryer and Iles (1972), *S. lidole* (Lowe (McConnell) 1957) and *S. mossambicus* (Bruton and Boltt 1975). Finally, after a variable time according to the species (22 days in *S. mossambicus*, Bruton and Boltt 1975; Russock and Schein 1977), the young, totally independent, are liberated by the female in shallow water where they live in schools and continue their growth.

In almost all mouthbrooders, guarding the young is undertaken by the female (uniparental maternal family) though the male may participate exceptionally, notably in *S. mossambicus* (Bruton and Boltt 1975). But in *S. melanotheron*, it is the male alone which incubates (uniparental paternal family) (Oppenheimer and Barlow 1968). In *S. galilaeus* (Iles and Holden 1969; Fishelson and Heinrich 1963) and *S. multifasciatus* (Fryer and Iles 1972) the two sexes form a stable couple and both practice mouthbrooding. This seems, therefore, to be an intermediate stage between the biparental family of substrate-spawners and the uniparental family of mouthbrooders (Ruwet 1968).

Table 7. Principal characteristics of development of eggs and alevins in eight species of tilapia (after Hanon 1975). (Temperature: 26 to 27°C in aquarium).

Species	Length of eggs (mm)	Hatching age (days)	length (mm)	First day of swimming age (days)	length (mm)
Tilapia					
T. guineensis	2.7	2	5.0-5.5	7	7.5
T. rendalli	1.8	2	3.9	6	6.0
T. sparrmanii	1.6	2½	3.5	5-6	5.0
T. tholloni	1.6	2	3.6	6½	6.1
Sarotherodon					
S. galilaeus	2.5	4	—	11	—
S. melanotheron	3.5	6	6.5-6.8	12-13	11.0
S. niloticus	2.8	4-5	4.5	11	8.0
S. saka	2.7	5	4.7	11	9.2

Guarding the young increases considerably the survival of the alevins and reproductive success, but mouthbrooding represents an even more remarkable specialization which confers on *Sarotherodon* great independence from the milieu. Mouthbrooders have a better capacity for adaptation (in cases of introduction) and resistance in water bodies subjected to rapid changes in water level (for example, the advantage of *S. macrochir* over *T. rendalli* in the man-made Lake Mwadingusha, Shaba Zaïre: Ruwet 1961-1962, 1963b, 1968, and the success of the introduction of *S. macrochir* in the artificial Lake McIlwaine, Zimbabwe, Marshall 1979b).

The territoriality of substrate-spawners is a regulatory eco-ethological mechanism which allows a certain number of spawners—generally the largest, the best-motivated and the most aggressive—to occupy the breeding space

offering optimal conditions for survival of the young (protection against predators and exploitation of the best physical sites for reproduction). The smaller and less motivated individuals occupy marginal zones of the spawning grounds, where habitat conditions are suboptimal and the exposure to predators is greater.

The social structure of the mouthbrooders, and their arenas comprise a system whereby those males with the strongest reproductive drive occupy the territories at a given time and attract the females. Less motivated and younger individuals are pushed to the edge of the spawning ground or outside it (marginal individuals).

Both in the substrate-spawners and the mouthbrooders, territorial aggression is shown mainly by displays and symbolic conflicts and rarely by true fights leading to wounds. However, the latter are known in nature, for example in *S. mossambicus* where, of a total of 323 territorial individuals, Bruton and Boltt (1975) recorded 10% carrying wounds. Individual aggression depends mainly on size of fish, the size of the territories (which varies with size of male, density of the population and the nature of the substratum) and the degree of visual isolation from the neighbors (influenced by the nature and the variety of the bottom). One can also see specific differences; certain species are considered aggressive *(S. niloticus)*, others intermediate *(S. macrochir)* and others feebly aggressive *(S. galilaeus)*. The degree of aggression is an important factor to consider in the intensive culture of tilapias in cages or in ponds (Mélard and Philippart 1980).

PRACTICAL IMPLICATIONS

The methods of reproduction and the social organization of tilapias have practical implications for culture, which we will review in passing. Substrate-spawners form stable territorial pairs and one can only stock a spawning pond with the number of pairs corresponding to the space available. Any surplus will not participate in breeding, and will disturb the spawners. For mouthbrooders, however, with breeding arenas, there is interest in planning a spawning pond comprising three zones with distinct uses: 1) a flat bottom, muddy or sandy, of medium depth (ca. 1 m) which one can stock with a number of males higher than the space available for nest making, in such a way that always the most motivated occupy the bottom territories and ensure continuous reproduction; 2) a vegetated zone to shelter the females separately from the males during the period of buccal incubation and 3) a shallow zone (10 to 20 cm) to harvest the alevins before sexing them and transferring them to growing ponds or floating cages (see Ruwet and Voss 1974).

A precise knowledge of the breeding habitat (depth, nature of substrate, slope, vegetation) would allow the design for each species of a model grow-out pond limiting breeding as far as possible and, in consequence reducing overpopulation and dwarfing. One can also envisage the possibility of harvesting the alevins by attracting them into traps by means of the sound emissions (Lanzing 1974) possibly used by the parents for reassembling the clouds of alevins, both in substrate-spawners and in mouthbrooders.

In taking into account the eco-ethology of reproduction, it is often possible to explain subsequently, or to foresee, the differential dynamics of substrate-spawning and mouthbrooding species in natural water bodies subject to fluctuations (for example changes in water level, development of vegetation) in man-made lakes or artificial reservoirs, or since the introductions of species. The rapid falls in level in certain man-made lakes can be catastrophic for populations of substrate-spawning species (of which the breeding males and females as well as the eggs and alevins are strongly attached to the nest and, moreover, often situated in sites close to the shores) but have little or no effect on mouthbrooding species in which only the males (which stay billeted on the arenas and always at greater depths than substrate-spawners) are eventually affected, for the females are capable of moving the alevins towards deeper water. In Lake Mwadingusha, ex-Katanga, Zaïre (Ruwet 1962, 1968) the variations in level affected *T. rendalli* much more than *S. macrochir*, a species which also coped successfully with water level fluctuations in Lake McIlwaine, Zimbabwe (Marshall 1979b).

In Lake Naivasha, Kenya, the development of the (introduced) population of *T. zillii* is associated with an evolution of the environment (rise in level and appearance of a six-year flood cycle) which has permitted the development of a fringe of riverine and marginal vegetation favorable for the reproduction of this species; this evolution has also favored *S. leucostictus* to the detriment of *S. spilurus niger*, a fluviatile species unable to adapt to the disappearance of bottoms suitable for its reproduction (Siddiqui 1979a, 1979b).

In Lake Kainji, Nigeria created in 1969, the tilapias are represented by *S. galilaeus*, *S. niloticus* and *T. zillii*, in the proportion 16:5:1. The predominance of *S. galilaeus* is partly explained by its less specialized requirements for breeding than those of *S. niloticus* and *T. zillii*, which need special bottoms and vegetation (Ita 1978). One can see, however, evolution from the original riverine situation in tilapia populations in several other man-made lakes (Lake Nasser, Latif 1976) characterized by a progressive substitution of *S. galilaeus* for *S. niloticus*, initially the more abundant.

Certain deceptive results in fish culture are explained largely by a modification of the frequency of spawning in species transplanted into an environment climatically different from their original environment. Thus, the good results obtained with *T. rendalli* in fish culture in Shaba where the existence of a cold dry season limits the numbers of spawnings (and in consequence population of the ponds and dwarfing) are not also found in the Zaïre basin at Yangambi, where reproduction is continuous (Gosse 1963). A comparable phenomenon is probably responsible for the failure of the transfer of *S. andersonii* from Zambia (a single reproduction per year and maturity at 12 to 15 months old) to Tanzania (maturity at 3 to 5 months old and excessive breeding) (Lema and Ibrahim 1975).

The relative aggression of the species at intraspecific (intensive monoculture) and interspecific (introductions, polyculture) levels and its variations with sex, size, age and environmental factors such as temperature, must be taken into consideration by fish culturists. In Taiwan, *T. zillii* is considered of little interest because it is too aggressive (Chen 1976); in ponds in Zaïre *T. zillii* competes with *T. rendalli* (Gosse 1963) and in Lake Victoria it competed with, and supplanted, *S. variabilis* (Table 2).

SELECTION OF MICROHABITAT

Information on spatial separation (horizontal, vertical) of numerous tilapias and their preferences for a habitat has been obtained either by analyzing statistics of commercial and artisanal fisheries, or by employing different sampling methods: trawling, gill nets, traps or rotenone (Ita 1978; Bruton and Boltt 1975; Balon 1974), echo-sounding (Bruton and Boltt 1975; Capart 1955), direct underwater observations by diving (Bruton and Boltt 1975) and also by electric fishing in lakes and rivers (Lamarque et al. 1975; Lamarque and Closset 1975; Pienaar 1968).

The general characteristic of the spatial distribution of tilapias in lakes is their restriction to the shallow littoral zones (see Table 4). Thus in Lake Kainji, Nigeria (maximum depth ca. 50 m), *S. galilaeus*, *S. niloticus* and *T. zillii* are caught in the littoral zone, at a depth of 0 to 7 m. The biomass there attains 107 kg/ha (Ita 1978).

The littoral distribution of lacustrine tilapias originates fundamentally from their physiological incapacity to descend to great depths (Caulton and Hill 1973, 1975), a characteristic which supports the riverine origin of tilapias. But ecological factors also affect this:

— temperature, through on one hand the existence of tolerance limits and specific temperature preferences, and on the other hand a direct influence on the physiological capacity of tilapias to adapt to depth (Caulton and Hill 1975), or to withstand certain unfavorable conditions of DO, toxic gases, etc.;

— DO and the presence of dissolved toxic gases (H_2S, NH_3, CO_2) which restrict the depth penetration to varying degrees according to the species and their tolerance and preferences;

— demands and specific preferences for a habitat or determined biotope in accordance with feeding (feeding grounds), nesting (spawning grounds), guarding the young in mouthbrooders (brooding areas) and protection against predators (refuges and shelters: escape range, see Gerking 1959).

On the whole, substrate-spawners with macrophyte feeding habits are more dependent on shoreline habitats (macrophytic vegetation has a maximum depth of 7 to 8 m) than are the mouthbrooders with their microphagous feeding and more pelagic habits, especially in waters rich in plankton (Lowe-McConnell 1959). It is interesting to note that in certain shallow lakes very productive of plankton, for example, Lake George, Uganda (maximum depth 2.5 m), the tilapias *(S. niloticus* and *S. leucostictus)* preferentially occupy a littoral band of 50 m even though the plankton food is abundant throughout the lake (Burgis et al. 1973; Gwahaba 1975). Caulton (1978a, 1978b, 1978c) has put forward a bioenergetic interpretation of this phenomenon.

The microseparation of tilapias in rivers is, as in most species of fish, influenced by current speed (in accordance with the swimming capacity) and by ecological factors which are closely associated with this: the depth, the nature of the substrate and the cover of vegetation (Hynes 1970; Brown 1975; Huet 1959). Gaigher (1973) showed that *S. mossambicus* avoided the

rapids and fast-flowing water and preferred still water and pools. In the same way, electric fishing in the Shire River, Malawi (Lamarque and Closset 1975) showed the absence of tilapias (mainly *S. mossambicus*) from the central part of the river where the current is rapid, and their concentration along the sheltered banks provided with vegetation.

The habitat of a species is especially more difficult to characterize as it differs with size, age and stage of sexual maturity and it varies for each intraspecific group with the seasons and even the time of day (variations which lead to daily movements and seasonal cyclical migrations).

a. Influence of size, age and stage of sexual maturity. The size of fish limits the physical accessibility of certain habitats (depth) in such a way that the alevins, juveniles and adults distribute themselves in depth zones from the shore towards open water; this spatial separation favors complementary exploitation of the feeding niches of different habitats, avoiding specific competition. The alevins and the juveniles generally have a much larger temperature tolerance range than the adults (16.5 to 39°C, with a preference for 19 to 35°C in the alevins and juveniles of *S. mossambicus*, compared with a tolerance range of 19 to 32°C and a preference for 22 to 30°C in the adults, Bruton and Boltt 1975), which explains why they are able to live throughout the year in the littoral zone (warmer than open water in summer but colder in winter) while the adults only stay there during the summer breeding period.

b. Seasonal changes of habitat. Bruton and Boltt (1975) studied the seasonal changes in the distribution of *S. mossambicus* of Lake Sibaya. During the cold season (May to July, 20°C), the juveniles and adults live in the pelagic zone at a depth of generally less than 12 to 13 m. When the water warms up (August to September), first the juveniles, then the adults migrate towards the shallower littoral zone which forms the feeding and breeding grounds until the end of the hot season. In January, there is a return migration towards deeper water. Seasonal migrations of the same type, between littoral and pelagic zones have been observed in *S. lidole* of Lake Malawi (Lowe 1953), *S. variabilis* of Lake Victoria (Fryer (1961a) and *S. macrochir* of Lake Mweru (Carey 1965).

Changes (seasonal or more irregular) in the spatial distribution of tilapias are introduced by the variations of salinity in certain saline lakes (*T. rendalli* and *S. shiranus chilwae* of Lake Chilwa; *S. macrochir* of Lake Mweru Wantipa) and by variations in the turbidity of certain river systems (Pienaar 1968).

Whitefield and Blaber (1979) showed equally important displacements of *S. mossambicus* populations in estuaries which take into account their open and closed phases. *S. mossambicus* are abundant in the lower reaches during the closed phase (salinity stabilized and current weak) but retreat into the upper reaches when the estuary is open (strong daily variations in salinity and faster current).

Finally, it is well known (Lowe-McConnell 1975) that important seasonal changes in habitat are produced in all rivers subject to alternating floods (colonization of the flood plain, partly for reproduction) and dry periods (withdrawn into the river bed and into the permanent pools of the intermittent streams). Whyte (1975) has studied the seasonal changes in the spatial distri-

bution of *T. busumana*, *T. discolor* and *S. multifasciatus* in Lake Bosumtwi and in the permanent and intermittent rivers flowing into it.

c. Daily changes of habitat. In Lake Magadi, Kenya, *S. alcalicus grahami* feeds mainly during the day in lake zones where the temperature is 25 to 28°C and where food is abundant; it then moves toward hotter zones (35 to 40°C) which it occupies at night (Coe 1966, 1967 in Caulton 1978b).

In tilapias living in lakes or lagoons (*S. variabilis* in Lake Victoria, Welcomme 1964; *S. mossambicus* in Lake Sibaya, Bruton and Boltt 1975; *T. rendalli* in Lake Kariba, Donelly 1969; *T. rendalli*, Caulton 1978b), the juveniles, but above all the alevins, make daily cyclical movements between the shallower littoral zones, occupied during the day, and the deeper zones towards the open water, occupied by night. The juveniles of *S. mossambicus* of Lake Sibaya move thus from 0.15-1.0 m to a depth of more than 1.0 m (alevins from less than 0.15 m to 0.15-1.50 m). In the course of these displacements the fishes undergo a large temperature difference (up to 10°C) between the shallow water heated up by day (sometimes to more than 35°C) and the deeper water which is colder during the night. The change of habitat occurs at nightfall when the littoral waters become cooler than the deeper water (Caulton 1978b for *T. rendalli*; Bruton and Boltt 1975 for *S. mossambicus* in Lake Sibaya). These daily movements are made possible because the little fish, unlike the adults, are capable of a very rapid adaptation to variations in pressure and depth (Caulton and Hill 1973), a phenomenon further facilitated by the high temperatures (Caulton and Hill 1975).

Concerning the ecological significance and the survival value of these daily changes in habitat, several interpretations have been proposed:

1. They are tactics for avoiding predators, present in deep water during the day (Fryer 1961a, 1965b; Donelly 1969) or in shallower water during the night (case of *Clarias gariepinus*, preying on *S. mossambicus* alevins and juveniles of less than 15 cm in Lake Sibaya, Bruton and Boltt 1975) although such movements also exist in the absence of aquatic predators (Welcomme 1964; Caulton 1975a, 1975b), or in spite of very heavy predation by day in shallow water by birds (Bruton and Boltt 1975).

2. They reduce feeding competition by the successive exploitation in the course of the day of abundant food in several habitats (Welcomme 1964).

3. They are required by physiological adaptations to give the best growth of the juvenile population (Caulton 1978a).

Caulton *(op. cit.)* has supported the last hypothesis by bioenergetic study of *T. rendalli* and has stressed its interest for the distribution (density and biomass) of the cichlid populations in lakes (i.e., their concentration in the littoral zones where temperature fluctuations are more marked, and this despite more abundant food in open water, for example, in Lake George) as well as certain natural examples of dwarfing apparently connected with a homothermal regime and due, for example, to water supply from a spring. On the practical level, it should be useful to find out if rearing tilapias would give better results if the temperatures were varied strongly during the course of the day (influence of pond depth).

SCHOOLING BEHAVIOR

After their liberation by the female, the alevins of many mouthbrooding tilapias remain in schools until a stage of development more or less advanced according to the species (see Fryer and Iles 1972). In *S. mossambicus* (Bruton and Boltt 1975) the juveniles (less than 8 cm) form schools of some hundreds of individuals (several thousands when they group together after an alarm) which mix closely and disperse during the night. Observations made on *S. variabilis* of Lake Victoria (Fryer 1961a) suggest that the schools of alevins and juveniles keep a certain coherence for up to 6 to 8 months. It seems, however, that the schools of juveniles finish by breaking up, except in some pelagic plankton-feeding species of Lake Malawi (*S. saka*, *S. squamipinnis* and above all *S. lidole*) where they are maintained throughout life (Fryer and Iles 1972; Berns et al. 1978).

In the breeding season, many types of extremely structured schools are to be found: migrating schools (with possible presence of a leader) in *S. macrochir* of Lake Mweru (Carey 1965), schools of males (*S. mossambicus*, Bruton and Boltt 1975) or of females (*S. lidole*, Lowe 1952) near the spawning grounds, schools of mouthbrooding females (*S. variabilis*, Fryer 1961a and *S. mossambicus*, Bruton and Boltt 1975).

It is also known that several *Sarotherodon* species (*S. galilaeus* of Lake Kinneret, Israel, Fryer and Iles 1972, and *S. niloticus* of Lake Edward) form very large schools of 100 m^2 or more at the lake surface. These are probably for feeding. Echo-soundings made in Lake Kivu (Capart 1955) showed that schools of *S. niloticus* which had dispersed during the night reformed at dawn.

Again, the existence is reported in certain species (e.g., *S. esculentus* of Lake Victoria) of schools of small individuals (immature juveniles) living at the surface and of schools of large individuals (adults) living on the bottom (Fryer and Iles 1972). Finally, it is interesting that *T. rendalli* of Lake Malawi, a macrophyte-feeding littoral species, does not form schools, even though this is the rule among the plankton-feeding pelagic species like *S. saka*, *S. squamipinnis* and *S. lidole*.

The ecological significance of schooling behavior in tilapias and cichlids in general has been discussed by Fryer and Iles (1972). These authors see it as a mechanism with multiple functions: protection against predators, facilitation of feeding and population regulation, i.e., information on the level of population density at the time of reproduction (see Wynne-Edwards 1962).

MOVEMENTS, HOME RANGE AND HOMING BEHAVIOR

There are relatively few studies on these aspects of tilapia ecology, even in lakes. We know with certainty that the reproductive migrations of *S. macrochir* in Lake Mweru (Carey 1965) and of *S. lidole* in Lake Malawi (Lowe 1952, cited by Fryer and Iles 1972) involve displacements of several kilometers. After the liberation of their young, the female schools of *S. variabilis* in Lake Victoria (Fryer 1961a) generally disperse a little way (less than eight km) from the place of capture and tagging on the brooding ground,

but certain individuals make much longer journeys (maximum: 100 km in 30 days). Tags carried by *S. mossambicus* juveniles in Lake Sibaya (Bruton and Boltt 1975) showed that most of the returns found within two days were in a radius of 400 m from the tagging point; one individual was recaught 400 m away from the tagging point after two hours and another at 3,100 m after 14 days. Lowe (McConnell) (1956b) recorded important movements in *S. esculentus* in Lake Victoria (56 km in 40 days; 10 km in 3 days) but most of the individuals were recaptured at the marking place after 228 to 700 days, which suggested well-circumscribed populations, fixed to a home range. Marking experiments made by Holden (1963, cited by Lowe-McConnell 1975) showed great spatial stability of *S. niloticus* and *S. galilaeus* in the pools of the Sokoto River, Nigeria.

The first case of homing in the Cichlidae was reported by Fryer (1961a) in Lake Victoria, Jinja region. Eight *S. variabilis*, captured and marked on the brooding grounds, were recovered after 45 to 805 days on the same brooding ground or in its immediate proximity. In Lake Sibaya (Bruton and Boltt 1975), three *S. mossambicus* marked during a breeding season were captured during the following season: two individual males exactly on the breeding site of the previous year (homing) and one individual on another spawning ground three kilometers away.

Ecological Effects of Introductions and Transfers

AFRICA INCLUDING MADAGASCAR AND MAURITIUS
(see Tables 2 and 3)

Introductions into natural waters not containing any tilapias or offering a vacant ecological niche for tilapias are often crowned with success when one uses a species for which the natural distribution area is near: e.g., *S. niloticus* in Uganda (Koki Lakes) and in Madagascar; *S. spilurus niger* in Kenya; *S. macrochir* and *T. rendalli* in Zambia (e.g., Lake Lusiwashi); *S. macrochir* in Lake McIlwaine; *T. zillii* in Lakes Naivasha, Kyoga and Victoria; *S. alcalicus grahami* in Lake Nakuru and *T. rendalli* in certain South African lakes.

On the other hand, many long-distance introductions, to a different climatic zone or to a different altitude, have been considered complete failures: *S. macrochir*, *S. andersonii*, *S. spilurus niger* and *T. rendalli* in certain regions too cold in South Africa; *S. spilurus niger* in Madagascar; *S. mossambicus* in the north of Egypt and in Malta and *S. spilurus niger* and *S. esculentus* in lakes at altitude in Uganda. This is explicable for the most part by the unsuitable temperature conditions. A certain number of other results disappointing for the control of vegetation (*T. rendalli* in the Sudan), for improving a fishery (*S. niloticus* in certain lakes at altitude in Uganda) or for fish culture are explained by 1) poor survival (e.g., fish kills of *S. mortimeri* and *S. mossambicus* in man-made lakes of the Zimbabwe plateau, Jubb 1974) and slow growth (for example in *T. rendalli* of Lake Itasy, 1,200 m altitude, Madagascar, Moreau 1975) observed in the species transferred into regions characterized by a well-marked cold season and 2) excessive repro-

duction (leading to overpopulation of ponds and dwarfing) in the species transferred from highlands where the reproduction is seasonal to lower and warmer regions where reproduction becomes continuous (e.g., *T. rendalli* from Shaba to the Zaïre basin and *S. andersonii* from Zambia to Tanzania).

