Environmental Physiology of Tilapias

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Tilapias in general do not grow at water temperatures below 16°C and are not able to survive water temperatures below 10°C for than a few days. Low water temperature tolerance limits are: *Tilapia sparrmanii* 7°C, *T. rendalli* 11°C, *Sarotherodon aureus* 8-8.5°C, *S. vulcani* 11-13°C and *S. mossambicus* 8-10°C. Hybrids between *S. niloticus*, *S. vulcani*, *S. hornorum* and *S. aureus* are similar to *S. aureus* in their low temperature tolerance. Low temperature tolerance is affected by prior acclimation temperatures. Tilapias are tolerant to high water temperatures, e.g., 42°C for *S. alcalicus grahami* and 41°C for *S. aureus*. Tilapias are euryhaline and are able to survive, grow and some species even reproduce in sea water up to 40‰ salinity. The lowest dissolved oxygen concentrations survived for short periods by tilapias are 0.1 