The introduction of tilapias into waters already containing indigenous tilapias have had rapid and unfortunate consequences on aquatic ecology (e.g., hybridization, competition for food and breeding sites) and on the fisheries: for example, in Lake Victoria, hybridization of *S. niloticus* with the indigenous *S. esculentus*, and of *T. zillii* with *T. rendalli* and competition of *S. niloticus* (but above all of *T. zillii*) with the indigenous *S. variabilis* (Fryer 1961a; Welcomme 1967b; Fryer and Iles 1972).

Another interesting problem is posed by the failure of the introduction of *S. macrochir* into the man-made Lake Kariba, where *S. mortimeri* is indigenous. Based on the existence of a flourishing fishery for *S. macrochir* in Lake Mweru, the new lake was stocked with this species, but the source of supply was not Lake Mweru in the Zaïre basin but the Kafue River, a Zambezi affluent. *S. macrochir* never prospered in Lake Kariba, perhaps because the supply source was wrong, perhaps because the conditions of life in the lake were very different from the water of origin, or perhaps again because it was subject to the concurrence of *S. mortimeri*, which, a little against all expectation, is very well adapted to withstand the transformation of the fluviatile environment to a lacustrine one (Balon 1974). However, the *S. macrochir* from the Kafue were transplanted successfully into Lake McIlwaine situated on the Hunyani River, an affluent of the middle Zambezi.

Variations in the success of interspecific introductions are apparent from introductions made simultaneously or successively of tilapias capable of competing or presenting differential capacities of population resilience and eco-physiological adaptations to new environmental conditions (degree of eurycity). Thus *S. spilurus niger*, originally from Kenya rivers, was not able to acclimatize in the Koki Lakes in Uganda and in many other lakes at altitude in this region at a time when, on the contrary, the introduction of *S. niloticus*, a very euryoecious species, was crowned with success. *S. spilurus niger*, a fluviatile species, was at first very well adapted in Lake Naivasha until a change of environmental conditions (rise in water level plus cycles of littoral flooding plus the creation of lacustrine conditions) led to its disappearance and progressive replacement by *S. leucostictus*, a lacustrine species which had been accidentally introduced (Siddiqui 1979b). This accidental introduction also permitted the hybridization of the two species and the production of apparently all-male offspring (Fryer and Iles 1972, p. 168). Lamarque et al. (1975) showed an identical phenomenon in Lake Itasy, Madagascar, where *S. macrochir* (introduced in 1958) prospered for several years before disappearing and being replaced by *S. niloticus* (introduced in 1961-62); the hybridization of the two species produced slow-growing and sometimes deformed individuals.

The introduction and proliferation of macrophyte-feeding tilapias and especially of *T. rendalli* has seriously perturbed the ecology of certain water bodies, for example, Lake Kyle, Zimbabwe (in Jubb and Skelton

1974) and rivers of the island of Mauritius (George 1976). Also in Lake Kinkony in Madagascar, *T. rendalli*, accidentally introduced, in three years devastated nearly 3,000 ha of *Ceratophyllum* and *Nymphaea* beds with in consequence the almost total disappearance of a valuable indigenous fish, *Paretropus petiti* (Lamarque et al. 1975).

OTHER REGIONS (see Table 3)

In environments characterized by suitable temperature conditions and offering a vacant ecological niche, tilapias are able to establish themselves and form stable populations, contributing to the augmentation of the local fishery resources (e.g., *S. niloticus* in Indonesia, Bangladesh and Mexico; *T. rendalli* in Sri Lanka and *S. mossambicus* in Hong Kong).

In most cases, however, the establishment of tilapias in natural waters has engendered, as in Africa, unfavorable consequences: 1) initial growth of the population followed by spontaneous regression with some of these failures (e.g., *S. mossambicus* in Thailand and Bangladesh and *S. niloticus* and *T. rendalli* in Thailand) resulting from competition from local species or the influence of unfavorable environmental conditions, which, even if they do not occur every year suffice to hamper the long-term survival of the populations; 2) disappointing practical results due to continuous reproduction (overpopulation and dwarfing) in equatorial and tropical environments (e.g., *S. mossambicus* in Indonesia and *T. rendalli* in certain Brazilian lakes) and to slow growth and winter mortalities in regions situated at the limit of the natural distribution of tilapias (e.g., *S. mossambicus* in the rice fields of Taiwan and *T. zillii* for the biological control of aquatic vegetation in California and 3) excessive destruction of aquatic vegetation by macrophyte-feeding tilapias (*T. rendalli* in Brazil), damage to the indigenous fauna (*S. mossambicus* in Florida and in Colombia), competition for food and predation affecting other valuable species (*S. mossambicus* in the brackish *Chanos chanos* (milkfish) ponds in the Philippines).

Introductions sometimes prove to be failures in an economic scale as the species introduced was not accepted by the local population because of its unfavored taste (*S. mossambicus* in Thailand, Welcomme 1979b), small size, or because it was not the most judicious choice to fulfill its assigned role. Considered as a 'miracle fish' at the time of its first introduction to Southeast Asia, *S. mossambicus* has given poor results which explains why this species is now being progressively abandoned for use in culture: *S. niloticus*, *S. aureus* (Bowman 1977) and various faster growing hybrids with a higher proportion of males are preferred. *S. mossambicus* is in Asia what *S. macrochir* is in Africa.

Finally, the introduction of tilapias (and of exotic species in general) may assist the dispersal of diseases and undesirable parasites; thus the construction of tilapia ponds in Puerto Rico has favored the habitat of the molluscan vectors of bilharzia and this malady may reach Florida (Courtenay and Robins 1973).

Conclusions

Tilapias constitute a diversified and plastic group of great interest to ecologists. But until now most studies have been qualitative and limited to one particular aspect of their biology. Future ecological research should above all consist of quantitative overall studies of populations (cf. Bruton and Allanson 1974 and Bruton and Boltt 1975 for *S. mossambicus*) and studies of population dynamics: analyses of the causes of temporal fluctuations of the populations; demographic comparisons of several species in the same water body; demographic comparisons on the same species in contrasting milieu; evolution of populations in water bodies subject to artificial modifications (cf. Dudley 1979), and interactions between indigenous and introduced populations (cf. Noble et al. 1976).

Another important objective is to show the precise geographical distribution of each species and the introductions and transfers with their effects in Africa and in the other regions (i.e., build up a data bank); this would provide a reference point for the easier evaluation of the evolution of future populations.

It is equally necessary to develop quantitative research on the environment in order to understand better the ecological factors which influence the distribution of different species and their absolute abundance, as well as their preferred habitats and microhabitats. This type of study should lead to preparation of an inventory of populations (ecophenotypes) adapted for particular conditions (temperature, salinity, etc.) and interesting to exploit for culture. But parallel to this research on the environment, it appears indispensable to undertake, in a more systematic manner, experiments on environmental tolerance limits and preferences. For this it is necessary to first define a standard methodology in order to eliminate the extreme variability of the results which appear in the literature. A systematic study of preferences and tolerance limits in regard to temperature (McCauley 1980) is especially important.

Finally, concerning introductions, the errors made and the past failures (notably with *S. mossambicus*) by stocking without sufficient knowledge of the biology of species and ecosystems, encourage very great prudence concerning introductions of new species *(S. aureus, S. hornorum, S. niloticus)* in all parts of the world. It is good to report that many countries, without doubt because they are subject to the unpleasant consequences of ancient and uncontrolled introductions, are starting to take control measures on the spreading of tilapias (e.g., Colombia, U.S.A. and Papua New Guinea). The burden of decision in this matter ought to rest on an evaluation of the risks of perturbation of the native biocenoses and ecosystems. However, often in such ecological studies it is difficult to generalize one way or the other (total prohibition or total liberty). Numerous examples show that the same species introduced into different waters often reacts in an unpredictable and unequal manner depending on the milieu and the action of physico-chemical factors and biocenotic characteristics. Only intensive research on the particular case will permit the understanding of the mechanisms involved and the implications for the management or conservation of the aquatic milieu.

Acknowledgments

Life Histories of Tilapias: An Evolutionary Perspective

D. L. G. NOAKES AND E. K. BALON

Department of Zoology
College of Biological Science
University of Guelph
Guelph, Ontario
Canada N1G 2W1

The early ontogenies of tilapias are shown to be of major importance in the evolution of life history styles. By applying hierarchical systems for classification of reproductive guilds, and a uniform system of categorization for developmental intervals, we show that the life history styles of tilapias fall into two clearly defined categories, altricial and precocial, and that a significant evolutionary mechanism exists for changes between these. The major evolutionary trend has been from a more altricial style, the nest-spawning guarders (equivalent to substrate-spawners), to the more precocial style, the mouthbrooding external bearing species (equivalent to mouthbrooders). The major distinction between these is largely a consequence of heterochronous shifts in ontogeny, particularly the lack of a larval period in the ontogeny of the bearers. A survey of published information shows the predicted differences between the two types of species, with some overlap. The overlap exists because individual species retain the ability to adapt somewhat more towards an altricial or a precocial life history style by ontogenetic shifts within their own reproductive guild (i.e., guarder or bearer). This predicts the adaptive responses expected of fish under varying ecological conditions, including aquacultural practices. Stunting, perhaps the most serious problem in aquaculture, is not only interpreted in our theoretical framework, it is predicted by us. We make some tentative suggestions as to how stocks of tilapias might be manipulated to better purpose for aquaculture production.

I ask the reader to remember that what is most obvious may be most worthy of analysis. Fertile vistas may open out when commonplace facts are examined from a fresh point of view. L. L. Whyte (in Koestler 1967)

Introduction

This review of the life histories of tilapiine cichlid species of the breeding morphs called *Tilapia* and *Sarotherodon* will focus in particular on early life history and developmental features. We believe this approach brings profitable insights to the understanding of the biology of these fishes. We also

believe that mouthbrooding likely evolved several times among the tilapias as an adaptation to stable and competitive conditions (Balon 1980, 1981a). If there has been this polyphyletic origin, it must be questioned as to whether to separate the generic names on this basis. An outline of our theories and some essential terms formulated by Balon (1979a, 1979b, 1980, 1981a) and of the theoretical framework we propose to apply will be given first. We will then consider the tilapias with some comparisons to related taxa and conclude with some practical considerations.

Although most terms we will use are by now established, confusion still exists as to precise meanings of some, or how some may be applied in particular circumstances. A number of recent reviews or textbooks, in addition to those cited above, have more than adequately discussed the basic ecological and epigenetical framework used later, so we refer interested readers to those sources (e.g., MacArthur and Wilson 1967; Emlen 1973; Ricklefs 1973; Løvtrup 1974; May 1976; Gould 1977; Stearns 1976, 1977; Krebs 1978; Pianka 1978).

Review of Terminology

The life history of any species (more properly, of individuals) is the sum of a number of events and processes with ecological and evolutionary consequences. Recent usage has introduced the term "strategy" in such discussions. While there is some confusion over both the etymology and application of this term, it can be a useful shorthand reference to evolutionary considerations. We do not propose to defend its uncritical acceptance or application, but find it a useful heuristic tool, at least in the early stages of discussing the evolution of life history patterns. For it is surely the evolutionary questions that will be of greatest interest at the level of the comparative approach we use. We employ the term and assume the phrase "as if", i.e., animals would be expected to respond to natural selection "as if" they were attempting to maximize fecundity, or minimize predation, or minimize energy expenditure, and so on. In all cases, the more formal argument could be made (Dawkins 1976) in a more orthodox fashion, to lead to the same conclusion.

A conventional consideration of life histories would likely discuss the biology of these species in terms of fecundity, growth and development, age at maturity, parental care, and longevity (Emlen 1973; Ricklefs 1973). The assumption is that natural selection acts so as to maximize the fitness of individual animals (but see Dawkins 1978) by adjusting some or all of these parameters in accordance with the ecological conditions faced, to produce an integrated whole, the life history strategy (= style).

The Pitfalls of "r" and "K"

A concept often applied to life histories, frequently uncritically or even inappropriately, is that of the so-called "r- and K-continuum" (MacArthur and Wilson 1967; Wilson and Bossert 1971; Emlen 1973; May 1976; Pianka

1978). These terms refer to the parameters of the widely-used logistic growth curve for populations, where "r" is the slope (growth rate of the population), and "K" the upper asymptote (sometimes referred to as the carrying capacity of the environment). We prefer the terms altricial and precocial life history style to "r-selected" and "K-selected", respectively, for reasons we explained earlier (Balon 1979b) and will elaborate below. First, some further implications of this general dichotomy in life histories are provided.

Species are said to be "r-selected" if they have a life history pattern that includes a short growth interval and early maturation, high fecundity, reduced parental care and short life (generation) span. These features characterize animals in environments where rapid colonization is favored, where catastrophic mortality is liable to act in a density-independent manner, or where environmental disruptions are liable to be serious and unpredictable. Species are said to have a "K-selected" strategy if they have a prolonged growth interval and deferred maturation, reduced fecundity, increased parental care and an extended life (generation) span. They are favored in environments where conditions are more stable, where competition is liable to be a more serious factor, where mortality is likely to be density-dependent, and where conditions are likely to be stable over long periods of time (May 1976; Horn 1978; Krebs 1978; Green 1980). In a relatively stable (numerically) population, with limiting resources and severe intraspecific competition, variation in juvenile survival is likely to be greater than variation in adult survival. In a population going through a series of colonizing episodes, the reverse is likely to be the case (Stearns 1977).

This is a simplification of what is clearly an idealization. But it is useful because it brings our attention to these aspects of life histories, and couches our considerations in evolutionary terms. It brings the important questions to our attention, even if it does not immediately provide the answers. And the consideration of "r- and K-selection" has its obvious limitations (Stearns 1976, 1977; Horn 1978; Green 1980). Certainly, the life history of any species, when considered in these terms may well be a compromise (i.e., a mixed rather than a pure strategy), and it may not even be correct to consider "r" and "K" as being on the same continuum (Horn 1978; Green 1980). As this concept has obvious limitations, we will refer to it largely because it has been so widely used, and carries at least some general connotations (Fryer and Iles 1972; Lowe-McConnell 1975, this volume).

Guilds and Ontogeny: Hierarchical Systems

Our consideration of life histories will focus on the ontogeny of individuals, especially early ontogeny. The reasons for believing that the early life history will be of critical importance and have the primary determining influence on the entire life history have been given elsewhere (Balon 1964, 1971, 1978, 1979a, 1979b, 1980, 1981a; Noakes 1978a, 1978b, 1981), and so need not be elaborated here. In particular, we will stress eco-ethological guilds (reproductive guilds), and an approach based upon an hierarchical model of ontogeny with a uniform system of nomenclature for development intervals (Balon 1975a, 1975b, 1981b).

The proposal (Balon 1975a) to define the ontogeny of fishes by uniform, objectively-recognized intervals in an hierarchical system, has lead to increasingly widespread reassessments (Balon 1978, 1980; Bond 1979; Noakes 1981), although the proposal itself has been considered by some as little more than a semantic exercise (Balon 1976; Richards 1976).

The life history (ontogeny) of any fish is composed of a series of intervals. By now most would accept this concept, but disagreements continue as to the definition and nomenclature for these intervals. The proposal of a uniform terminology for these intervals, based on a hierarchical system from the smallest recognizable stages in development to the broadest periods in the life history has significant and far-reaching implications (the fundamental implications of hierarchical systems in biology are well-established, Koestler 1967). These intervals are arranged, in sequence from broadest to smallest, as periods, phases, steps and stages. Each interval is composed of one or more at the next lower level in the hierarchy.

These terms overlap somewhat with previous usage, especially as they have been applied by some developmental biologists and ecologists, but they impose an order on otherwise ambiguous usage (e.g. Keenleyside 1979) and align with current theories of ontogeny.

The life history of a fish can consist of a maximum of five periods; embryonic, larval, juvenile, adult and senescent. These encompass the entire life of an individual, from beginning to the end of its life. The embryonic period begins with activation (insemination) of the egg, and terminates with the transition to exogenous feeding. The larval period begins with the transition to exogenous feeding and terminates with metamorphosis, when most of the temporary embryonic structures are replaced by permanent "adult" organs (typically including differentiation of the median fin fold, and ossification of vertebral centra). The juvenile period extends from this point until the first maturation of the gonads. The first gonadal maturation marks the beginning of the adult period, which continues until the last reproduction. The senescent period includes that time after the fish has ceased reproduction (or gametes are very few and of inferior quality), and ends with death.

At least some of these intervals may be greatly extended (e.g., larval period of several years in anguillid eels), or be entirely eliminated (as is the larval period in mouthbrooding cichlids (Fig. 1), the coelacanth, *Latimeria chalumnae*, and many cyprinodontids). Recognition of the alterations of life histories by the relative timing and duration of these intervals (usually referred to as heterochrony; Jones 1972; Gould 1979) leads to productive insights (Balon 1980). We must again emphasize that hatching (or parturition) plays no role in defining these intervals. This is perhaps the most common and persistent misunderstanding in considerations of ontogeny and life history features (Balon 1980, 1981a; Noakes 1981). We tend to date most things from birth (parturition) or hatching, and assume that the event has general significance in ontogeny, likely as a result of peculiarities of our own development (Noakes 1981). It does not.

Our terminology provides a uniform scheme to apply to any organism for the sake of comparisons. Typically, authors attempting such comparisons have assumed (usually implicitly) that hatching (or birth) should be the "zero point" at which to adjust the scales of measurement for the species in

question, instead of activation, insemination, or fertilization. Our system allows us to recognize the comparable intervals for any species, and thus to make meaningful (biological) comparisons of life history styles across virtually all organisms (Balon 1975a, 1981a; Noakes 1981).

Reproductive Guilds

The second basic point for our discussion is the earlier (Balon 1975b, 1975c, 1978; Balon et al. 1977) proposal to define fishes according to reproductive guilds. Again, this has been described in detail elsewhere, and so will be outlined here only in summary fashion. Basically, the assumption is that the reproductive style, or guild, of each species will be determined by factors relating to oxygen supply for the developing young, and predation upon them (Kryzhanovsky 1956; Soin 1968). The full set of proposed guilds will not be discussed here, only the major categories (again, this system is hierarchical). The most inclusive category, the section, contains a number of sub-sections, each of which contains the individual reproductive guilds. There are three sections; nonguarders, guarders and bearers. Within these are, respectively: open spawning nonguarders and brood-hiding nonguarders, substrate-choosing guarders and nest-spawning guarders, and external and internal bearers (Table 1).

Table 1. Reproductive guilds of fishes (after Balon 1975b), with most guilds omitted for the sake of brevity.

Section	Subsection	Guild	
A. Nonguarders	A.1 Open spawners	A.1.1	Pelagophils
		A.1.6	Psammophils
	A.2 Brood-hiders	A.2.1	Lithophils
		A.2.5	Xerophils
B. Guarders	B.1 Substrate-choosers	B.1.1	Lithophils
		B.1.4	Pelagophils
	B.2 Nest-spawners	B.2.1	Lithophils*
		B.2.2	Phytophils*
		B.2.3	Psammophils*
		B.2.5	Speleophils*
		B.2.8	Actiniariophils*
C. Bearers	C.1 External	C.1.1	Transfer brooders
		C.1.3	Mouthbrooders*
		C.1.6	Pouch brooders
	C.2 Internal	C.2.1	Ovi-ovoviviparous
		C.2.3	Viviparous

*Indicates guild known to contain cichlid species.

Overview of Tilapia Life Histories

The question of reproductive guilds is an obvious one to apply to tilapias. Several authors have proposed categorizations of these fishes on this basis (e.g., Baerends and Baerends-van Roon 1950; Wickler 1966a; Barlow 1974; Keenleyside 1979). The usual distinction has categorized the cichlids, including especially tilapias, as either substrate-spawning or mouthbrooding species (Lowe-McConnell 1975). The distinctions are obvious and clear, with few if any ambiguities assigning species to either category. The only problematic species are those few which behave initially as substrate-spawners (i.e., they do not take the fertilized eggs into the buccal cavity but direct custodial care towards embryos outside the body), but subsequently (up to as long as a few days later) take the embryos into the mouth and complete the cycle in a fashion essentially similar to that of a typical mouthbrooding species (Timms and Keenleyside 1975; Keenleyside 1979).

Further elaborations of these schemes include considerations as to whether young are taken back into the parent's mouth after they are first released (in mouthbrooding species), and the precise location of spawning. These generally assume (usually implicitly) that release from the mouth or hatching from the egg envelope(s) is a significant event for interspecific comparisons in ontogeny. However, as we have shown, this is misleading, as these events are not involved in defining any of the developmental intervals.

The distinction between mouthbrooding and substrate-spawning habits is also significant in taxonomic considerations of tilapiine fishes (Trewavas 1973a, 1978, this volume), consistent with the generic divisions of *Sarotherodon* and *Tilapia*, respectively. However, if mouthbrooding has evolved independently a number of times from nest-spawning guarders, it may not represent an evolutionary trend.

In our scheme of reproductive guilds, the substrate-spawning species are categorized as nest-spawning guarders (guarders, for convenience). The mouthbrooders are mouthbrooding external bearers (bearers, for convenience). There is little significant difference between the (usually) accepted classification of reproductive styles of these fish (Barlow 1974) and our guilds. The (apparently) intermediate species have been omitted at present, for lack of detailed information to decide on their guild. The utility of the guild concept extends beyond tilapias, however, so our adherence to it is more than just an attachment to our particular terminoloy.

The life histories of the tilapias can be profitably reviewed from the combined model of ontogeny and reproductive guilds. The close association of these, and their apparent relationship to other ecological aspects of life histories have been described for a *Labeotropheus* species (Balon 1977) and charrs (*Salvelinus* species; Balon 1980). There is good reason, both empirical and theoretical, for believing that heterochronous shifts in early development have been of major importance in the evolution of not only life history styles, but also consequently of independent species (Balon 1980, 1981a). This could be a plausible mechanism for sympatric speciation, perhaps to account for some of the endemism in African cichlids (Fryer and Iles 1969, 1972). We will return to this suggestion later.

We have surveyed published life history data for tilapias, especially as

related to growth and development, age at maturity, fecundity, parental care and longevity (Lowe-McConnell 1959; Berns et al. 1978; Gwahaba 1978; Hodgkiss and Man 1978; Babiker and Ibrahim 1979; Dudley 1979; Marshall 1979a, 1979b; Vareschi 1979; and the more general works mentioned previously). At times we have had to paint with a broad brush to complete our picture, as necessary data were not always available, but the fit to our hypothesis has been gratifyingly close, as will be seen.

We wanted to see if life histories fell into categories in our consideration, and whether they fit an evolutionary progression as proposed from our model, i.e., an evolutionary sequence, or back and forth alteration from altricial to precocial in life history styles. We propose that selection should act through heterochronous shifts of character anlagen in early ontogeny, to favor increasingly precocial forms (i.e., species adapt to conditions which tend to become more uniform and stable over time). However, the mechanism exists for this trend to be reversed, so that species will not necessarily become "trapped" in an evolutionary "dead end" of a highly specialized (and therefore unadaptable) precocial form (Balon 1980, 1981a).

We use the terms altricial (generalist) and precocial (specialist) in the general ecological sense, i.e., altricial young being those that are relatively small and incompletely developed, whereas precocial young are relatively larger and more completely developed, at a particular time in ontogeny (the term precocial is not to be confused with *precocious* breeding at a small size in tilapias which can occur in both bearers and guarders, i.e., in association with either 'precocial' or 'altricial' young).

So, for example, if we compare young tilapias at the onset of exogenous feeding (Figure 1), young of mouthbrooding species are clearly more advanced and better developed, i.e., precocial. At the corresponding time in development (onset of exogenous feeding), young of guarding species are smaller and less well-developed, i.e., altricial. For this reason, we refer to the guarding species as having a more altricial life style, and the bearers a more precocial style. The same kind of comparison can be made between species within a guild, or between forms within a species, to determine which is more altricial or precocial (since the terms are relative).

The relative position of a species (in terms of its life history style) will be apparent in terms of the relative timing of the developmental intervals in ontogeny. Precocial forms will include a truncated larval period and delayed maturation, and a senescent period of some length. Altricial forms, on the other hand, will have the early periods (embryonic and/or larval) prolonged, an early maturation and a reduced senescent period.

The only study of ontogeny in a species similar enough to tilapia to serve directly as a model (Balon 1977 on *Labeotropheus* species) will form the basis for much of what we will say regarding bearers. There have been several studies of guarding tilapias (e.g., Fishelson 1966a, 1966b; Peters 1963, 1965, 1973) but most have focused on descriptions or compilations of stages of development (not corresponding to our saltatory steps of ontogeny, Balon 1979a), and descriptions of certain important features (e.g., adhesive organs, Ilg 1952) of interest in these species. Data on fecundity are available for a number of tilapias (although still surprisingly few species) and are by no means complete. Data on growth and development (including age at first

reproduction) are available for even fewer species, and information on longevity is sketchy at best. Ironically, behavioral data (i.e., reproductive and parental behavior) are perhaps most nearly complete, partly as a result of the popularity of these fish with aquarists, and for interest in them as representative of some of the most specialized parental and social behavior among fishes (Balon 1975b; Maynard Smith 1977; Keenleyside 1979). Consequently, we summarize data for generalized guarders and bearers, as representative of the two alternative life history styles, altricial and precocial, while acknowledging that these data may at times be drawn from different species in a variety of circumstances, including non-tilapiine species in some cases (Balon 1959a, 1959b; Noakes and Barlow 1973a, 1973b; Noakes 1978a, 1978b, 1979; Lowe-McConnell, this volume).

Parental Roles and the Evolution of Parental Care Patterns in Tilapiine Fishes

There is convincing evidence from different sources (e.g., Fishelson 1966a, 1966b; Fryer and Iles 1972; Trewavas 1973a; Barlow 1974; Balon 1975b) that mouthbrooding tilapias (bearers) evolved from substrate-spawning (guarder) species (see Oppenheimer 1970 for a general discussion of mouthbrooding in fishes). As Keenleyside (1979) has noted, tilapias are remarkable, not so much for their well-developed parental care (which is in fact universal among the Cichlidae), but for the fact that uniparental custodial care (of whatever type) is almost invariably carried out by the female. This, paradoxically, resembles the pattern commonly encountered in birds and mammals, but is opposite that found in most other fishes which show custodial (parental) care. The typical pattern among teleosts is that the male is the responsible parent (Barlow 1974; Blumer 1979). In fact, this has given rise to a number of efforts (Dawkins and Carlisle 1976; Maynard Smith 1977; Baylis 1978, 1981; Barlow 1978; Ridley 1978; Perrone and Zaret 1979; Werren et al. 1980) to suggest why the male should so often be the responsible teleost parent.

The tilapias clearly differ from this pattern, and so require either a different, or an extended explanation. All guarding tilapias are biparental, the pattern typical for cichlids in this guild (Barlow 1974, Keenleyside 1979). The bearers are remarkable. All bearing (mouthbrooding) species have been assigned to the genus *Sarotherodon* (Trewavas 1973a, 1978, this volume) a designation we might question, as we have already mentioned, although the generic status is not critical to our discussion, as will become apparent. A few bearer species (e.g., *S. galilaeus)* are biparental (i.e., both male and female parent carry developing young in their buccal cavities) (Iles and Holden 1969; Fryer and Iles 1972). In a few others (e.g., *S. melanotheron),* the male is the sole custodial parent (Aronson 1949; Barlow and Green 1970; Ridley 1978). All other *Sarotherodon* forms are maternal bearers (i.e., only the female carries the developing young).

Various proposals (e.g., Trewavas 1978) have been suggested as possible alternative evolutionary pathways for the different bearer strategies from the guarding ancestral condition. We do not propose to resolve that controversy,

nor suggest a possible explanation for the overwhelming incidence of maternal bearer species beyond the following comments, as this issue is not central to our discussion.

All female-uniparental *Sarotherodon* forms are lek species in courtship and breeding (Fryer and Iles 1972; Lowe-McConnell 1975; Loiselle and Barlow 1978). Field observations on reproductive behavior of male-uniparental *Sarotherodon* forms are insufficient to draw any firm conclusions from (Lowe-McConnell, Trewavas, pers. comm.). This by itself is not a remarkable correlation, since a number of other teleosts also have lek breeding systems, but with uniparental male custodial care (e.g. Centrarchidae, Belontiidae, Gasterosteidae; Loiselle and Barlow 1978; Keenleyside 1979). Such communal mating displays (leks) have been noted (Southwood 1976) as typical of "K-strategists" but irrespective of whether this is a valid generalization, we shall see that it does not necessarily restrict these *Sarotherodon* forms to a strictly K-selected strategy.

Nor is it mouthbrooding (bearing) which is responsible for the parental roles in *Sarotherodon*. The general pattern of parental roles in mouthbrooding (bearing) teleosts does not appear significantly different from that in parental teleosts in general (nonbearers) (Oppenheimer 1970), although the data are very sketchy (Breder and Rosen 1966). There must be some aspect of the ecology and/or life history of the *Sarotherodon* forms which predisposes them to, or necessitates, the predominant role for the female in parental care (see also Maynard Smith 1977). Neither their position as cichlids, nor as lek breeding species nor as bearers can account for the female parental role. The proposal by Barlow (1974) of an evolutionary progression from biparental care, to polygyny and uniparental female care certainly agrees with the major trend in tilapias, assuming selection favors parental care.

If we assume that these species were likely adapted for riverine existence in their ancestral form(s) (Fryer and Iles 1972; Liem 1973; Greenwood 1974), they would be better adapted (over an evolutionary time scale) as altricial rather than precocial forms. The evidence of such fluvial species is that they tend to be adapted to breed seasonally, often in flooded or inundated habitats with strong seasonal and/or yearly fluctuations (Lowe-McConnell 1975; Welcomme 1979a). But if conditions did not permit guarding (e.g., unsuitable substrate for a nest, with danger of exposure, etc.) and hence bearing were favored, maternal bearing (mouthbrooding) would most likely be the end result of an extended evolutionary progression (Barlow 1974; Loiselle and Barlow 1978; Balon 1981b; but see Timms and Keenleyside 1975). Perrone and Zaret (1979) hypothesized that lake-dwelling cichlids, because of the rather constant environmental conditions, with extended or continuous breeding seasons, should be maternal mouthbrooders (bearers). They suggested that riverine cichlids should have a greater incidence of male parental care, including biparental guarding, because of stronger seasonal changes and more restricted breeding seasons. The correlation may be a general one, but may also be difficult to apply rigorously to all tilapias (e.g., Lowe-McConnell, this volume).

Bearing and its attendant adaptations are clearly an advanced, precocial life style, seemingly ill-suited to the kind of habitat we have described for a

fluvial species invading a recently-inundated area (but see Philippart and Ruwet, this volume). The key point is the saltatory nature of development we have described. In a very real sense, these fish can have the best of two worlds and both life styles. Through heterochronous shifts in development during ontogeny they can quickly adapt towards a more altricial mode to take advantage of new habitats (e.g., seasonally flooded lagoons), or revert to a more precocial mode under other circumstances (e.g., more stable, long term conditions in large lakes, high competitive diversity of fish taxa) while remaining in the same reproductive guild.

Tilapiine Life Histories and Ontogenetic Inferences

The relevant life history data for guarding and bearing tilapias under natural conditions are summarized in Table 2. There is clearly a correspondence between the reproductive guild (and, hence the genus; Trewavas 1973a, 1973b, this volume) and other aspects of the life history style. Guarders are generally more altricial, bearers more precocial. There can be little doubt that the bearers are more specialized, and almost certainly derived from ancestral guarding species (Fishelson 1966a; Peters 1965; Lowe-McConnell 1959; Trewavas 1973a, this volume). The guarders are more primitive, also, as proposed in the system of reproductive guilds (Balon 1975b, 1981b). As already mentioned, bearing may have evolved several times independently among the tilapias (Trewavas, this volume), and if so it cannot likely be the basis for taxonomic distinctions. In any event, the multiple evolution of bearers is consistent with our hypothesis of altricial and precocial "twin forms".

Comparisons between tilapias in the two different guilds are informative, with at least some confirmation of our predictions. There are some apparent exceptions however. These seem to be the result of adaptive shifts in life history features within each guild, causing the ranges of certain values to overlap between guilds. This will become more apparent when we discuss

Table 2. Comparison of tilapiine species in natural populations*, according to reproductive guilds (modified from Fishelson 1966a; Fryer and Iles 1972; Peters 1973; Lowe-McConnell 1975; Balon 1975b, 1977; Balarin and Hatton 1979).

Characteristic	Guarders	Bearers
Fecundity (fertility)	up to 7,000 eggs	up to 1,000 eggs
Egg diameter (mm)	1-1.5	up to 5
Yolk—% lipid	less than 25	up to 45
Yolk color	clear, pale yellow	opaque orange
Size at onset of feeding (mm)	5-6	9-10
Age at first reproduction (years)	0.5-2	1-4
Total length at first reproduction (cm)	up to 20	up to 40
Courtship	prolonged, monogamous	brief, polygamous
Juvenile mortality	relatively higher	relatively lower
Longevity (years)	up to 7	up to 9

*Extreme values associated with fish stocked in non-native conditions, held in intensive rearing facilities, or other exceptional circumstances have been excluded.

such ecological (rather than evolutionary) shifts in life history features.

The bearing species have a relatively lower fecundity, larger ova (with higher yolk density), a longer growth interval, later age at maturity (with overlap between guilds), and possibly (the data are few) greater longevity than the guarding species (see also Lowe-McConnell, this volume). The bearers lack the larval period in their ontogeny (Balon 1977), an adaptation for increased protection of the young. The young are released in an advanced state of development (as juveniles), at a relatively large size (up to 15 per cent adult body size) (Figure 1). The guarding species have significantly higher fecundity, with correspondingly smaller, less energy-rich eggs (Fishelson 1966a; Fryer and Iles 1972; Hanon 1975; Balon 1977). Their development includes an abbreviated but distinct larval (alevin) period. Maturation (onset of the adult period) is relatively earlier, the growth interval shorter, and life span appears to be shorter (again, these data are not strong) (see also Shine 1978).
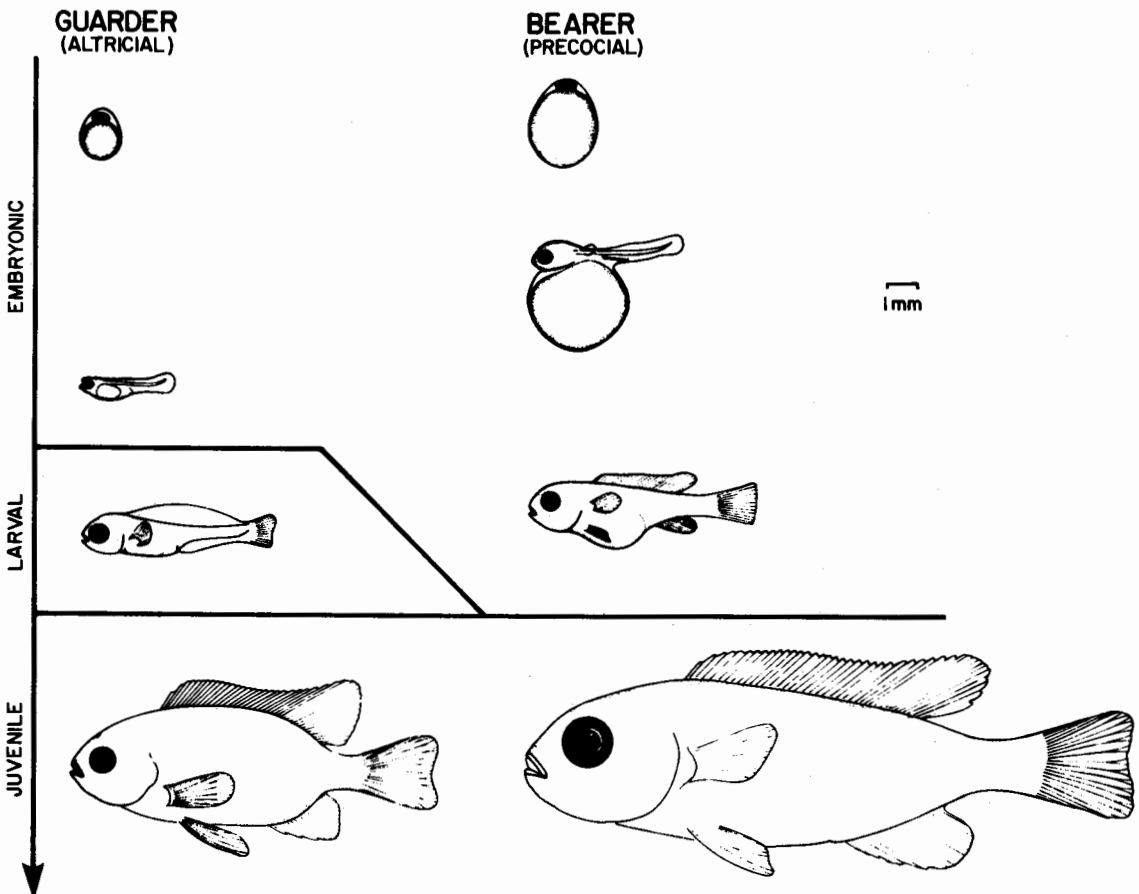

Figure 1. Diagrammatic representation of developmental intervals in idealized guarding (altricial) and bearing (precocial) tilapiine fishes (adapted from Fishelson 1966a; Fryer and Iles 1972; Axelrod and Burgess 1973; Peters 1973; Balon 1977, 1981a). Durations of intervals as indicated by vertical extent in the diagram, are not to scale.

This correspondence in life history features of the two groups of tilapias is not surprising, and at least some of these features have been noted by almost all previous investigators who have studied more than a few species (e.g., Baerends and Baerends-van Roon 1950; Fryer and Iles 1972; Lowe-McConnell 1975, this volume). We emphasize it since it agrees with our basic hypothesis, and leads to some interesting predictions. These are particularly relevant as they may apply to management of these fishes, and their responses to environmental perturbations over an ecological time frame (i.e., during the ontogeny of individual fish).

Saltation of Ontogeny, and Altricial to Precocial Tilapias

The hypothesis of saltatory development predicts that species should respond to environmental situations, both on the time scale of ontogeny and of phylogeny, by heterochronous rates in development. These rates will provide a more appropriate "match" to existing environmental conditions by moving the individual more towards the altricial or towards the precocial trend of the life history style. Since these conditions correspond, in the general way we have already described, to "r- and K-selection", respectively, they are of some considerable significance.

Heterochrony is the "shifting of gears" in development (Jones 1972; Gould 1977, 1979; Balon 1980), or change in ontogeny as a result of relative timing of developmental events and intervals. Since we have a uniform set of terminology to apply to ontogeny, we can ask whether heterochrony has occurred, and if so, at what point(s). The answers appear to be directly related to considerations of selective pressures acting on life history styles.

Heterochrony provides the ability to adapt to a fluctuating environment by shifting the timing of appearance of structures and functions. It likely varies among species, or even forms within a species, depending on previous evolutionary history. The trend in evolution will be from altricial to precocial (Balon 1980; Noakes 1981). This is based on the assumption that, other things being equal, communities will tend towards a more mature, competitive ("K-selected") condition through ecological succession, favoring a more precocial life style in the fishes. But juvenilization (paedomorphosis) remains as the process available for "retracing" phylogeny, and prolonging early ontogeny, with its concomitant flexibility and adaptability. By this mechanism, fish will retain some flexibility in ontogeny, and be able to shift back more towards an altricial life style.

In theory, at least, we can derive an altricial form (more or less equivalent to "r-selected"), or a precocial (more or less equivalent to "K-selected") form for a particular tilapiine species by altering the timing of ontogeny (heterochrony). A shortened (or absent) larval period would be related to a longer growth interval, to a later reproductive maturation, and consequent shifts in life history (and vice versa). Since size (a consequence of growth) and fecundity are typically positively correlated in fishes (bigger fish have bigger gonads with more gametes; Lowe-McConnell, this volume), fecundity would also be altered, as would longevity (Balon 1981b). But the net effect of such shifts in ontogeny would depend on the details of each case, as an

earlier age of first reproduction will often dramatically increase "r" (Lewontin 1965; Green 1980). Thus earlier age of first reproduction will likely be more significant than changes in fecundity. Ecologists have provided extensive discussions of these considerations, particularly the concept of reproductive value, i.e., the allocation of resources to growth or reproduction at a particular time (Southwood 1976; Horn 1978; Krebs 1978; Hirschfield 1980). More altricial forms would either occupy habitats with persistent, unpredictable fluctuations, or invade "new" habitats before they stabilize (e.g., Courtenay and Hensley 1979). More precocial forms would be better suited for stable conditions and resultant competition, or specialization, or both (Baker and Stebbins 1965; Southwood 1976; Horn 1978; Balon 1981a). In this regard, it is worth noting the generalizations made by Philippart and Ruwet (this volume). They conclude that the macrophagous, substrate-spawning (guarders) *Tilapia* species of the *Coptodon* group all have wide distributions, exclude each other geographically, have been slow to speciate and are closer to the original stock. The microphagous, mouthbrooding (bearers) *Sarotherodon*, on the other hand, are diversified and specialized into small local populations with restricted distributions in the Rift Lakes (with a few exceptions). The distinctions they draw correspond well to the separation we have suggested between the altricial life style of the guarders and precocial life style of the bearers, with attendant adaptations as "generalist" and "competitive" species, respectively.

Also, the report by Lowe-McConnell (this volume) of the results of simultaneous stocking of *T. zillii* (a guarder) and *S. leucostictus* (a bearer) in the Teso dams of Uganda fits the same pattern. *T. zillii* predominated at first, but was later overtaken in numbers by *S. leucostictus*, even though the fecundity of the latter was lower. As we would predict, the more altricial guarder would be better suited (ecologically) for the initial invasion, but with time (and presumably increasing ecological maturity of the system) the more precocial life style of the bearer would be increasingly favored. However, not all such cases of apparent competition fit this pattern: see discussion of the advantage of *S. macrochir* over *T. rendalli* in initial colonization of the man-made Lake Mwadingushu, Shaba (Philippart and Ruwet, this volume) and ousting of *S. variabilis* by *T. zillii* in L. Victoria (Lowe-McConnell, this volume).

But the intrinsic appeal of our formulation is that it does not require dramatic or drastic alteration in a species to produce substantial evolutionary changes, i.e., a species would not necessarily require major new genetic "mutations" to shift its life history style. Such shifts could be the result of relatively minor, genetically-determined changes in the timing of ontogenetic processes. In fact, a more precise formulation provides a mechanism for evolutionary change in either direction between altricial and precocial forms. The sympatric occurrence of two forms of a species, altricial and precocial, has been discussed at length elsewhere (Balon 1980, 1981a, 1981b).

Such a heterochronous shift could make possible a kind of sympatric speciation (through allochronic speciation, perhaps), or only lead to adaptive changes in life histories. As an aside, however, as we mentioned previously, it is worth noting the possible significance of this as a mechanism for the proposed dichotomous splitting of taxa (Løvtrup 1974; Balon 1981b). The

possibility that such a mechanism may have been responsible for at least some of the adaptive radiation in African cichlids, as seen in the Great Lakes, is obvious, and clearly warrants attention in the future.

The responses of tilapias during ontogeny to either natural or man-made changes in ecological conditions are perhaps the best evidence to support our hypothesis of heterochrony and saltatory development. Our hypothesis predicts, for example, that as environmental conditions change (or are changed by human intervention) towards either of the extremes described previously, the fish should alter their ontogenetic development accordingly. Sudden and marked alterations in environmental conditions (e.g., flooding of river banks or lake shore lagoons, increases in adult mortality and/or decreases in juvenile mortality) should all favor a more altricial life style. Consequently, we would expect that any or a combination of these environmental features (or changes) should lead to one or more of: an earlier maturation, increased fecundity (clutch size), smaller eggs, faster growth and shorter life span in the fish. Conversely any change(s) in the opposite direction in those environmental conditions would favor a more precocial ontogeny and life style. We would predict the fish should respond by showing some or all of: delayed maturation, decreased fecundity, with slower, larger eggs, and increased longevity.

The data available, both from field and aquaculture observations, appear to support these predictions (see, in particular, extensive reports summarized in Fryer and Iles 1972; Lowe-McConnell, this volume). The comparisons can be made in a number of ways. Fish living (native) in habitats differing in the above ways can be compared. Fish artificially stocked from one habitat to another can also provide data to test these predictions, especially since the introductions could take place either into a habitat the same as, or different from the original one. The responses of tilapias to naturally-occurring environmental changes can also be used here. The responses of these fish in aquaculture facilities, particularly to different types of management procedures, can also be interpreted to test the predictions (Table 3). A brief summary of some examples will illustrate our case.

Table 3. Size at sexual maturity (beginning of adult period), maximum size and longevity in different stocks of tilapiine species. A smaller size at first maturation (within a species, and to a lesser extent within a guild) indicates a more altricial life history style (see text for full discussion) (adapted from Worthington and Ricardo 1936; Ricardo 1939; Lowe (McConnell) 1955b, 1957, 1958; Lowe-McConnell 1975; Garrod 1959; Cridland 1961, 1962; P.J.P. Whitehead 1962; R.A. Whitehead 1962; Iles and Holden 1969; Hyder 1970a, 1970b; Iles 1971; Fryer and Iles 1972; Balon and Coche 1974; Ben-Tuvia 1978; Hodgkiss and Man 1978; Silverman 1978a, 1978b; Bruton 1979; Siddiqui 1979a; De Silva and Chandrasoma 1980). (All *Tilapia* species are guarders, all *Sarotherodon* species are bearers).

Species	Locality	Typical (T) or Dwarfed (D) Stock	Maturation Size (mm)	Maximum Size (mm)	Longevity (years)
T. mariae	Nigeria, Osse River	T	165	300	—
T. mariae	Jamieson River	D	100		
T. rendalli	Lake Kariba	T	—	450	5
T. zillii	L. Kinneret	T	135	270	7
T. zillii	Egypt, ponds	T	130	250	—
T. zillii	L. Naivasha	D	90		
T. zillii	aquaria	D	70		

Table 3 (cont.)

S. lidole	L. Malawi	T	285	390	5
S. mossambicus	Egypt	T	—	300	7
S. mossambicus	Hong Kong	T	165	310	4
S. mossambicus	Sri Lanka	T	150	340	—
S. mossambicus	L. Sibaya	D	100		
S. mossambicus	South Africa	T	—	390	11
S. mossambicus	Buffalo Springs	D	100		
S. mossambicus	aquaria	D	45		
S. m. mortimeri	L. Kariba	T	300	390	8
S. m. mortimeri	lower Malolo River	T	180		
S. m. mortimeri	upper Malolo River	D	90		
S. niloticus	Egypt	T	200	330	9
S. niloticus	L. George	T	—	400	—
S. niloticus	L. Rudolf	T	390	640	—
S. niloticus	L. Rudolf, Crater Lake A	D	250		
S. niloticus	L. Edward	T	170		
S. niloticus	L. Baringo	T	260	360	
S. alcalicus grahami	L. Magadi	D	25	100	
S. aureus	L. Kinneret	T	190	315	5
S. esculentus	L. Victoria	T	230	375	10
S. esculentus	Kavirondo Gulf	T	230	330	7
S. esculentus	Jinja	T	225	340	7
S. esculentus	Mwanza	T	240	325	7
S. esculentus	aquaria	D	105		
S. esculentus	pond	D	164		
S. galilaeus	L. Kinneret	T	220	345	7
S. galilaeus	Sokoto River	D	110		
S. grahami	L. Magadi	D	25	100	—
S. leucostictus	L. Naivasha	T	180	250	—
S. leucostictus	L. Edward	T	210	240	—
S. leucostictus	L. George	T	140	280	—
S. leucostictus	L. Albert	T	260	280	—
S. leucostictus	L. Albert, lagoon	D	100		
S. leucostictus	Uganda, pond	D	120		
S. leucostictus	Kenya, pond	D	70		
S. niloticus	L. Albert	T	280	500	—
S. niloticus	L. Albert, lagoon	D	100		
S. rukwaensis	L. Rukwa, tributary	D	280		
S. saka	L. Malawi	T	275	340	5
S. shiranus	L. Malawi	T	220	290	5
S. s. chilwae	L. Chilwa	T	200	290	5
S. squamipinnis	L. Malawi	T	240	330	5
S. variabilis	L. Victoria	T	220	300	7

(Only the maturation size is given for Dwarfed stocks, since the evidence strongly suggests that these stocks are only phenotypically dwarfed, and so the maximum size remains that for the Typical stocks, in theory.)

The situation of *S. mossambicus* in Lake Sibaya is a well-documented example of a shift in the life history of a species as an adaptive response to (native) environmental conditions (Bruton 1979; Bowen, this volume). It clearly fits into the category of "stunted" or "dwarfed" natural populations of tilapia, known from a number of regions (Fryer and Iles 1972; Bruton 1979).

Both juveniles and adults are dependent upon feeding on benthic detritus. Juveniles feed in shallower, more inshore water, adults in deeper offshore locations. There is a strong correlation between protein content of benthic

detritus and depth (and therefore, distance offshore), and consequently, between depth and quality of diet. Thus, juveniles obtain a diet adequate in protein for growth, but as they become larger and feed in deeper waters, they progressively encounter protein deficiency, and as a result adults in the lake are severely emaciated (Bowen 1979, this volume).

The smallest juveniles are released by female *S. mossambicus* in the shallowest, inshore waters. Older (larger) fish are increasingly excluded from the richer (shallow) feeding areas, and so growth declines progressively with age, particularly in comparison with more typical *S. mossambicus* populations in other, nearby areas.

With water levels at or below normal, only the larger adult males are reproductively active. With higher than normal water levels, successively smaller (younger) males are recruited into the breeding stock, indicative of a shift towards a more altricial mode (i.e., earlier age of first reproduction). These smaller males attempt to breed in the most marginal waters around the edge of the lake, including particularly any recently inundated by flooding.

This shift in life history style, together with the typical food-restricted conditions in Lake Sibaya, is obviously the type of adaptive response we would predict in such circumstances. The generally harsh (i.e., food-restricted) environment, together with fluctuating lake levels, produces earlier maturation (onset of the adult period) in Lake Sibaya. *S. mossambicus* in this lake typically breed at about 0.43 (length at first breeding/maximum length), compared to the more typical value of about 0.70 for African cichlids (Iles 1971; Table 3). Others (most notably Iles 1971; Fryer and Iles 1972; Lowe-McConnell 1975) have also mentioned similar cases of dwarfed tilapia stocks, and have correctly interpreted them as representing adaptive responses to particular environmental conditions. Our proposed mechanism, saltatory development and heterochronous shifts in development (ontogeny), appears to be the mechanism involved in these cases.

An earlier age of first reproduction (thus a shorter generation time) tends to have the greatest effect on net reproductive effort, and to greatly accelerate population growth (Krebs 1978) (i.e., it increases "r" very markedly). If fish were to delay onset of sexual maturation, more of their available resources would be channelled into somatic growth. Thus, they would be larger (in size) at the time of their (later) maturation, and likely have higher fecundity (more or less equivalent to fertility, but see Welcomme 1967b, 1970). However, increased fecundity and longevity generally have much less significant effects on "r" than does an earlier age of first reproduction. Since food (and therefore potential for future survival, growth and maturation) is severely and progressively limited for *S. mossambicus* in Lake Sibaya, it is clearly adaptive for these fish to begin breeding when resources are still available to allow diversion into reproduction (and before adult mortality rate begins to increase because of protein deficiency) (Horn 1978).

Lowe-McConnell (1975, this volume) summarized a number of studies of growth and maturation in tilapia species throughout their range. She reports that the same species delay their maturation when living in large, deep lakes, whereas in smaller water bodies (floodplain pools, fish ponds, etc.) the fish breed at smaller sizes and younger ages. The growth rates of fish in the latter cases do not suggest physical "stunting", i.e. they are not small because they

are slow-growing. For example, they may breed for the first time at an age of less than one year (compared to three or four years in a big lake); they produce smaller eggs in these situations, and they may spawn repeatedly at relatively short intervals. Inshore species in a lake tend to breed earlier (in age) than do offshore species (e.g., in Lake Malawi), and the same species living in smaller (and therefore more "harsh") lakes breeds at an earlier age (and smaller size) than when living in larger lakes. She also draws attention to an example we shall return to in some detail, that of tilapias in fish culture ponds. Under these conditions the fish (e.g., *S. mossambicus* and *S. niloticus*) can breed when only a few months old, at about one-half the typical size at first reproduction in the field, and produce relatively more, but smaller eggs than fish of comparable size would if they bred at that size in the field.

Fryer and Iles (1972) cite a number of examples, too numerous to repeat here in their entirety, but worth mentioning in a summary fashion. Again, they clearly drew attention to the adaptive nature of such responses in tilapias, for which we are proposing the mechanism. They reported the response of fish in "confined" conditions (i.e., dams, pools, ponds) to breed at smaller sizes (earlier ages), to breed more frequently, and to produce smaller eggs than normal (the extremes of these sometimes being reported from aquarium conditions). Under natural conditions, bigger species grow faster (but these data need to be extended), mature at a later age, and live longer (observations remarkably in accord with our description of the precocial life style) (see also Lowe-McConnell, this volume). From the evidence available, they concluded that these responses, especially the "stunting" of body size, were due to a phenotypic (rather than genetic) change in the fish (i.e., reversible). They also concluded, quite correctly, that the phenomenon is not one of "stunting", but of relatively earlier breeding in the fish (they described the situation as "neoteny") (but see Balon 1981b for a discussion of this term). They defined neoteny as the ability to breed successfully while still in the juvenile interval of development, and elaborated on the potential survival value of this property for tilapias. They suggested that this property is at least in part responsible for the widespread distribution, plasticity and success as colonizers of tilapias, particularly in shallow lakes subject to fluctuations in water levels. Others have noted such "generalist", "colonizing" abilities of these fishes, and have also drawn attention to the apparent relationship between this and the relative lack of adaptive radiation in these species (only about 100 species of tilapia *sensu lato*), compared to the explosive speciation in genera adapted for stable, lake conditions (e.g., *Haplochromis, sensu lato*).

Some Comments on Culture

In a very real sense, the interests of fish culturists are working at odds with the biology of these fishes. The culturist wishes to raise the fish in a monoculture (or simple polyculture) system, with a high density of fish, high growth rate, and a harvest (yield) of large individuals in as short a time as possible.

As we have outlined, the biology of these fishes is such that under these conditions of rapid turnover, simple ecological community, and frequent environmental perturbations (e.g., draining ponds for stocking, harvest, etc.) they are forced strongly into a more altricial life style. This tends to result in fish showing earlier sexual maturation, and directing much of their resources into reproduction, with consequent lack of somatic growth (especially in females, in the bearers). In fact, these circumstances might well favor one of the guarding species over any of the bearers, since the former are, as a guild, more altricial.

The task in this case would be to select a guarder species that would not mature (sexually) so rapidly as to cancel the inherent benefits of its life style (high fecundity, general ability as an "invader" species). Furthermore, there might be disadvantages associated with the guarding guild (substrate require-ments for breeding, decreased likelihood of producing hybrids between species because of prolonged, monogamous courtship and pair formation) that would mitigate against them. However, some evidence (Caulton, this volume, pers. comm.) suggests that under appropriate circumstances, a guarder species (in his case *T. rendalli)* may have considerable potential for aquaculture.

"Stunting": A Misunderstood Phenomenon

Perhaps the most striking aspect of the literature on the culture of tilapias is the so-called "stunting" problem (Balarin and Hatton 1979; Avtalion, this volume; Hepher, this volume; Jalabert and Zohar, this volume; Lowe-McCon-nell, this volume) encountered in many attempts at intensive aquaculture. In fact, as we and some others have indicated (e.g., Fryer and Iles 1972), the problem is not one of inhibited somatic growth but one of accelerated ontogeny (sexual maturation).

Not only has the problem apparently been widely misinterpreted, and therefore misunderstood, it is also perhaps the clearest possible verification of the predictions of our hypothesis of altricial and precocial trends in ontogeny. Such early maturation is the classic response of an altricial form. There is little doubt that an earlier age of first reproduction will have the greatest effect on the rate of population increase (Lewontin 1965; Wilson and Bossert 1971; Emlen 1973; Southwood 1976; Horn 1978; Krebs 1978; Pianka 1978). It is clearly a heterochronous shift towards a more altricial form, as we would predict.

Tilapiine fishes are almost certainly derived from fluvial ancestors and still retain (at least in some species) the ability to successfully invade newly-created marginal aquatic habitats (Welcomme 1970; 1979a; Lowe-McConnell 1975, this volume). Stocking these fish in a pond or other aquaculture facility under the usual conditions (Balarin and Hatton 1979; Lovshin, this volume) is as close to a replication of those natural (ecological) phenomena as one could imagine. A relatively small number of adults or juveniles is introduced into a previously unpopulated pond, creating a low density, non-competitive situation. Often supplemental food is also provided for the fish (Hepher, this volume; Lovshin, this volume). A natural invasion into

a newly-created river floodplain pool or marginal lagoon (Welcomme 1970, 1979a) would be the ecological equivalent of this man-made event. The response of the fish is identical in both situations. There is a shift towards a more altricial life style, with a shorter interval of somatic growth (inferred from smaller body size), an earlier onset of reproductive maturity (again inferred from smaller body size) (Table 3), as well as production of more numerous, smaller eggs (Lowe (McConnell) 1955b; Fryer and Iles 1972).

The apparent misinterpretation of this response in aquaculture conditions as one of "stunting" has serious practical consequences (beyond any theoretical implications). The fish clearly are stunted, in that they are physically smaller than (large) adults known for the same species. But the real phenomenon is of course as we have described it. The fish are not "small for their age", they are "old for their size". The difference is not only semantic, and the consequences of the correct understanding are profound.

This also requires an understanding of the distinction between ultimate and proximate factors regulating these responses of the fish. Our discussion has centered on ultimate (i.e., evolutionary) factors. These must not be confused with proximate (i.e., immediate) factors influencing the animals. The latter might include food supply, water temperature, chemical signals from conspecifics and so on (Guerrero, this volume; Mires, this volume). For example, one result of the misunderstanding that the fish in ponds are "stunted" has been a misguided effort to provide ever more food for the animals. On the assumption that the fish are truly (somatically) stunted, from lack of sufficient food, the solution would appear to lie in providing more and more food. Ironically, this may worsen the problem. Not only may such attempts lead to serious problems of oxygen depletion (Balarin and Hatton 1979; Caulton, this volume; Hepher, this volume), but they may exacerbate the basic problem. If we assume that the fish are responding to what they perceive (by whatever means) as their invasion into a "vacant", low-competition habitat, then providing ever more food may simply add to that perception. Perhaps fish culturists should adopt the opposite strategy. Some evidence for the success of this exists in the literature, but it does not appear to have been fully appreciated or investigated (Hauser 1975; Balarin and Hatton 1979).

We would predict that if one wanted to produce large fish, with late onset of breeding (in ontogeny), and with a long interval of somatic growth, one should do things to push the fish more towards a precocial life style. This would mean that conditions should favor high intraspecific competition, with relatively higher mortality (rate) for younger fish and a lower rate for older individuals (see our previous discussion of the environmental conditions associated with precocial life history styles). We predict, for example, conditions such as restricted food, stable conditions over relatively long time periods, and high population density should favor the precocial life style.

Some evidence from aquacultural practices supports this. For example, in some cases, intensive stocking in aquaculture facilities has practically eliminated reproduction and led to production of desirable (i.e., large body size) fish in a relatively short time (Balarin and Hatton 1979). In fact, Allison et al. (1979) found an inverse relationship between stocking density and reproduction in *S. aureus* (but note the small tanks used by these authors

from which it is probably invalid to extrapolate to large culture ponds—Editors). The so-called "paradoxical stunting" reported at lower or intermediate stocking densities, ascribed to the action of "living space on growth" seems at best a *post hoc* attempt to explain the situation. Our hypothesis not only predicts the supposedly anomalous responses at different densities, but makes specific predictions as to the manipulation of tilapias for management purposes.

We feel our approach may be more rational than the great variety of attempts to produce monosex cultures of tilapias for pond culture, to produce all-male hybrid broods, to chemically or surgically castrate fish to inhibit reproduction, or the search for growth-inhibiting factors that operate differentially at different densities. Since it is based on the evolutionary (and ecological) features of the life histories of these fish, and manipulates their biology with a minimum of intervention requiring high technology or direct human action, it should also be the desired course of action for those with a solely practical interest in these fish, particularly in developing countries.

It is rewarding to find that the activities of basic science, particularly taken from first principles and theory, may in the end yield something of value comparable to that normally expected only from so-called mission-oriented research. If our efforts have such an effect in this case, we would view them as a success.

Acknowledgments

Discussion

LOVSHIN: I found the paper very interesting and stimulating as a culturist. I have thought along the same lines for quite a while, and I think the points you raise have importance. For example, why does a fish dwarf in a pond? What are the environmental, behavioral or density-related factors involved? However, I have a very strong resistance to your basic conclusion. You said that restrictive food and stable conditions would mean that the fish would not reproduce at such an early age, whereas Dr. Lowe-McConnell has said that tilapia in poor condition will switch to reproduction at a smaller size than those in better condition. I have also found that to be true in culture ponds. You also said there is some evidence that at high densities, reproduction is restricted. There is probably no doubt about that, but you have to understand that, at these high densities, if you do not feed fish they are not going to grow. You have to feed fish to get them to a large size particularly at high densities. This conflicts with your idea of restricting food. Your basic theory is very interesting, but I think we have to determine whether we can manipulate the environment, or manipulate something in some way so that we can eliminate the reproduction of tilapias in their first year. If so, we would in fact have solved many of our culture problems. This would be a tremendous advancement to tilapia culture, especially in developing countries. The high stocking densities to which you refer will reduce reproduction but these are only achievable with high cost, intensive, aerated circulation systems and they require much feeding.

NOAKES: I don't disagree with anything you have said. Obviously, fish are not going to grow unless you feed them. I will try to clarify that position. The question is not so much whether you feed, but given that you feed a certain amount, what leads the fish to channel that food into reproduction or into somatic growth? The problem is that we don't really know to what signal the animal is responding when making such a physiological shift.

LOVSHIN: But you make a very strong point in your paper—"We feel that our approach is not only more rational than a great variety of attempts to produce monosex culture of tilapias fishes for pond culture . . . to chemically or surgically castrate fish to inhibit reproduction . . . prospect for ultimate success." The way it is stated in this paper, it will not work at those high densities; not for culturing large fish.

HEPHER: I would like to support Len Lovshin. You said that you think that at a sufficiently high density, reproduction will stop. I would like to quote an experiment done at Auburn University by Allison who stocked 50,000, 100,000 and 200,000, densities you would suggest will make reproduction stop. Reproduction did decrease, but even at 200,000/ha, he got 38,380 fry/ha produced, which means there was still reproduction enough to affect the whole system and to cause stunting in the population. I would also like to quote the work of Miranova (1969). She held *S. mossambicus* in aquaria and the food was very limited. Fish of 6 g spawned in her aquarium. Of course, they didn't grow much because of lack of food, but they did spawn.

NOAKES: The particular density value we gave is simply a value we took from the literature. I am sure you are well aware that it is difficult to find data to test our ideas. I do not disagree with what you are saying. What I would like to say is that our hypothesis predicts that there should be a trend: if you decrease stocking density, it should tend to increase reproduction. The important thing is not so much to what extent stocking density is a factor, but that we find out what the fish are responding to—whether they spawn or whether they grow. It may be density; it may be any of a number of things.

BOWEN: I think we can divide the factors that are likely to be important into two categories: physicochemical types of cues, and cues related to food. When I need fry for experiments, I can always put juvenile *Sarotherodon mossambicus* of about 4 cm standard length in aquaria and raise the temperatures to 25°C and they will begin to reproduce, even in the presence of abundant food, at this very small size.
    Some groups of fishes, such as cyprinids, are known to secrete pheromones when in densely packed communities. These have a negative feedback effect on growth and

tend to trigger spawning. The food obviously has a role to play both in terms of quantity and quality. To my knowledge there has been very little attention paid to food quality with regard to this switching mechanism.

NOAKES: In temperate species, in highly seasonal conditions, food itself may not be so critical. The animal will be committed to enter a reproductive cycle. In the tropics, however, food may be much more important.

CAULTON: I would like to make one comment. About three years ago, we tried some high density rearing of *T. rendalli*. We found that they bred very easily, but we did not find many offspring in the pond because they are very cannibalistic. We were really recycling the gonadal products back into the food chain, and we got very good size fish from this system. As the fish has a short reproductive cycle, not too much energy is devoted to breeding and this is a useful way to combat it.

NOAKES: I would like to suggest that anything which alters the juvenile survivorship, or which decreases their mortality, will induce the fish to put more effort into growth and less into reproduction.

TREWAVAS: I would like to suggest that we avoid using the terms precocial and altricial in connection with tilapias. I do not think they help much, and they cause confusion as we already use the word 'precocious' for tilapias which breed at a small size, whether they are substrate-spawners or mouthbrooders—this dwarfing occurs in both groups. In Dr. Noakes' paper these terms appear to be used in two ways: (i) equated with substrate-spawners (altricial) and mouthbrooders (precocial), and (ii) with early and late development, a phenomenon which occurs in both groups. Thus, for example, the dwarf populations of *S. niloticus* breeding precociously in lagoons have, according to Dr. Noakes' terminology, become more altricial (hence *less* precocial) than the larger-growing lake populations.

Then there is heterochrony. The contact reaction of juveniles to parents is activated at an early stage. The reaction can then go on for some weeks. In *S. melanotheron*, which has a large egg, the young are said to exhibit no contact reaction after release. But Bauer's (1968) experiments with extra-orally reared embryos show that the reaction, though a weak one, is initiated at the usual time, but because of the large yolk, the embryos are normally then still in the parental mouth. This can hardly be called heterochrony.

It has been shown that certain structural and behavioral features develop at the same time in both substrate-spawners and mouthbrooders. These are incapable of expression in terms of function in the mouthbrooders, because the embryo is still attached to a heavy egg and is passive in the parental mouth. Hence, the temporal factor is constant, the key difference being the size of the egg, as Fishelson (1966b) showed.

Tilapias in Fish Communities

R. H. LOWE-MCCONNELL

Formerly Overseas Research Service
(Present address: c/o Fish Section, British Museum (Natural History)
Cromwell Rd., South Kensington, London, S.W. 7, England)

This paper reviews the information available on the ecology and behavior
of tilapias in natural fish communities, the species interactions and factors
controlling tilapia numbers, particularly conditions under which tilapias switch
from growth to reproduction. Maturation and maximum sizes tend to be
smaller (i.e., the fish 'dwarf') in small bodies of water than in larger ones, and
populations of fish with low weight for length switch to reproduction at a
smaller size than whose in which the fish are in better condition. Males tend
to grow larger than females in 'dwarf' populations, even in species in which
the two sexes grow to comparable sizes in large lakes.

Comparison of tilapia growth rates from different lakes and rivers shows
that within a water body the various species grow at different rates, the
faster-growing species reaching a larger size. But the same species will grow at
different rates in different water bodies, suggesting that environmental
differences are more potent than genetic ones in determining maturation and
maximum sizes.

Studies of biomass, production, yield and turnover rates from the Kafue
floodplain and Lake Kariba show that only a small part of the total production
is cropped as yield in natural waters; the turnover rate (production/biomass
ratio) is higher in the substrate-spawning *Tilapia rendalli* than in the associated
mouthbrooding *Sarotherodon.* Studies in the equatorial Lake George (Uganda)
have shown that the highest yield of tilapia from a natural water body is
comparable with yields from unfertilized fishponds. But despite this high
sustained yield here, it represents less than 1% of the very high primary
production (blue-green algae on which the tilapia feed).

The great plasticity of tilapia growth in natural waters suggests that
concentrating research on environmental and behavioral factors affecting
growth and the switch to reproduction is likely to be more helpful for tilapia
culture than the search for faster-growing genetic strains.

Introduction

For this meeting I had been asked to review work on the behavior of
tilapias in natural fish communities and species interactions, to see if any
inferences could be drawn from this for tilapia culture in polyculture systems.
But as feeding and breeding behavior, microhabitats and the dynamics of
spatial segregation have already been reviewed in an earlier paper (Philippart
and Ruwet, this volume) the emphasis in this paper has been changed to

include data on growth and production of tilapias in natural waters.

From the title one might expect discussion of the role of tilapias in relation to their competitors and predators, and the partitioning of resources where more than one tilapia species is present in a community. There has, however, been little direct study of competition with other species, or of differential predation, though more is known about partitioning of resources.

While reviewing the main sources of information on ecology and behavior of tilapias in natural and semi-natural fish communities (for the species listed in Table 1), the aim here was to consider:

1. The partitioning of resources of (i) food, and (ii) space and time breeding (now dealt with by Philippart and Ruwet).
2. Some of the factors which appear to control tilapia numbers in fish communities, with special reference to the size and age at which different populations switch from growth to reproduction.
3. Growth rates in different water bodies.
4. Production and yield from various natural waters.

Tilapias are preadapted by their breeding and feeding habits to thrive in still water and most of the important tilapia fisheries are in lakes. In rivers, tilapia fisheries are usually important only where there are extensive floodplains, and the fishery is then a seasonal one, geared to the annual flood cycle. In the last two decades the creation of large man-made lakes behind hydroelectric dams on African rivers has stimulated pre- and post-impoundment surveys, which have taught us much about the ecology and behavior of the riverine fish communities and how they adapt to lacustrine conditions.

As we have already seen in the previous papers, riverine tilapias tend to be widely distributed, for example, those of the 'soudanian' region and in the Zambezi system. The main river systems of these regions cross savanna floodplains lying at comparable distances north and south of the equator, where seasonal floods follow the overhead sun, so that they flood in their summer season after temperatures and day lengths have started to increase.

The aquatic life is geared to the well-defined seasonal cycles, the high-water season being the main feeding and growing time for the fishes, including the tilapias, when growth is fast and fat stores are laid down to last through times when food is scarce in the low water season. In these vast river systems floods do not necessarily coincide with local rains, as they may result from rain far upstream arriving downriver after local rains are over. Tilapias are less dependent than are the ostariophysan fishes living with them on the start of the rains, or flood, to initiate spawning. These riverine tilapias generally spawn at the end of the dry season, producing at least one batch of young before the water level rises, and continuing to produce batches in succession through part of the highwater season. The growth checks in the dry season show on the tilapia scales as annual rings, so more is known about ages and growth rates of floodplain tilapias than about those dwelling in large lakes, where more climatically stable conditions throughout the year lead to continued growth, making scale ring analyses very difficult. As the floodplains dry out, the tilapias along with the other fish retreat to the main rivers, or are trapped in pools on the floodplain until released by rising waters the next year. Predation from piscivorous fishes, the numerous aquatic birds and other animals, including man, is most intense as the waters

shrink, and also in the dry season when the fish may be trapped in pools and riverbeds where there is very little aquatic vegetation to give cover from predators.

Lacustrine tilapia populations include many of the same species found in the rivers, for example the nilotic species in many East African lakes. Some, like the Luapula/Mweru populations of *S. macrochir*, may make regular movements between river and lake. But in some long-enough isolated lakes endemic tilapia species have evolved: for example the *Sarotherodon* species flocks of Lake Malawi, and tilapia species in small crater lakes in West Africa.

As tilapias support the main commercial fisheries in most African lakes (except Lake Tanganyika) it was predicted that they would become the dominant fish in the new man-made lakes, such as Lakes Kariba and Kafue on the Zambezi system, Lake Volta in Ghana, and Lake Kainji on the Niger. The speed with which the tilapia populations have built up from indigenous riverine populations has depended on factors such as the draw-down for hydroelectric needs (which can destroy tilapia nests in shallow water), and perhaps flow-through/storage ratio, a high flow-through militating against the buildup of planktonic food sources. Tilapias became predominant species within two years in Lake Volta and three years in Lake Kariba (Petr 1969), but took longer to build up in Lake Kainji (Lewis 1974).

Ecological Information from Particular Water Bodies

The tilapias most studied in natural and semi-natural communities, and on which this review is based, are listed in Table 1.

1. NILOTIC TILAPIAS FROM RIVERS AND LAKES

Fish communities in the soudanian region include three relatively common tilapias, *Sarotherodon galilaeus* and *S. niloticus*, and *Tilapia zillii*, plus the smaller less common *S. aureus* (syn. *S. monodi*), which is more abundant in the Nile delta and Israel. These fish communities also include many much larger fishes, some of which may compete for resources with tilapias, such as *Labeo* and *Citharinus* which share the bottom detritus used as food by *S. galilaeus* in Lake Chad (Lauzanne 1972). Others are large piscivores, such as *Lates niloticus*, *Hydrocynus* species and *Gymnarchus niloticus*, all known to include tilapias in their diets. The tilapias are generally restricted to pools, lagoons and edges of the river and floodplain, places where aquatic vegetation provides cover. Daget (1954) pointed out that in the Upper Niger *S. galilaeus* predominates over sandy bottoms, *S. niloticus* over muddy ones (as Holden 1963, also found in Sokoto river pools), while *T. zillii*, an ecologically tolerant species, lives over rock, sand or mud, in still or running water. A macrophyte-feeder, *T. zillii* is generally found near plant stands; riverine *S. galilaeus* are detritivores using bottom algae, and *S. niloticus* takes epiphytic algae, diatoms or plankton according to the conditions.

In the lacustrine conditions of the huge but shallow Lake Chad, *S. galilaeus* is the common species, except in the north and northeast where *S.*

Table 1. *Tilapia* species for which ecological information is available from natural and semi-natural waters. These species may be Indigenous (I), Endemic (E), Stocked (S), or have just Appeared (A), probably escapes from dams or ponds.

Locality	*S. alcalicus*	*S. andersonii*	*S. aureus*	*S. caroli*	*S. esculentus*	*S. galilaeus*	*S.g. multifasciatus*	*S. jipe*	*S. karomo*	*S. karongae*	*S. leucostictus*	*S. lidole*	*S. linnelli*	*S. lohbergeri*	*S. macrochir*	*S. sp. nov.*	*S. melanotheron*	*S. mortimeri*	*S. mossambicus*	*S. niloticus*	*S. pangani*	*S. rukwaensis*	*S. saka*	*S. shiranus*	*S.s. chilwae*	*S. squamipinnis*	*S. steinbachi*	*S. variabilis*	*T. busumana*	*T. discolor*	*T. rendalli*	*T. sparrmanii*	*T. zillii*
RIVERS																																	
Niger		I			I															I													I
Nile		I			I															I													I
Upper Zambezi	I														I																I	I	
Middle Zambezi	A														S			I													I	I	
Lower Zambezi																			I												I		
Pangani							E														E												
Malagarasi								E								E																	
MAN-MADE LAKES																																	
Volta					I															I													I
Kainji					I															I													I
Nasser					I															I													I
Kariba	A														S			I													I		
Kafue	I														I																I		
McIlwaine															S			S															
Nyumba ya Mungu			S					I													I										S		
LAKES																																	
Kinneret (Israel)		I			I																												I
Chad					I															I													I
Albert					I						I									I													I
Turkana (Rudolf)					I															I													I
George/Edward											I									I													
Victoria					E						S									S								E					S
Malawi										E		E											E	E		E					I		
Chilwa																									E							I	
Mweru															I																		
Rukwa																						E											
Magadi	I																																
Nakuru	S																																
Naivasha											S																						
Bosumtwi						E																							I	E			
Barombi Mbo			E										E	E													E						
W. Afr. lagoons																	I																
Sibaya																			I														
Hong Kong Res.																			A														
Nicaraguan lake																			S														

niloticus predominates, and in the southern deltas of the inflowing rivers where *T. zillii* lives over varied types of bottom (Blache et al. 1964). The daily food consumption of *S. galilaeus* in Lake Chad, studied by Lauzanne (1978a, 1978b), depends on the water temperature; the conversion of the detritus eaten is very low (only 3%). In the new man-made lakes of Volta (Ghana), Kainji on the Niger, and Nasser/Nubia on the Nile, *S. galilaeus* has become the dominant tilapia, though in the Volta lake *S. niloticus* also became fairly abundant on the eastern side of the lake, and *T. zillii* in certain western arms. In Lake Kainji the buildup of tilapia populations was delayed for some years, perhaps because the large annual drawdown (10m) affected potential spawning grounds; furthermore *Citharinus* became very abundant when Kainji first filled, the lake filling coinciding with, or stimulating, a good *Citharinus* spawning year, and conditions for the survival of the young were good as predator populations had not yet built up. In Lakes Turkana (Rudolf) and Albert, which both have nilotic faunas, *S. niloticus* is the larger-growing and more abundant tilapia, feeding mainly on phytoplankton. Though here again *S. galilaeus* is found off sand banks; *T. zillii* is rarely seen in the main lake. Lake Albert also has another inshore-dwelling *Sarotherodon*, *S. leucostictus*. In Lakes George/Edward, which drain into Albert, *S. niloticus* and *S. leucostictus* are abundant (the latter in the inshore zone), but *S. galilaeus* and *T. zillii* are absent from the fauna. Both Albert and Turkana have populations of dwarf *S. niloticus*, living in lagoons along the Albert lake shore, and in crater lakes on Central Island in Lake Turkana.

S. niloticus was also stocked into many lakes and dams in Uganda. In some of these the fish grew very large while the populations were small, but then multiplied rapidly and became dwarfed; in other lakes they apparently never grew large, which may have reflected the paucity of suitable food. Data on *S. niloticus* from many of these lakes and dams, summarized by Lowe (McConnell) (1958), brought out the following points:

1. The distribution of *S. niloticus* within a water body varied with the ecological conditions. Phytoplankton, epiphytic diatoms or bottom algae were used as food according to whatever was available.

2. The size to which the fish grew, and at which they matured, varied greatly; fish from large lakes matured at, and grew to, a larger size than those from lagoons or ponds. (The largest up to 64 cm TL came from Lake Rudolf, Worthington and Ricardo 1936). (Figure 1)

3. In the lakes the males and females did not differ significantly in maturation size or final size, but in small bodies of water where the fish were dwarfed, males were larger than females, and also much more numerous than the females.

4. Fish in poor condition (low weight for length) matured at a much smaller size than fish in good condition (Figure 2). The growth rates and ages of large and small fish at maturation were not known, but in some newly stocked waters *S. niloticus* grew to 350 g (equivalent to about 26 cm TL) in one year, whereas in ponds they grew to 17 cm TL (98 g) and started to breed when 7 to 8 months old.

5. In equatorial waters *S. niloticus* in breeding condition may be found at any time of year, but peak spawning coincides with the two rainy seasons (a finding later confirmed by Gwahaba 1973). At higher
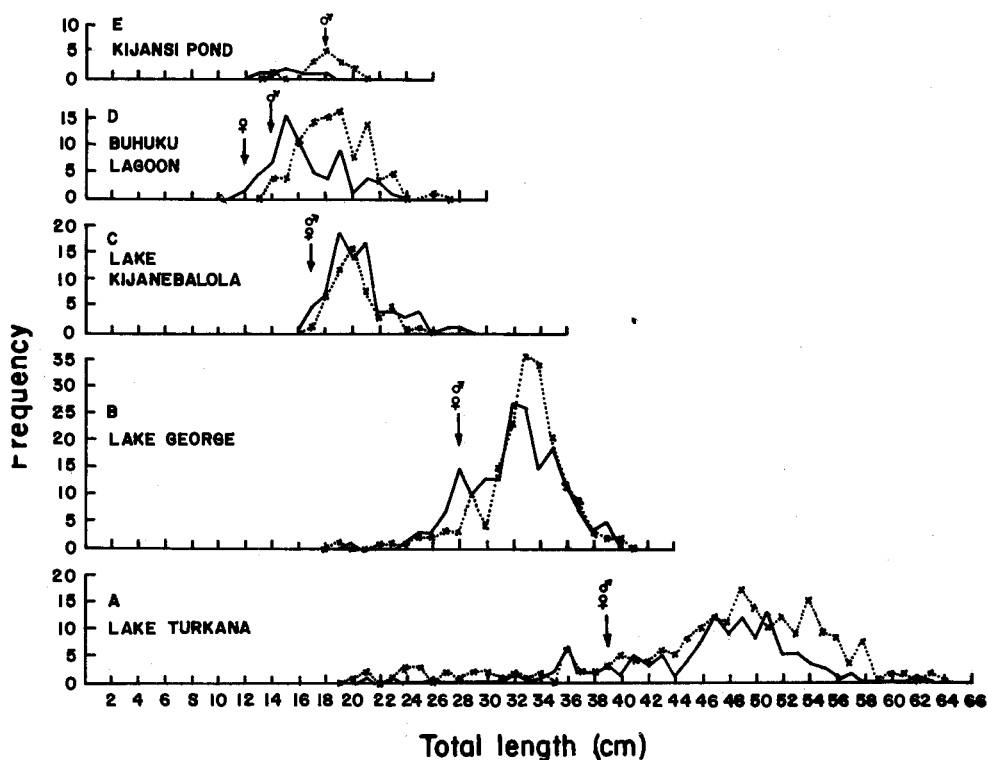
Figure 1. Length frequency distributions of male (x . . . . x) and female (●——●)
Sarotherodon niloticus from various East African waters (after Lowe (McConnell)
1958). A, Lake Turkana, seined fish, maturation size (m.s.) 39 cm TL, both sexes;
B, Lake George, gillnetted fish, m.s. 28 cm both sexes; C, Lake Kijanebalola, gill-
netted fish, m.s. 17 cm both sexes; D, Buhuku lagoon, Lake Albert, seined fish,
m.s. 14 cm male, 12 cm female; E, Kijansi pond, Uganda, fish examined alive
when pond drained, males of 18 cm in breeding colors.
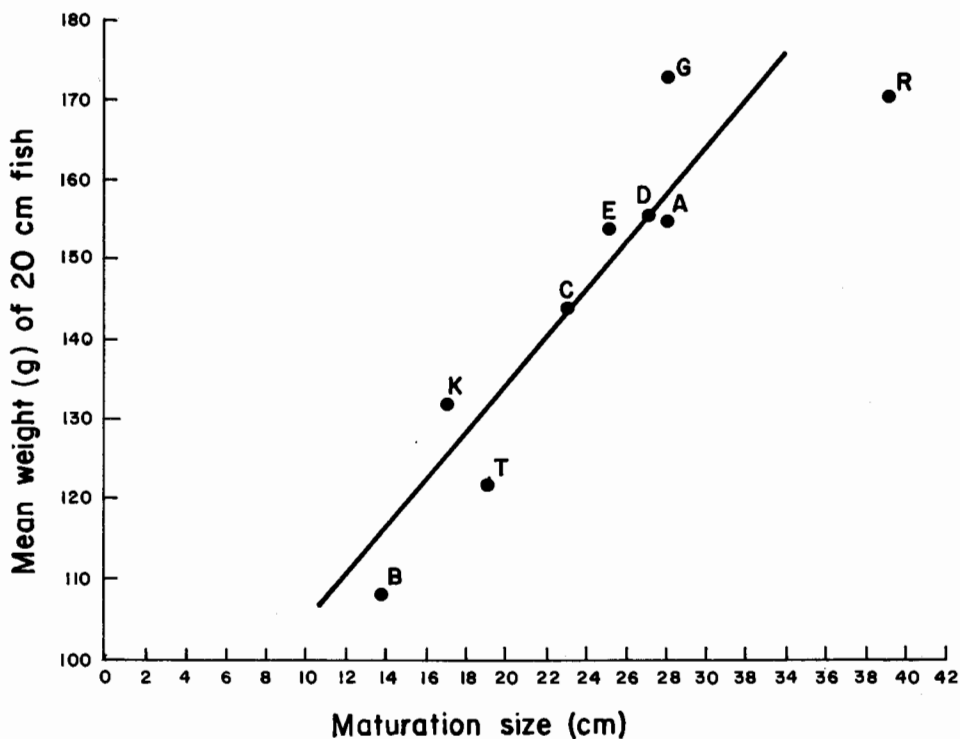
Figure 2. The relationship between weight for length ('condition') and maturation size of *S. niloticus* populations in various East African waters (after Lowe (McConnell) 1958). Mean weight of 20 cm TL fish plotted against maturation size of population for fish from Lake Turkana (R), Lake Albert (A), Lake George (G), Lake Edward (E), Lake Katinda (D), Lake Chanagwora (C), Lake Kijanebaĺola (K), Tonya lagoon of Lake Albert (T), Buhuku lagoon of Lake Albert (B). (Calculated means are used for Lakes Turkana, Albert and Chanagwora as samples from these waters had no 20 cm TL fish).

latitudes this species breeds mainly in the rainy season.

6. The dwarfed *S. niloticus* from shallow waters were often heavily parasitized, those from the large lakes relatively free of parasites.

7. Some hybridization had occurred between *S. niloticus* and *S. spilurus niger* both stocked in Lake Bunyoni, and possibly between *S. niloticus* and *S. esculentus* both stocked in an Ankole crater lake.

During the intensive International Biological Programme studies on the ecology and production of *S. niloticus* in the equatorial Lake George (Uganda), Gwahaba (1973) found that the maturation size of these fish had diminished since earlier studies (Figure 3). This he attributed to the effects of intensive fishing. Early in the history of the fishery, 50% of the females were mature at 27.5 cm TL, by 1960 this had fallen to 24.5 cm, and in 1972 was 20 cm. Data on *S. leucostictus* in Lakes George/Edward and Albert, where it is indigenous, and from numerous lakes, dams and ponds where it has been introduced, summarized by Lowe (McConnell) (1957), show that, in this species too, maturation size varies greatly with the conditions (from 26 cm TL in Lake George to 7 cm TL in ponds). And about twenty years later Gwahaba (1973) found the maturation size in Lake George had declined to 14 cm TL, though the reason for this decline was not clear. In certain waters male *S. leucostictus* matured at, and grew to a larger size than the females; in ponds this species bred when only three months old. In some ponds immature males were known to have grown faster than the females.
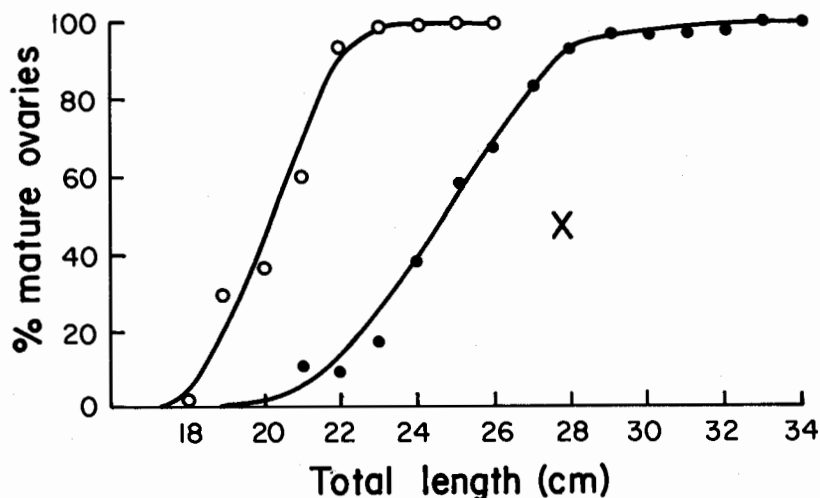

Figure 3. The decline in maturation size of female *S. niloticus* in Lake George, Uganda. Gwahaba's 1971-72 maturity curve (o) compared with Fry and Kimsey's 1960 curve (●) and Lowe (McConnell's) (1958) mean maturation size (x) (after Gwahaba 1973).

In natural waters *S. leucostictus* occupies an inshore zone and is common in lagoons. In equatorial lakes, as in ponds, breeding occurs throughout the year, without well-defined seasons. Egg numbers increased about 100 in a 7 cm female to roughly 1,000 in a 26 cm female, a relationship later studied by Welcomme (1967a). Small females tend to produce smaller, less robust fry than large females. Eggs hatch in about six days after fertilization and young are brooded for a further three weeks, though for the last week only at night. Lake George individuals caught in midlake showed a preponderance of

blue-green algae in the gut, whereas fish in the inshore regions had ingested detritus; since this species is more abundant inshore, it is essentially a detritivore (Moriarty et al. 1973).

Introductions of *S. leucostictus* showed how rapidly tilapias can be established in new waters from very few fry. All the *S. leucostictus* in Kenya waters appear to have originated from six specimens between 6 and 11 cm TL taken to Kisumu ponds from Uganda. In the Teso dams (Uganda) where *T. zillii* and *S. leucostictus* were stocked simultaneously, *T. zillii* predominated in the first few years after stocking, but were gradually overtaken in numbers by *S. leucostictus*, although this species lays fewer eggs at a time (Lowe (McConnell) 1955b). Such changes may have been related to food supply; in one of the dams *T. zillii* predominated while dense stands of macrophytes existed, but as it cleared these from the dam, *S. leucostictus* became the predominant species.

S. leucostictus introduced into Lake Naivasha, Kenya, in 1956 hybridized with another introduced species *S. spilurus niger*. Hybrids were abundant in 1961, but had disappeared by 1974 when Siddiqui (1977b) studied the lake. He found *S. leucostictus* then to be the dominant species, and to spawn throughout the year, though Hyder (1970a) had previously maintained they had a relatively quiescent period here from July to September. Males matured at 18 cm TL, females at 16 cm. Fecundity ranged from 320 to 1,328 eggs in 16 to 32 cm females. Males predominated in the catches.

2. Lake Victoria

The nilotic *S. niloticus* and *T. zillii*, together with *S. leucostictus*, have been studied in Lake Victoria to see how they have fitted in with, and taken over from, the indigenous *S. esculentus* and *S. variabilis*. Earlier studies (Lowe (McConnell) 1956a; Fryer 1961a) had indicated that these two indigenous tilapias were ecologically complementary species with little or no competition between them; *S. esculentus* predominated in land-locked bays where the bottom was of soft flocculent mud from phytoplankton deposition, while *S. variabilis* was most abundant off more exposed shores, in water lily lagoons and in the outflowing River Nile. Both species occupied different biotopes according to the size and sexual condition of the fish. *S. variabilis* spawned in shallower water than *S. esculentus* (spawning behavior observed in a water lily swamp, Lowe (McConnell) 1956a), and juveniles occurred in different nursery zones.

In an attempt to boost the tilapia fisheries, *T. zillii* from L. Albert was introduced to Lake Victoria in 1954, and along with it came *S. niloticus* and *S. leucostictus*. Tilapias in ponds draining the lake may also have gained access to the lake around this time. *T. zillii* appeared in gillnet catches by 1956, *S. niloticus* and *S. leucostictus* both appeared in commercial records for the first time in 1960 (Welcomme 1967a). Some suspected hybrids between (i) *T. zillii* and *T. melanopleura* (from pond escapes), and (ii) *S. variabilis* and *S. niloticus*, were described by Welcomme (1967b). The spread of the introduced species was described by Welcomme (1966): *T. zillii* spread rapidly at the northern end of the lake, appeared in the southern

and eastern parts in 1960, and was abundant by 1964; it later became the dominant species in the former *S. variabilis* areas. Meanwhile *S. niloticus* and *S. leucostictus*, both rarely seen in commercial catches before 1962, became much more abundant from 1964 onwards, *S. leucostictus* becoming the dominant species in lagoons around the lake and near the papyrus and in the shallows of muddy bays, *S. niloticus* on the former *S. esculentus* grounds, where they were caught both in surface and bottom set gillnets. *S. niloticus* from offshore areas grew much larger than the indigenous tilapias (personal observation c.1970). The *T. zillii* lived in shallow marginal waters all round the lake, fry and juveniles (to 5 cm TL) inhabiting sandy shelving rock shores in sheltered places, situations favored as *S. variabilis* nurseries.

Welcomme considered possible competition between juveniles, and also between adults for feeding and breeding places. There appeared to be little competition for food between adults: *T. zillii* taking higher plant material, *S. esculentus* planktonic diatoms, while *S. niloticus* and *S. variabilis* had more flexible diets, feeding either on the bottom or on epiphytic or planktonic diatoms depending on the habitat. *S. leucostictus* seemed to feed exclusively on bottom material (Welcomme 1966, 1967b). Spatial segregation of feeding individuals helped to reduce any competition, *S. leucostictus* being confined to shallow margins of the lake near, and often behind the papyrus fringe (in water 30 cm to 5 m deep), a habitat shared with young *S. esculentus* (of 13 to 18 cm TL), while *T. zillii* and *S. variabilis* tended to spread into harder-bottomed habitats and more exposed waters. The larger *S. esculentus* remained in mud-bottomed bays 5 to 10 m deep. *S. niloticus* was found in most of the habitats. All the introduced species grew to a large size in the lake and were in good condition (high weight for length).

Competition for breeding grounds was more apparent. The possible lack of suitable areas for spawning, and of nursery grounds for the very young, appeared to be a factor limiting population expansion. This view was supported by the dramatic increase in *S. esculentus* catches in 1964/65 following the unprecedented increase in lake level (1.4 m above the previous highest recorded level) in 1961-62. This flooded lagoons behind the papyrus fringe, places then used as *S. esculentus* nurseries (Welcomme 1970). Clean, firmer substrates were needed on which to spawn by the guarder species *T. zillii*, and by the very small *S. variabilis*, and the ousting of *S. variabilis* by *T. zillii* appeared to be due to competition between them for such places for breeding and nursery grounds. *S. leucostictus* spawned in shallow (30 cm deep) water in mud-bottomed areas at the edges of lagoons; here the males in breeding colors guarded their nests at sites not frequented by other species. *S. esculentus* evidently spawned deeper, where it could find firm enough bottom in the sheltered gulfs, but the juveniles lived in the lagoons at the lake edge. *S. niloticus* appeared more catholic in its habits and could be found in association with any of the other species; its preference for hard substrates was reflected in some hybridization with *S. variabilis*, but later it thrived in *S. esculentus* areas.

Welcomme's (1964) study of juveniles on nursery beaches showed that juvenile tilapia were abundant on gently sloping 'gradient' beaches, *Haplo-*

chromis off more steeply shelving 'non-gradient' beaches. The small tilapias could withstand temperatures up to 38°C, lethal to the *Haplochromis*. Tilapias moved on and off these gradient beaches in accordance with the diurnal temperature fluctuations, the shallows cooling rapidly at night and the fish then moving into deeper water. An approximately linear relationship was found between the size of fish and depth of water. This enables small tilapia to feed without disturbance from larger individuals. Also they are then out of reach of the piscivorous catfishes, *Clarias mossambicus* and *Bagrus docmac*, often caught just off the tilapia beaches. The nursery beaches, though sharing high temperatures, differed in their dissolved oxygen tensions (DO), for which the different species had characteristic, though to some extent overlapping, preferences. *S. leucostictus* young were confined to areas of low DO (0.6 to 2.0 ppm), *S. esculentus* and *S. niloticus* lived in slightly better aerated water (1.0 to 3.0 ppm and 2.0 to 4.0 ppm respectively), while *T. zillii* and *S. variabilis* needed well-aerated slightly exposed areas. Competition for nursery areas appeared greatest between *T. zillii* and *S. variabilis*.

The introduced *Lates niloticus* fed mainly on cichlids in Lake Victoria and included some tilapia in its diet (Gee 1968, 1969).

3. ZAMBEZI SYSTEM

Zambezi system tilapias have been much studied as part of the pre- and post-impoundment surveys of hydroelectric schemes at Kariba and Cabora Bassa on the Middle Zambezi and on the Kafue tributary (see Balon and Coche 1974; Bowmaker et al. 1978; JFRO Annual Reports, and for information on the Barotse floodplain on the Upper Zambezi, Duerre 1969). Tilapias flourish better in the more lake-like 'reservoir rivers', which retain water and a good growth of aquatic vegetation throughout the year, than in the 'sandbank rivers', which dry out into pools devoid of plant cover in the dry season. Throughout the Zambezi system the presence of large piscivores, especially *Hydrocynus vittatus (Hepsetus odoe* in the Kafue), appear to control the ecology of the tilapias. The Upper Zambezi and Kafue have two indigenous species of *Sarotherodon*, *S. macrochir* and *S. andersonii*, and two *Tilapia*, *T. rendalli* (which greatly resembles *T. zillii* in the northern soudanian floodplains) and the smaller *T. sparrmanii*. In the Middle Zambezi *S. mortimeri* (which greatly resembles *S. mossambicus* in the Lower Zambezi) is the dominant species, though *S. macrochir* is also present; *S. andersonii* had not been recorded from the Middle Zambezi until 1971, after Lake Kariba had been established for twelve years. This example stresses that tilapias may move about more than realized, but strays do not get established unless they find suitable ecological conditions, in this case due to a man-made change.

Summarizing information on Upper Zambezi tilapias, Bell-Cross (1974, 1976) described *S. macrochir* there (the subspecies with a 'volcano' shaped nest) as being well distributed and abundant throughout the Upper Zambezi and its larger tributaries, growing to 1.8 kg. It feeds mainly on periphyton and detritus, though other algae are taken in summer months when they are abundant. Breeding starts early in the summer, probably triggered by increas-

ing water temperature and/or light periodicity; there appears to be a correlation between onset of rains and breeding activity, in the river at least one brood of young is produced before the floods, and one or more during the highwater season (in ponds four broods may be produced between September and February). The female mouthbroods the young. Once juveniles leave the floodplain, where they grow fast, they are restricted to lagoons and backwaters until they reach a size large enough to coexist with piscivorous *Hydrocynus*.

The Mweru/Luapula system has a subspecies of *S. macrochir* which has a characteristic star-shaped nest; this undertakes seasonal migrations from the deeper north end of Lake Mweru to the shallower southern end and up the Luapula River during the period July to October (it breeds September to March), with a reverse movement northwards in February-May; it appears to need shallow water in which to spawn, and cover for the young. Juvenile *S. macrochir* have a higher tolerance of low DO than adults, and remain on the spawning grounds up to a length of 18 to 20 cm. Marshall (1979b) gives egg numbers ranging from 1,000 to 1,500 in 16 to 27 cm SL female *S. macrochir*.

S. andersonii, a larger-growing species (males up to 3.2 kg) occurs widely except in small streams and is found in all types of habitat, but it is a shy fish which likes to hide in deep pools. Though it takes the same food as *S. macrochir*, it appears to be less specialized and will also eat aquatic and terrestrial insects and small Crustacea. The female mouthbroods, and seems to produce only one brood a year, between November and January. The eggs are large (374 to 593 eggs in females of 17 to 25 cm TL; Mortimer 1960).

T. rendalli, widely distributed and abundant throughout the Upper Zambezi, moves up tributary rivers and onto the floodplain, but spawns once in the dry season before leaving the river as well as on the floodplain; juveniles in tributaries continue to move upstream. This species prefers water with dense growths of aquatic plants. In addition to macrophytes and detritus, it eats aquatic and terrestrial insects. It grows to 1.4 kg. A multiple spawner, it breeds during the rains between October and February; the nest is a series of small holes made in shallow water where both parents guard eggs and young.

The smaller *T. sparrmanii* (growing to 0.25 kg in rivers—the largest, up to 25 cm in Lake Young) is the commonest cichlid in the Upper Zambezi and distributed throughout the system; it prefers quiet water with good weed cover, in riverine, swamp and lake habitats. It is a fairly omnivorous species, feeding primarily on periphyton, aquatic plants, detritus and algae, but Crustacea, insects (terrestrial and aquatic) and even worms and fish may be eaten. A multiple spawner, batches of eggs are produced between October and February, both parents guarding the eggs and young. In Lake Young Ricardo-Bertram (1943), who described the spawning behavior there in shallow water, considered that suitable breeding grounds with sandy bottom were very limited, and there was great intraspecific competition for nest sites, the nests almost touching one another.

Predators on these Upper Zambezi cichlids include piscivorous cichlids, *Serranochromis* spp. (though these feed mainly on cyprinids and cyprinodonts). The characoid *Hydrocynus vittatus* takes many cichlids and its

presence appears to be a factor limiting cichlid populations. Underwater observations have confirmed that cichlid distribution in the openwaters of the main rivers is limited to those tilapia which have managed to reach a size large enough (c.19 cm TL) to withstand predation by *Hydrocynus*. In the Kafue *Hepsetus odoe* is the common openwater predator, but in the Upper Zambezi *Hepsetus* is apparently restricted by competition to habitats not frequented by *Hydrocynus*, such as lagoons, backwaters and smaller tributaries. Bell-Cross (1974) commented that in years of poor rainfall, when the main river is confined between sandy banks for most of the year and the isolated floodplain pools, which serve as reservoirs for tilapia stocks, dry up, the predation on juvenile and small adult cichlids must be extremely severe. Preimpoundment studies on the Kafue floodplain suggested that predation is particularly high at two periods a year: for tilapia in the rivers in the dry season, and for juvenile fishes as the floodplains dry up, a time when piscivorous fishes *(Hepsetus* and *Clarias)* and the numerous birds and other animals can catch them very easily (Williams 1971).

The preimpoundment survey for Lake Kariba in the Middle Zambezi showed *S. mortimeri* (then called *S. mossambicus*) to be the commonest tilapia, but not nearly as abundant as *Labeo, Distichodus, Hydrocynus* and *Alestes*. The tilapia hugged the shore or lived in vegetation rather than in openwater, the juveniles in very shallow water. Some *T. rendalli* (then called *T. melanopleura*) lived in weedy shallows. In an attempt to provide a more openwater-living species the new Kariba lake was stocked with *S. macrochir*, known in Lake Mweru to live in openwater, but in the event stock was taken from the nearby Kafue, so was what was later known to be the 'volcano-nest' subspecies, not the 'star-nest' one used to openwater conditions. In the four months after dam closure in 1959 over 11,000 fingerlings of *S. macrochir* and *T. rendalli* were stocked. For many years these *S. macrochir* were not seen; many of the stocked fish were apparently consumed by *Hydrocynus* in the new lake, a piscivore not previously encountered by the Kafue fishes (Van der Lingen 1973). It was the indigenous *S. mortimeri* which thrived and underwent a population explosion in the new lake, becoming very abundant within three years. Recently *S. macrochir* have reappeared and are slowly increasing in numbers (Bowmaker et al. 1978). In Lake Kariba, after the flooded terrestrial vegetation rotted (by 1963) there was a hiatus before the establishment of rooted macrophytes, and tilapia numbers then fell until these were established (Bowmaker et al. 1978). Perhaps these recently found *S. macrochir* came from upstream, for *S. andersonii* also appeared for the first time (in 1971) when conditions had been altered by the new lake and there was cover for the fish.

In Lake Kariba, Donnelly (1969) found that juveniles less than 10 cm TL of both *T. rendalli* and *S. mortimeri* lived in water less than 30 cm deep, the 'primary nurseries' on gently sloping shorelines. Fish of 11 to 19 cm TL (age one year) tend to leave these for adult habitats, though they are not sexually mature till at least a year later. *S. mortimeri* over 20 cm TL live in a variety of habitats and in water up to 15 m deep. *T. rendalli* is confined to macrophyte beds, though adults return to shallows to breed, or during a rise in lake level to feed on decomposing grasses. These Kariba tilapias breed throughout the year, but with spawning peaks from October to

December. Their nesting sites are ecologically distinct. *T. rendalli* nests along the lake margins in water 60 to 100 cm deep, sometimes in colonies, the parents depositing the alevins in pits. The *S. mortimeri* nests appear to be in water 4 m deep. The juveniles move from the nurseries into deeper water at night, but in Lake Kariba tilapia keep near weed cover till 17 to 19 cm TL (though in dams which lack *Hydrocynus*, tilapia schools of all sizes mingle at varying depths). The largest tilapia in *Hydrocynus* stomachs were 18 cm TL. In Kariba *Hydrocynus* seldom enter water shallower than three times their own length; small *Hydrocynus* taken in the primary nursery areas were still feeding on invertebrates. Other piscivores here are the catfishes *Clarias gariepinus* and *Eutropius depressirostris; Mormyrus deliciosus* also forage in the deep nurseries. The combination of active predation (mainly by *Hydrocynus)* and fluctuating water levels has enhanced the importance of submerged plants in providing cover for tilapias in Lake Kariba.

The Lower Zambezi is the type habitat for *S. mossambicus*, now a circum-tropical pond fish. Bell-Cross (1976) described this species as an omni-vorous feeder, taking plankton, algae, aquatic and terrestrial insects, shrimps and vegetable matter. A polygamous mouthbrooder, several broods are produced during the summer (starting about September but varying with water temperature). Some move up tributaries to spawn. The most thorough ecological studies of this species in natural waters are those made in Lake Sibaya (Kwazulu, South Africa).

4. LAKE SIBAYA

S. mossambicus lives in Lake Sibaya with *T. rendalli swierstrae* and *T. sparrmanii* (see Bruton 1979). *S. mossambicus* nests on terraces in open, shallower water than that used by the other two species, whose nests are among macrophytes. Male *S. mossambicus* move in to establish territories in September, when the water temperature first exceeds 20°C. There may be up to 13 nests per 1,000 m^2. There is intense intraspecific conflict between males prior to excavating nests. Small males (10 to 13 cm SL) are repulsed and returned to deeper water; they may establish nests if the lake level rises, but not at low lake level. After a brief active courtship the female leaves the nest and mouthbroods eggs and fry for 14 to 22 days in the macrophyte beds. The fry when about 9 mm SL are released in very shallow water (10 cm deep) along barren sandy shores or in marginal pools. They occupy pro-gressively deeper water by day as they grow larger, but all move into deeper, warmer water at night, where they lie motionless. The juveniles, which return to the shallows when the temperatures first exceed those of the main lake in the morning, form small schools (up to 20 fishes) on terraces by day for feeding; the composition and size of the feeding groups change constantly.

Scale studies have shown that males grow faster than females after the first year, as discussed below. This Lake Sibaya *S. mossambicus* population is breeding precociously, then growth deceleration occurs and the final size is smaller than in other natural systems in southern Africa, for reasons discussed by Bowen (this volume).

The large adult catfish *Clarias gariepinus* feeds almost exclusively on *S. mossambicus* in this lake (as studied in some detail by Bruton), and both juveniles and adults are preyed on by the numerous birds: cormorants, darters, herons, kingfishers, fish eagles and ospreys.

5. PANGANI RIVER SYSTEM

Another east-flowing river, the Pangani in Tanzania, has two endemic tilapias, *S. pangani* with a subspecies *S. pangani girigan* in Lake Jipe where it is sympatric with *S. jipe*. In Lake Jipe *S.p. girigan* feeds on water weeds *(Najas)*; the former pharyngeal teeth of *S. jipe* suggest it consumes smaller particles (Lowe (McConnell) 1955a). A new man-made lake on this Pangani system, Nyumba ya Mungu reservoir completed in 1965, studied by Bailey and Denny (1978) and Bailey et al. (1978) has three species of *Sarotherodon* (the indigenous *S. pangani* and *S. jipe*, introduced *S. esculentus*) and *T. rendalli*. These indigenous *Sarotherodon* grew to a large size, about 50 cm TL and 1.75 kg (much larger than previously recorded from Lake Jipe). They were found mainly in the littoral areas of the southern part of the lake, where *S. jipe* clearly predominated. The *S. esculentus* lived in the southern deeper offshore waters, where it consumed phytoplankton. *T. rendalli* found in shallows close inshore to fringing reed swamp was surprisingly rare in the north of the lake which has marked development of macrophytes. *S. jipe* and *S. pangani* were chiefly browsers of periphyton and bottom deposits (phytobenthos). In both these species males grew to a much larger size than females (*S. jipe* males to 48 cm, females to 27.5 cm; *S. pangani* males to 47 cm, females 31.5 cm TL). In Lake Jipe and the Pangani River, where males were much more numerous than females in catches of these species, male maturation and maximum sizes were also larger than in females (Lowe (McConnell) 1955a).

6. MALAGARASI SWAMPS

Two endemic species of *Sarotherodon* live sympatrically in the Malagarasi swamps (over 1,100 km^2) which drain westwards into Lake Tanganyika: *S. karomo*, whose breeding behavior in the swamps was studied by Lowe (McConnell) (1956a), and a new species (then referred to as a form of *T. nilotica*). These breed at different times of year. *S. karomo*'s teeth appear beautifully adapted for rasping epiphytic algae off the abundant water lilies and other macrophytes.

7. LAKE MALAWI

Lake Malawi has a unique species flock of four endemic *Sarotherodon* species adapted for openwater life: *S. squamipinnis*, *S. saka* and *S. lidole* distributed round the lake where there are areas of water less than 40 m deep, and *S. karongae* apparently confined to the northern end of the lake (Lowe 1952, 1953). These fish, often in mixed schools living in midwater,

feed on phytoplankton. *S. lidole*, the most openwater-living, may move considerable distances to do so (80+ km), the others may turn to bottom feeding if phytoplankton is scarce. These tilapias have evolved relatively short annual breeding seasons at staggered times. Season and place of spawning, reinforced by differences in colors of the breeding males, keep the species distinct. *S. saka*, which has a black breeding male, spawns from August to November, the hot weather before the rains in relatively shallow water (4 m deep) near macrophyte beds, off weedy or sandy shores; brooding females move into weed or reed beds. *S. squamipinnis*, the non-breeding fish of which are scarcely distinguishable from *S. saka*, spawns in the rainy season, December to February, in deeper water (about 16 m), generally off more sandy, open shores; brooding females also retire into the weed and reed beds; the breeding male is sky blue with a white head which is clearly visible to the ripe females which swim above the nesting arenas (see Berns et al. 1978). *S. lidole*, like *S. saka*, also has a black breeding male and breeds before the rains, but in much deeper water or off open sandy, clean weedless beaches.

Fecundity appears to be much reduced in these Malawi *Sarotherodon*, by late maturation (not spawning till three years old), the production of but one brood a year (rarely two?), and of relatively few but large ova (370 to 549/fish in *S. squamipinnis*), the young being brooded to a larger size than in other tilapias (to 30 mm TL in *S. squamipinnis*, 52 mm in *S. lidole*). In Lake Malawi, *S. saka* and *S. squamipinnis* mature when about 25 cm TL, *S. lidole* at 28 cm TL, with no size difference between the sexes; in aquaria they can mature at a smaller size (10 cm SL—for details of aquarium behavior see Berns et al. 1978).

S. shiranus, of different stock, lives in a more inshore zone of Lake Malawi and has a more extended breeding season, but mainly December-January. *T. rendalli* appears to be confined to vegetated lagoons round the lake.

Malawi tilapias show adaptations to inhabit increasingly openwater conditions, from the inshore-dwelling *S. shiranus* to the most offshore living *S. lidole*, viz: (a) the food contains a higher proportion of phytoplankton rather than bottom diatoms and bottom debris; (b) the tendency to collect in small, close schools increases; (c) the amount of movement increases, *S. shiranus* populations being very localized and *S. lidole* far-ranging fish; (d) the young are brooded to an increasingly large size; (e) the rate of growth in length appears to increase, but growth in weight for length decreases, giving a more streamlined form in openwater species. Each species spawns in the clearer water end of its range, but broods young in the richer, greener water. The brooding females carry the eggs and young inshore, from spawning to brooding or nursery grounds. It is possible to tell from the characteristics of the water, such as clarity, color, and whether the shore is of mud, silt, sand or rock, shore vegetation, etc., which species are likely to predominate off a particular beach, though mixed catches are often taken. *S. shiranus* predominates in muddy swampy areas, *S. saka* off sandbanks near weedbeds close to swampy *(Papyrus)* and reedy *(Phragmites)* shores, *S. squamipinnis* off more open beaches with *Phragmites*, and *S. lidole* off open, clean, clearwater beaches or where the bottom shelves steeply, and out into openwater.

8. LAKE CHILWA

Lake Chilwa, lying southeast of Lake Malawi, has a subspecies of *S. shiranus*, *S. s. chilwae* as a predominant member of its very small fish fauna (which includes *T. sparrmanii*, one species of *Barbus*, one of *Haplochromis* and two of *Clarias*). Mass mortalities of the fish occurred when this lake virtually dried out in 1965-68 (see Furse et al. 1979). Tilapia populations started to decline ahead of the main drying out—possibly due to sandy shallows used as spawning grounds being reduced in area (which seems to happen about every six years or so in this lake). Populations of dwarfed tilapia survived in the permanent streams of the basin and pools in the marshes; these fish were able to repopulate the lake when it refilled. But aided by stocking, it still took three years before tilapia numbers were high again. This subspecies is smaller in adult size than *S. shiranus* in Lake Malawi, matures earlier, produces smaller and more numerous eggs, and has two main spawning periods in an extended breeding season. It also matures more quickly in freshwater when rains come again. In Lake Rukwa in Tanzania, Ricardo (1939) had found *S. rukwaensis* to have dwarf populations in river pools near the lake after it dried out. These appeared adapted to repopulate the lake after it refilled.

9. WEST AFRICAN CRATER LAKES

Endemic lacustrine tilapias have also evolved in small crater lakes in west Africa. Lake Bosumtwi (Ghana), whose fish communities have been studied very comprehensively by Whyte (1975), has three tilapias, *Sarotherodon galilaeus multifasciatus* (an endemic subspecies), *Tilapia discolor* (endemic and very like *T. zillii*), and *T. busumana*. The adult *S. g. multifasciatus* live in midwater feeding on phytoplankton, here mainly blue-green algae and desmids. Unlike other tilapias (and *S. galilaeus* in Lake Chad) this species is said to feed at night, between 6:00 P.M. and 5:00 A.M. undergoing a diurnal vertical migration to do so; sinking to 30 m by day and rising to surface waters at dusk to feed. Adults of both *Tilapia* species are bottom dwellers. *T. busumana* feeds mainly on aufwuchs on stony and sandy substrates by day and moves into deeper water (3 to 7 m) by night. *T. discolor* feeds mainly on periphyton on reeds *(Typha)* and water plants, and on aufwuchs, but feeds mostly by night, moving into deeper water (5 to 10 m) by day. The juveniles of all three species are surface dwellers round the lake edge, using different foods from their adults; they all share the allochthonous insects on the surface, eaten together with phytoplankton in juvenile *S. g. multifasciatus* and *T. discolor*, while *T. busumana* juveniles take aufwuchs instead of phytoplankton. There is thus separation in feeding habits between species, between juveniles and their adults, and also in vertical use of space, juveniles living in surface waters, *S. g. multifasciatus* in midwater, both *Tilapia* species at the bottom, one feeding by day the other by night.

Other cichlids in Lake Bosumtwi are *Chromidotilapia guentheri*, a benthos feeder in which the juveniles take the same food sources as the adults, and *Hemichromis fasciatus*, the juveniles of which share the allochthonous fauna at the lake surface with juvenile tilapia, as do the juveniles of the catfish *Heterobranchus isopterus*. Adult *Hemichromis fasciatus* and *Heterobranchus isopterus* are both piscivorous, eating juvenile tilapias. Once the tilapias reach a certain size they are relatively safe from predation.

The breeding places and habits of these three tilapias also segregate them. Most *S. g. multifasciatus* spawn between November and April (though some ripe fish may be found at any time of year). Nests are made at 1 to 3 m in the littoral zone over a *sandy* substrate, among reed beds *(Typha australis)* or in openwater; eggs are brooded by both parents and brooding fish may be found 5 to 20 m from shore. Of the two *Tilapia* species, *T. discolor* has a protracted breeding season from December to May, making nests with axillary pits at 1 to 7 m in the littoral zone over *muddy* bottoms (240 to 700 eggs per nest). *T. busumana* peaks from October to February (though some are ripe at any time of year), making a bowl nest in permanent streams and the littoral zone over *sandy* or stony shores in 10 cm to 1 m water (60 to 280 eggs per nest). The nests are of very different form: the *T. busumana* nest is a simple bowl; the *T. discolor* nest has axillary pits around the main nest. These tilapias do not seem to grow very large.

In west Cameroons the oligotrophic Lake Barombi Mbo has four endemic species of *Sarotherodon*, of which two species, the *galilaeus*-like *S. steinbachi* and *S. lohbergeri* share organic debris obtained in shallow water, from sandy areas by *S. steinbachi* and aufwuchs sucked off rocks by *S. lohbergeri*. Both species also probably take some food when skittering at the surface (Green et al. 1973). The other two species (*S. linelli* and *S. caroli* probably related to the *S. melanotheron* group) share phytoplankton-feeding a meter or so below the lake surface; possibly differences in breeding seasons help to keep these two species apart (Trewavas et al. 1972). Another Cameroon crater lake, Lake Kotto is eutrophic with a dense bloom of blue-green algae, food of three tilapias, *S. galilaeus*, *T. mariae* and the endemic *T. kottae*. The two *Tilapia* species both take some bottom food (invertebrates in *T. kottae*) as well. This lake lacks the aufwuchs-feeding niche found in the oligotrophic Barombi Mbo. The phytoplankton eaten by adults is so abundant in Lake Kotto that tilapia numbers are more likely to be limited by availability of food and feeding habitats for the young stages which live and feed inshore (Corbet et al. 1973).

10. KENYA RIFT SODA LAKES

Lake Magadi in the Kenya rift, a very alkaline lake (pH 10.5), with hot springs (43°C), and a high specific gravity (1.01 to 1.03) is inhabited by a little *Sarotherodon*, *S. alcalicus grahami* (formerly known as *S. grahami*) whose ecology and behavior was studied by Coe (1966). These fish browse on blue-green algae on the stony bottom, together with small crustaceans (copepods), and dipteran larvae, in the warm shallows near the hot springs, moving into deeper water at night when the surface temperature begins to

fall. High temperatures (above 32°C) appear necessary for the males to assume breeding colors in these fish, and at high temperatures they breed almost continuously. Females move to brooding areas, and somehow manage to take some food while brooding; they release the brooded young in shallow nursery areas. Here the young escape predation by adult fish, but are open to attack from numerous kinds of birds, especially pelicans. There is also some cannibalism of eggs.

This species was introduced into Lake Nakuru around 1960, where it is now one of the main herbivores and has altered the whole ecology of the lake (Vareschi 1979). Fish distribution here is very patchy. At noon they concentrate near the shore, at night offshore, a migration pattern probably reflecting preference for high temperatures. They feed primarily on the very dense cyanophyte *Spirulina platensis*, 80% of the tilapia living in the top 100 cm where they feed. The total ichthyomass of *S. alcalicus* in this lake was estimated to increase from 90 t (dry weight) in 1972 to 400 t in 1973 (2.1 g/m^2 to 10.2 g/m^2). The main impact of this introduction on this lake has been to increase diversity by extending food chains to fish-eating birds. Before the introduction such birds only occasionally visited the lake, now over 50 species are recorded there, of which the great white pelican *(Pelecanus onocrotalus roseum)* predominates. Adult pelicans are estimated to eat 1,330 g (fresh weight) of tilapia a day, the young some 770 g/day from hatching to fledging. Calculations suggest pelicans remove 16 to 20,000 kg fresh weight of fish per day from the lake. Since they nest on a neighboring lake, taking fish there to feed their young, they have been calculated to export some 13 t phosphorus a year from the Nakuru system.

11. WEST AFRICAN COASTAL LAGOONS

In west African coastal lagoons *Sarotherodon melanotheron*, a species which can withstand high and changing salinities, has been studied as a possible candidate for fish culture with mullet *(Mugil* sp.) by Pauly (1976). This tilapia only grows to 25 cm TL, the adults feeding on bottom mud (30% organic content, 1.2 Kcal/g calorific content). Daily food intake of a 20 g fish was estimated to be 1.5 g (dry weight) and the calorific assimilation 900 cal/day. Juveniles take zooplankton and phytoplankton. *S. melanotheron* is a male mouthbrooder (whose behavior has been much studied in aquaria under the name *T. macrocephala* or *T. heudelotii*, e.g., papers by Aronson 1951). In the field this species breeds throughout the year with equinoxial peaks. Parasitism is low, attributed to the varying salinity in the lagoon.

12. EXOTIC COMMUNITIES

One of the best-studied examples of the role of a tilapia in an exotic fish community is that of *S. mossambicus* in Plover Cove Reservoir, Hong Kong, where an arm of the sea has been turned into a freshwater storage reservoir (Hodgkiss and Man 1977a, 1977b; Man and Hodgkiss 1977a, 1977b).

An initial twenty species in the reservoir fish fauna included marine species which survived but did not reproduce, rice paddy and riverine fish from the drainage basin, and Chinese carps stocked in 1967-71. The *S. mossambicus* were escaped pond fish which established themselves and soon became the dominant species in gillnet catches. Chiefly a detritus-feeder, the tilapia here had the most diverse food spectrum of any species studied, thus proving to be a good reservoir fish since almost all items were exploited, and when certain items were scarce a change to others was possible. Tilapia also helped to control algae and chironomids, and to remove nutrients and decaying organic detritus from the mud, thus indirectly helping to reduce algal growth. Earlier studies on *S. mossambicus* in Indonesia had provided much basic information about this species in Asian waters (Vaas and Hofstede 1952).

In Lake Moyua in Nicaragua (Central America) the stocked *S. mossambicus* matures between 12 and 14 cm (90 to 100 g) when 5 to 6 months old. This lake lacks piscivorous fishes, but numerous water birds feed on the tilapia fingerlings.

13. HYBRIDIZATION

Where several tilapia species share a water body, nesting areas are usually distinct in place (depth or type of bottom) or time. In substrate-spawners the elaborate courtship behavior probably helps to prevent any hybridization. Courtship behavior is generally much briefer in the mouthbrooders. Cases of hybridization, or suspected hybridization in natural waters, due to introductions include those of:

S. niloticus x *S. spilurus niger* in Lake Bunyoni (both introduced)(Lowe-McConell 1958)

S. niloticus x *S. esculentus* in Lake Nkugute (both introduced) (Lowe-McConnell 1958)

S. niloticus (introduced) x *S. variabilis* (indigenous) in Lake Victoria (Welcomme 1966)

T. zillii x *T. rendalli* (both introduced) in Lake Victoria (Welcomme 1966)

S. amphimelas (indigenous) x *S. esculentus* (introduced) in Lake Kitangiri (Trewavas and Fryer 1965)

S. s. niger x *S. leucostictus* (both introduced) in Lake Naivasha (Elder et al. 1971, who considered how these hybrids fitted into the ecological zonation in the lake). These hybrids, abundant in 1961, following introductions in 1956, had disappeared by 1974 (Siddiqui 1977b).

Tilapia Growth Rates in Natural Waters

The most reliable growth rate data come from waters with marked seasonal changes which affect the biology of the fish, leaving marks on scales, bones, otoliths, etc., and where seasonal spawning allows length-frequency mode progressions to be traced in the young fish. Examples are given in Figure 4, based on data from nilotic tilapias by Blache et al. (1964), Ben-Tuvia (1959), Daget (1956), Jensen (1957), Lauzanne (1978), Payne and Collinson (in
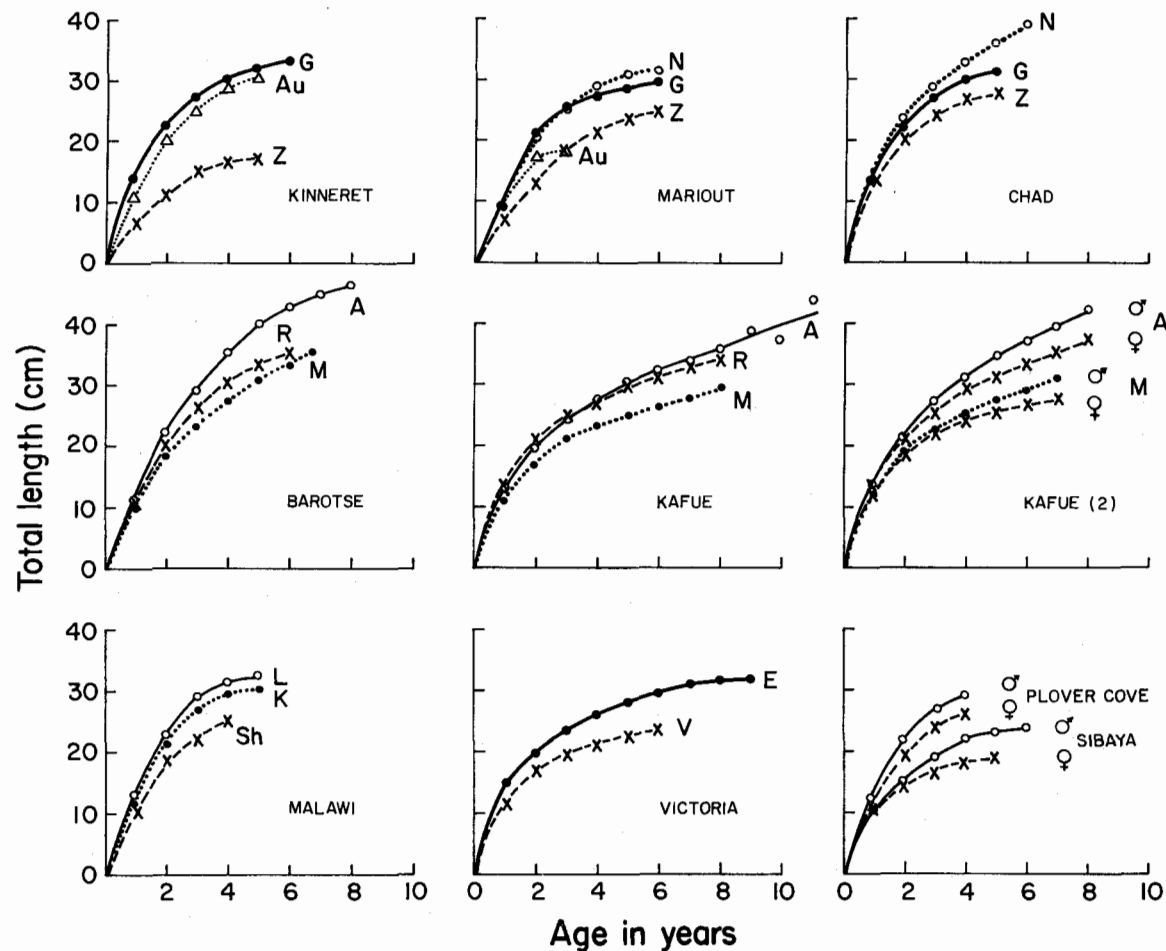
Figure 4. Comparison of tilapia growth rates in various natural waters (for sources of data see text). Nilotic species: *Sarotherodon niloticus* (N), *S. galilaeus* (G), *S. aureus* (Au), *Tilapia zillii* (Z), from Lakes Kinneret (Israel), Mariout (Egypt) and Chad. Zambezi species: *S. andersonii* (A), *S. macrochir* (M), *T. rendalli* (R), from Barotse and Kafue floodplains. Lacustrine species: *S. lidole* (L), *S. saka* (K), *S. shiranus* (Sh) from Lake Malawi; *S. esculentus* (E), *S. variabilis* (V) from Lake Victoria. Male and female curves are shown separately for Kafue (2) and for *S. mossambicus* from Lake Sibaya (S. Africa) and Plover Cove Reservoir (Hong Kong).

press), from Zambezi tilapias by Duerre (1969), Kapetsky (1974), Dudley (1974), for *S. mossambicus* by Bruton and Allanson (1974), Hodgkiss and Man (1977b) and from the Great Lakes from Lowe (1952) and as summarized by Fryer and Iles (1972, Table 14). Total lengths were calculated from standard length data for Lakes Chad and Sibaya.

Growth data for the nilotic tilapias all indicate that within a water body *S. niloticus* grows to a larger size than *S. galilaeus* (though *S. galilaeus* is deeper bodied so weight differences are not so marked): both grow faster and larger than *T. zillii*. *S. aureus* also grows faster and larger than *T. zillii*, but not as large as *S. galilaeus*. Payne and Collinson (in press) have suggested that the extended breeding season of *S. aureus* in Lake Mariout (Egypt) slows somatic growth, for here *S. niloticus* and *S. aureus* grow at comparable rates until they mature at one year old, after which *S. niloticus* with its more restricted breeding season grows faster and larger than *S. aureus*.

In riverine populations *S. niloticus* males grow larger than females (Banks et al. 1965). This also occurs in lagoons and ponds as we have already seen (Figure 1), but in large lakes, where growth is good, males and females may mature at, and grow to, comparable sizes. This phenomenon has also been noted in *S. esculentus*, where growth of the two sexes was not significantly different in lake populations (Lowe (McConnell) 1956b; Garrod 1959). Again, in *T. zillii* in Lake Kinneret, Israel, males and females were of comparable sizes (maturing at 13 to 14 cm) though in the Dor aquaculture station ponds, where they mature at a smaller size than in the lake, males grow faster than females, even though the pond fish grow faster than the lake fish, achieving 18 to 20 cm in one year instead of two years as in the lake (Chervinski 1971).

All three Zambezi tilapias *(S. andersonii, S. macrochir* and *T. rendalli)* grow faster and to a larger size on the Barotse floodplain than on the Kafue floodplain (Figure 4). But on both floodplains *S. andersonii* grows fastest and to the largest size, followed by *T. rendalli*, while *S. macrochir* does not grow as fast or as large. It is interesting that in this case the *Tilapia (T. rendalli)* grows better than one of the accompanying *Sarotherodon (S. macrochir)*, unlike the soudanian region where all the *Sarotherodon* grow better than the *Tilapia (T. zillii)*. The Zambezi region does, however, have an additional smaller *Tilapia (T. sparrmanii)*.

In natural waters, *S. andersonii* rarely matures when less than three years old (at 27 cm TL); a few *S. macrochir* spawn at the end of their first year (when 13 to 16 cm TL). In *T. rendalli* some fish start to spawn in their second year (when 17 cm TL). In the Zambezi, *Sarotherodon* sexual differences in size become marked after maturation, female growth slowing down more than male growth, and all the large fish are males. *T. rendalli* showed no sex differentiation in growth for the first two years. After the sixth year these tilapias grew very little.

From the Kafue, tilapia scale rings permit growth to be backcalculated enabling variations in growth from year to year in the different age groups to be examined in relation to environmental factors such as water temperatures and flood levels. Such data for fifteen years examined by Dudley (1974, 1979) indicated that: a) there are significant variations in growth rate from year to year for most age groups of all three species and b) growth

of the young and extent of flooding are positively correlated, suggesting that high flooding would increase growth and survival (Dudley 1974). Later studies, however (Dudley 1979), indicated that year-classes are larger following low-flood years. These *Sarotherodon* will not spawn if the water is too deep, but Dudley considered that high year-classes following low-flood years might be due to the *Sarotherodon* entering a stressed condition and breeding at a smaller size in dry, low-flood years. In support of this view he found ripe females of *S. andersonii* of 18 cm TL in 'dry' years, compared with a minimum breeding size of 26 cm TL in high-flood years (Dudley 1979).

The relative growth rates of young and older fish may differ in different lakes. For example, *T. rendalli's* first year growth appeared to be slower in Lake Kariba than on the Kafue floodplain, but the Lake Kariba population nearly caught up in weight in the fourth year and in length in the fifth year (Kapetsky 1974).

For *S. mossambicus* in Lake Sibaya, South Africa, growth rates were lower and fell off more rapidly (Bruton and Allanson 1974) than for this species in Plover Cove Reservoir, Hong Kong (Hodgkiss and Man 1977b) (Figure 4). The precocious breeding in Lake Sibaya has been explained in terms of food quality (Bowen, this volume), the adults being in poor condition as the food available to the deeper-living adults is less nutritious than that available to the juveniles living in the warm shallows. Female growth rates fell off more rapidly than male growth rates in both places. In Lake Sibaya, females may breed at one year (8 to 10 cm SL), males when one or two years old (12 cm SL); maximum age was 7 to 8 years, the largest males 23/29 cm SL/TL, the largest females 18/22 cm (Bruton 1979).

Tilapia Production In, and Yield From, Natural Waters

For natural waters we have to distinguish clearly between the biological production, i.e., the total elaboration of fish tissue during a given time interval (generally taken as a year), and the yield, i.e., the harvestable part of the production. The catch, sometimes loosely called 'fish production,' is really a yield. Ecologists considering energy transfers from one trophic level to another are concerned with total production (all the fish tissue produced in the time interval, whether or not it survives to the end of that time), whereas fishery biologists are more interested in the available production (the amount of fish tissue surviving at the end of that time). In natural waters the yield (catch) is generally only a small proportion of the available production, depending on the selectivity and efficiency of the fishing method (both the gear used and how much the fish move about). Also, due to the many causes of mortality in natural waters, the available production may be much less than the total production (Table 2 and Figure 5 of data from the Kafue floodplain show this well). In ponds, where fish are cropped by draining the pond, the yield reflects the available production much more closely, and, if predation and diseases are controlled, available production may be much nearer to total production than it can be in natural waters.

Analyses of catch statistics are used for determining whether a fishery

is declining, but for computations of production in natural waters growth rate and biomass data are essential. The relatively few comprehensive studies of tilapia production yet made in natural waters include those for the Kafue floodplain and Lake Kariba, both in the Zambezi system, and for the equatorial Lake George in Uganda. For these sites the computed abundances of the fish, their biomasses, production, yield and turnover are indicated in Table 2.

Table 2. Examples of tilapia *(Tilapia* and *Sarotherodon)* production, yield and turnover rates in natural waters.

|	Abundance n/ha	Biomass kg/ha B	Production kg/ha/yr Total A	Production kg/ha/yr Available P	Yield kg/ha/yr Y_A	Yield kg/ha/yr Y_P	Turnover A/B
1. Kafue eastern floodplain							
lagoons (31 spp.)	11,053	680					
channels (24 spp.)	3,894	333					
weighted mean (all spp.)	8,191	541		c. 1,000			
3 spp. tilapia lagoons	2,282	364					
3 spp. tilapia channels	2,351	246					
3 spp. tilapia mean		317					
T. rendalli (lagoons:channels)	706: 187	125	198	110	18	8	1.59
S. macrochir	737:1,327	145	145	96	39	23	1.0
S. andersonii	839: 837	147	119	92	23	15	0.75
2. Lake Kariba							
20 spp. (revised estimate)	—	827	1,224	720	400	202	
of these 'preferred' spp.							0.7
'accompanying' spp.							2.3
mean turnover ratio (revised)							1.48
T. rendalli (revised estimate)	957	38	44	30	19	12	1.15
S. mortimeri (revised estimate)	2,122	216	178	133	139	103	0.83
3. Lake George (Uganda)							
All (10+) spp. mean		220 (60-900 inshore)			catch 137		
S. niloticus (offshore:inshore)	63:1,094	37(?) mean			catch 111		
S. leucostictus (offshore: inshore)	7: 649	5(?) mean					
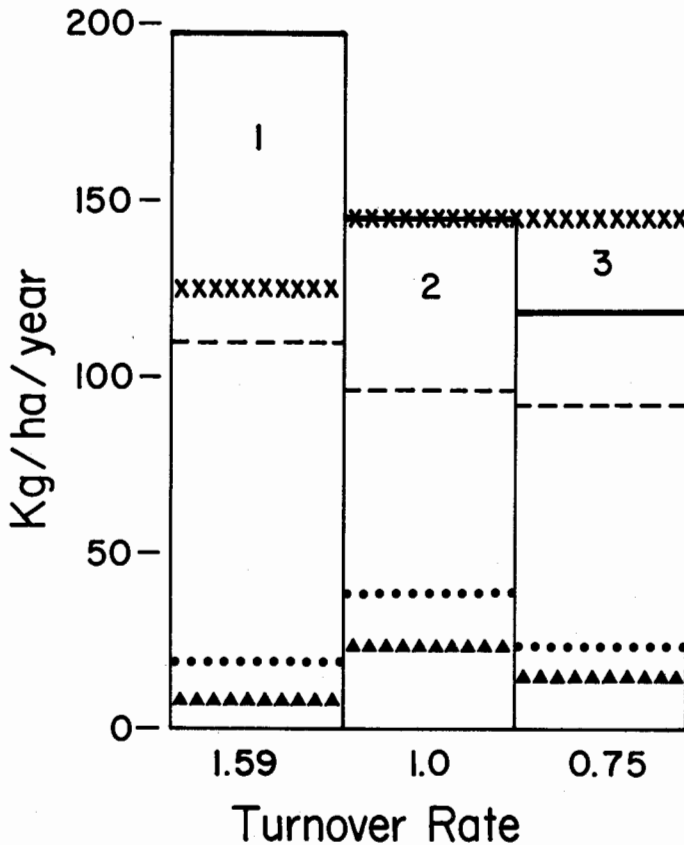
Figure 5. Kafue floodplain production of: 1, *T. rendalli*; 2, *S. macrochir* and 3. *S. andersonii*. Total production (———), Biomass (XXXXX), Available production(— — —), Yield (available) (● ● ● ●), Yield (production) (▲▲▲▲▲): see Table 2 and text (data from Kapetsky 1974).

The Kafue eastern floodplain (38,880 ha) is part of the 6,000 km² Kafue floodplain lying at 15° 30′S, 900 m, which produces an annual crop of 5,000 t of fish, over half of the catch (59%) being three tilapia species: *S. andersonii*, *S. macrochir* and *T. rendalli*. The building of the Kafue Gorge hydroelectric dam, closed in 1971, stimulated pre- and post-impoundment studies. Here fish biomasses were determined by chemofishing 25 sample areas (Lagler et al. 1971; Kapetsky 1974). First estimates ranged from 64 kg/ha in grass marsh, 337 kg/ha in open lagoons, 337 kg/ha in river

channels, to 2,682 kg/ha in vegetated waters. The areas of different types of habitat, at low and high water, were calculated from planimeter measurements on 1:50,000 maps. Meanwhile tilapia growth rates were determined by scale ring analyses (Chapman et al. 1971; Kapetsky 1974). *S. macrochir* and *T. rendalli* were considered harvestable at the end of the second year, *S. andersonii* end of third year.

The resulting computed biomass, production (total and available), yields and turnover rates of the tilapia populations on the eastern floodplain (Table 2) are shown in Figure 5. This brings out clearly that the total production is considerably greater than the biomass present in *T. rendalli* (turnover rate A/B, 1.59), equal to the biomass in *S. macrochir* (A/B, 1.0), and less than the biomass in *S. andersonii* (A/B, 0.75).

Kapetsky then computed a yield for the whole Kafue floodplain (121,000 ha), weighting for areas of lagoons and channels. This gave an estimated total tilapia production of 70,000 t/yr from the whole floodplain, total yield 13,000 t/yr and available yield 7,000 t/yr. Present catch is 5,000 t/yr of all species (Dudley and Scully 1980), so if computations are realistic it looks as though only about half the possible tilapia crop is being caught (my interpretation of the findings).

The Kariba dam across the Zambezi was closed in December 1958. Here chemofishing in lake coves was used to determine fish biomasses (Balon 1974). The calculations of production etc., for each species and the whole lake had, however, to be revised (Mahon and Balon 1977, whose revised estimates for total production, available production, total yield and available yield, all species, were 38%, 105%, 67% and 107% respectively of the original estimates). Tilapias were a much less important part of the catch (20 species considered) than on the Kafue floodplain. However, *S. mortimeri* (then called *S. mossambicus*), though present at a 'low population density' (2,122 fish per inhabited ha), had a mean biomass of 215.7 kg/ha and was estimated to give the third highest total production (178.5 kg/ha/yr) (after a mormyrid and *Alestes* sp.), and the highest total yield (139 kg/ha/yr) of the nine economically preferred species. *T. rendalli* was much less abundant, but had a higher turnover rate than *S. mortimeri* (1.15 compared with 0.83).

Lake George (Uganda). In an attempt to determine how this shallow equatorial lake, mostly less than 3 m deep (250 km^2) continues to produce such good catches of tilapia *(S. niloticus*, which forms 80% of the catch, and *S. leucostictus)* an International Biological Programme team spent six years studying production at different trophic levels (Dunn 1972; Burgis et al. 1973; Burgis and Dunn 1978; Burgis 1978; Gwahaba 1975, 1978). Fish biomasses (of 10 species) were determined using openwater seines; they were computed to range from 60 kg/ha in openwater to 900 kg/ha inshore (mean 220 kg/ha). The determination of fish growth rates proved very difficult in this equatorial lake, but for *S. niloticus* was indicated by length frequency analysis, of a particular cohort of young fish, to be about 1.2 cm/month (Gwahaba 1978). The fish yield based on catch statistics over twenty years fluctuated around a mean of 3,461 t/yr for all (10) species, 2,790 t/yr for *S. niloticus*, equivalent to 137 kg/ha/yr for all species, 111 kg/ha/yr for *S. niloticus*. The weight of fish landed had been maintained but, as already discussed above, the maturation size of *S. niloticus* had

declined (i.e., the numbers had risen). (This high, maintained catch suggests to me that the biomasses to produce these fish must have been considerably higher than recorded here.) This yield is very high for a natural water body, comparable with unfertilized fish ponds.

Lake George was found to have a very high gross primary production $(82,400 \text{ kJ/m}^2/\text{yr})$ made up primarily of the bluegreen alga *Microcystis*, consumed and digested by the tilapia. (Net primary production proved very difficult to determine; respiration rates of microorganisms were very high at the prevailing high temperatures.) The production of the main herbivores *(S. niloticus* and *S. leucostictus* which also took some bottom debris, *Haplochromis nigripinnis* and the cyclopoid copepod *Thermocylops hyalinus)* was computed to be equivalent to 650 $\text{kJ/m}^2/\text{yr}$ (Burgis and Dunn 1978; Burgis 1978), a mere 0.8% of the estimated net primary production. Burgis and Dunn compared this figure with Prowse's (1972) finding that fish production was 1.02 to 1.79% of net primary production in Malacca fish ponds containing tilapia and grass carp. Thus, despite the sustained high fish yield, the Lake George system appears to be inefficient as so little of the high initial primary production is passed on to fish flesh. The reason for this is not clear; it was suggested that perhaps the lake has too few herbivores; fish numbers do not seem to be limited by food here, but possibly they are by availability of suitable spawning grounds in this soft-bottomed lake.

Discussion: Factors Controlling Tilapia Numbers in Natural Conditions

1. PHYSICO-CHEMICAL FACTORS

Physico-chemical events, such as drying up of lakes (as has occurred for Lake Rukwa, Lake Chilwa and much of Lake Chad) have decimated tilapia populations from time to time. The role of deoxygenation, silt stress, alkalinity stress, heat stress and effects of drying out the shallow spawning grounds in the decline of the Lake Chilwa fishes were studied by Furse et al. (1979). Deoxygenation when bottom water was brought to the surface sometimes causes massive fish kills (as in Lake George). Increased alkalinity may kill fishes in the soda lakes and lagoons. Winter temperature drops also kill or stress the fish at high latitudes (as in Hong Kong, Israel). On floodplains, the variations in flooding from year to year affect tilapia survival and growth rates, as has become clear from scale studies backcalculating growth in previous years (Dudley for Kafue fish, Duerre for Barotse fish). But in large lakes biotic pressures may be relatively more important than physico-chemical ones in controlling tilapia numbers.

2. GROWTH AND REPRODUCTION

Tilapia numbers are greatly affected by their ability to switch from growth to reproduction in unfavorable conditions. Though there appear to be some limitations (presumably genetic) to growth possibilities (for instance

T. sparrmanii is basically a small species, *S. andersonii* a large one), in all the tilapias investigated growth varies with the conditions. Certain 'stress factors' evidently switch the physiological state of the fish from growth to reproduction at a smaller size ('dwarfing', 'nanism') and at a younger age than in normal populations, irrespective of the rate of growth to achieve this size. The mechanisms for this are not yet known, but are reflected in the condition (weight for length) of the fish. Pond experiments at Malacca (Chen and Prowse 1964) demonstrated that the size of the inhabited water body influences maturation size and final size in some as yet unexplained way.

Is this ability more marked in species living in habitats likely to dry up? Even species endemic to the Great Lakes of Africa, such as *S. esculentus*, evidently have this ability. In Lake Victoria, *S. esculentus* only matures when two or three years old and at least 20 cm TL, but it can mature at five months old when only 10 cm TL in aquaria (Cridland 1961). The mechanisms for such a switch need investigation. In aquaria fast growth and precocious spawning in *T. zillii* was stimulated by keeping the fish at a high temperature (up to 31°C); changes in illumination had little effect (Cridland 1962).

Field studies have presented a number of clues about the switch: (i) tilapia in poor condition (low weight for length) switch to reproduction at a smaller size than those in better condition (see Figure 2). (ii) In Lake George, Uganda, marked declines in maturation sizes both of *S. niloticus* and of *S. leucostictus* were recorded after twenty years intensive fishing had reduced the general size of fish caught. (iii) In the Kafue, Dudley (1979) found some evidence that *S. andersonii* matures at a smaller size in dry years than in years when the water level remains high at the end of the dry season. (iv) In Lake Sibaya precocious breeding in *S. mossambicus* is associated with decline in food value of the food available to the fishes as they grow and move into deeper water (as discussed by Bowen, this volume). But quite possibly the tilapias are responding to some factors that we are not yet considering.

In addition to (1) the size and age at which the fish mature, tilapia populations are also affected by: (2) the length of the breeding season and number of broods produced a year. This may vary from only one (rarely two) as in Malawi *Sarotherodon* of the *S. squamipinnis* flock (Lowe 1952; Berns et al. 1978) and *S. andersonii* (according to Mortimer 1960), to a succession of broods, as seems more usual. These may be produced either through a defined breeding season, where environmental conditions are more seasonal, or throughout the year as in some equatorial waters; (3) The number of eggs produced at a time ('fecundity') which increases with the size (weight) of the female fish; (4) The egg size which is species-specific, substrate-spawners producing smaller and more numerous eggs than mouth-brooders (Lowe 1955b listed increasing egg size in *T. zillii*, *S. galilaeus*, *S. leucostictus*, *S. niloticus*, *S. variabilis*, *S. esculentus*, *S. karomo*, *S. lidole* and *S. saka*). Egg size shows some latitude, however, as females of dwarf populations produce somewhat smaller eggs than normal sized populations (Lowe (McConnell) 1957, Peters 1963), which helps to counteract the effect of fewer eggs per female in populations with dwarf females; (5) The number of young that can be mouthbrooded, which tends to increase to a

maximum then decrease with increasing size of fish. Thus the 'brooding efficiency' (number of young brooded/number of eggs produced) falls as females increase above a certain size: this aspect has been studied in most detail in *S. leucostictus* by Welcomme 1967a).

The survival of the young depends on many factors. Great variations in survival from year to year have been found in the Kafue populations, which have obscured any effects due to the change from riverine to lacustrine conditions as the new lake filled (Dudley 1979). Under the more climatically stable conditions in the Great Lakes, biotic pressures including predation, competition for suitable spawning grounds, or nursery sites, or food among the juvenile fishes, may be particularly important.

3. PREDATION

Though there has been much discussion on the effects of predators on cichlid speciation (see Fryer 1965; Lowe-McConnell 1975), facts concerning differential predation are much needed. Tilapias, particularly juveniles, are known to be eaten by *Protopterus* (lungfish), *Lates, Hydrocynus, Hepsetus,* catfishes such as *Clarias* (see Bruton 1979), *Bagrus* and *Eutropius* and also by piscivorous cichlids in the Great Lakes (e.g., *Haplochromis squamipinnis* in Lake George) and *Serranochromis* spp. in the Zambezi system. Some of these piscivores are diurnal feeders, but the catfishes are nocturnal, taking sleeping tilapias. The reversal of the feeding rhythm in Lake Bosumtwi tilapia was thought by Whyte (1975) to be an anti-predation measure.

The numerous kinds of fish-eating birds that will take tilapias include pelicans, cormorants (though these 'prefer' cylindrical fish) darters, herons, kingfishers, gulls and waders in the shallows (see lists in Coe 1966; Vareschi 1979 and JFRO reports).

4. RIVERINE AND LACUSTRINE TILAPIA POPULATIONS— 'r' AND 'K' STRATEGISTS?

Ability to breed at a dwarf size is shown by all tilapias tested, but in natural waters we find a range of adaptations. Floodplain species tend to have seasonally fast growth, early maturity (1 or 2 yr), high fecundity producing numerous rather small eggs, several broods in succession; rather generalized bottom-feeding habits. Many of these characteristics are typical of 'r strategists' found in pioneer habitats (as indeed the floodplains are—new habitats opened up each year). Lacustrine species in large lakes (Malawi, Victoria), on the other hand, tend to grow more slowly, have delayed maturity (2 to 4 yr) so the maturity/final size ratio is higher (see Iles 1971; Fryer and Iles 1972), reduced fecundity, producing only one (rarely two) brood a year in Malawi species, with relatively few, large ova, and they brood the young to a correspondingly large size. They tend to be specialized phytoplankton-feeders. (Thus they appear to have many features of 'K-strategists'). *S. andersonii* also has some of these features, such as brooding only

one brood a year (which suggests that this species may have evolved under more lacustrine conditions).

Substrate-spawners have smaller, more numerous eggs than mouthbrooders, and their populations can build up very quickly in the comparative absence of predators, as, for example, did those of *T. zillii* in Lake Victoria, a species adapted for life with nilotic riverine piscivores, many of which are not found in the lake. The neotropical cichlids are nearly all substrate-spawners, including the *Cichlasoma* adapted for lacustrine life in Central American lakes (papers by McKaye 1977; Perrone 1978; Perrone and Zaret 1979). Lake Tanganyika is the only African lake to include numbers of both substrate-spawners and mouthbrooders among its endemic species (list in Lowe-McConnell 1975); in all other African lakes most cichlids are mouthbrooders. Why should this be so?

5. POLYCULTURE AND INTRODUCTIONS

These field studies have shown that it is quite usual for several species of tilapia to share resources in a water body (see Table 1). The main riverine fish communities in the soudanian region and Upper Zambezi each have two *Sarotherodon* species and one or two *Tilapia* species living together in most of the region. The lakes too, unless they dry up (like Lakes Rukwa and Chilwa, which each have one species) tend to have three or more tilapias sharing resources. The experimental addition of more species to the Lake Victoria fauna has led to the decline of the two indigenous species, but five tilapias are still present in this lake. In Lake Malawi the unique *S. squamipinnis* species flock (four species) appears to have evolved in response to the increasingly openwater conditions available in this lake, in one case by the splitting of early and late breeding populations into two species *(S. saka* and *S. squamipinnis)*. In the Cameroon crater Lake Barombi Mbo, colonizations from the river may have recurred at different times, and the resultant tilapias have managed to coexist (again possibly by differences in breeding seasons, but more information is needed on this).

In Lake Victoria the coincidental phenomenal rise in lake level appears to have helped the introduced species to get established. In a number of lakes the indigenous tilapias have thrived better than introduced species, for example in Lake Kariba, where despite heavy stockings with *S. macrochir* (albeit from the Kafue, so a riverine form, not the Mweru, lacustrine subspecies intended) it was the indigenous *S. mortimeri* which underwent a population explosion, while *S. macrochir* vanished for many years. However, as ecological conditions change, so may the tilapias; *S. macrochir* is now said to be increasing in Lake Kariba, and *S. andersonii*, previously unknown from the Middle Zambezi, has been recorded here. Again, in the Nyumba ya Mungu reservoir on the Pangani river, it has been the indigenous tilapias, *S. pangani* and *S. jipe* which have grown so well (to 50 cm TL) and dominated catches, not the introduced *S. esculentus* or *T. rendalli*. And in multispecific stocking of Tanzanian dams, Payne (1974) found the indigenous *S. esculentus* to do better than the introduced *S. macrochir; T.*

rendalli was introduced here before *T. zillii* and the *T. zillii* failed to get established.

The establishment and dominance of *S. mossambicus* from pond escapes in Plover Cove Reservoir, Hong Kong, formerly an arm of the sea, stocked with Chinese carps, shows what hardy persistent fish these tilapias are; their ability to use many food sources was thought to have contributed to their success here. This also emphasizes how easily pond escapes occur, and how difficult it may be to eradicate a species once it has gained access to a water body.

6. CONCLUSIONS FROM GROWTH STUDIES

Collated information on tilapia growth from many natural waters indicates:
a. That within a water body, the different species tend to grow at different rates, the faster-growing species reaching a larger size (see Figure 4).
b. The same species will grow at different rates in different water bodies, suggesting that environmental differences are more potent than genetic differences in determining maturation and maximum size.
c. Under natural conditions both maturation and maximum size of a species tend to be smaller in small bodies of water than in larger ones (see Figure 1).
d. Populations with low weight for length tend to have a lower maturation size than populations where the tilapia are in better condition (see Figure 2).
e. Maturation size of a species can change within a water body, e.g., rising as lagoon fish escape to the main lake, or falling after intensive fishing (as in Lake George), or in low-flood years (as on Kafue flats).
f. In riverine populations (also in lagoon and aquarium kept-fish) males grow larger than mature females, but in lakes males and females of the same species may mature at, and grow to, comparable sizes.
g. The relative growth rates of young and old fish may be different in different water bodies.
h. An extended reproductive season may slow somatic growth.
i. Both Kafue and Kariba studies indicate that *T. rendalli* has a higher production/biomass ratio than the associated *Sarotherodon* species.

Finally, the great plasticity of growth in natural waters shows that tilapia growth rates are very greatly affected by environmental and behavioral conditions. This suggests that concentrating research on the environmental and behavioral factors affecting growth and the switch to reproduction is likely to be more helpful for fish culture than a search for faster-growing genetic strains.

Acknowledgments

SESSION 2: PHYSIOLOGY

Chairman's Overview

D. J. W. MORIARTY

Tilapias are mainly lacustrine fish and are well adapted to enclosed waters. They produce high yields and thus are an important source of protein in many tropical countries. But what are the biological attributes which suit them for this role? What is known of the biology of tilapias that would improve cultural practices and what gaps are there in our knowledge which limit successful culture? The ability of tilapias to utilize blue-green algae has been cited as a major reason for their high yields in shallow tropical lakes, where blue-green algae are often abundant. I think that other factors are also involved, but food is obviously important.

Dr. Bowen examines the nature and quality of the food of tilapias and their digestive physiology. All large juveniles and adults feed on plant material or detritus. (Zooplankton feeding has been described for *S. aureus* in Lake Kinneret; Spataru and Zorn 1978—Editors.) Some species feed on macrophytes, but many feed on phytoplankton or detritus. Most of the important, cultured tilapias feed on bacteria, especially the blue-green algae (or cyanobacteria as they are now commonly called). These microorganisms are lysed by stomach acid and subsequently digested in the long intestine. Tilapias which feed on macrophytes make use of their especially adapted pharyngeal teeth to break open cells, and then digest them by similar methods.

Tilapias are generally slow moving, and do not need as much energy for movement as predatory fish. For rapid synthesis of body protein they require a relatively high protein content in their diet. They would get this from blue-green algae or bacteria, which have C:N ratios from about 4:1 to 10:1. Tilapia fry feed on zooplankton and zoobenthos as well as algae and bacteria, which they collect around shallow lake margins. It is not known whether they can utilize animal protein more efficiently at this stage. As they grow larger, they move into deeper water and their preferred diet changes to phytoplankton (or macrophytes or detritus in some species).

Dr. Bowen's work with *Sarotherodon mossambicus* shows that the fish select food with a high nitrogen content. The requirement for nitrogen and its supply in the diet is one aspect of feeding biology which needs to be investigated in more detail. Tilapias feed at or near the base of the food web in natural systems. This fact could be exploited in tilapia culture and it may be considered economically wasteful to supply manufactured food to tilapias. Many of the phytoplankton-feeding species may not be able to utilize readily other forms of food.

In studying feeding, digestion and growth, temperature is an important factor to consider. Dr. Caulton has shown how *Tilapia rendalli* utilizes

temperature variations in its lake environment to maximize growth. By constructing careful energy budgets, he has demonstrated that faster growth rates were achieved when fish moved into warm inshore areas during the day (where feeding and digestion rates were faster) and then retreated to cool, deeper areas at night where energy demands were less, than if the fish remained at a constant temperature. The conclusion is that yields will be much higher in shallow waters where diel temperature changes are more pronounced. This temperature effect helps explain some of the distribution of tilapias in lakes, but it is probably not the only reason why the fish in Lake George, Uganda, are concentrated around the edge. This shallow lake stratifies thermally each day, so the fish could obtain more than a 10°C variation in temperature by varying their position in the water column. Other environmental factors may therefore be involved.

Temperature also limits the distributon of tilapias. Their inability to withstand temperatures much below 16°C confines them to tropical or warm temperate regions. For culturing tilapias near the limits of their range, an optimum water body size and depth is needed, which ideally allows the diurnal temperature variation that Caulton has shown and yet which does not cool down too much in winter. Many tilapias are euryhaline, which increases the potential areas of water available for their culture. Oxygen requirements are also important, but we need more data relating oxygen levels and temperature to the energetics of metabolism and the switch from growth to reproduction. Where there are dense blooms of algae, oxygen may be depleted at night or below the photic zone, to the point where respiration of the fish is affected. Perhaps an effect of this nature might be part of the explanation for preference of tilapias in Lake George for the lake edges, where phytoplankton densities are much lower than in the middle of the lake. The combination of high temperature and low oxygen levels would be stressful and, as Caulton has shown with *Tilapia rendalli*, there is likely to be a fine balance between energy supply in the diet and energy losses for maintenance. If metabolic losses are too high, or low oxygen availability decreases assimilation efficiency and limits energy supply, then growth and reproduction will be affected. There is evidence that growth is rapid and the onset of sexual maturity is delayed in highly oxygenated water.

In addition to food, the high reproductive potential of tilapia is an important factor governing their success in tropical lakes. This also leads to problems, however, because stunting may occur, particularly in overcrowded conditions, with attainment of sexual maturity at an early age. Like other fish, gametogenesis in tilapias is regulated by the influence of external and internal events on the nervous system and by a complex interaction of hormones from the hypothalamus, pituitary and the gonads. We need to know a lot more about the biochemistry of the hormones and the physiology of reproduction before practical benefits can flow to culturists. An example of the influence of social factors on breeding may be seen in Lake George, Uganda. As fishing pressure increased, the minimum size at which females reached sexual maturity decreased from 28 cm to 20 cm. As breeding sites are limited (because most of the substrate is too soft and flocculent for

nest-building), there may be competition for sites and the large fish would be dominant. Thus, it may be that occupancy of breeding sites by large fish inhibits the onset of sexual maturity, and as the large fish are removed by fishing, smaller fish become mature.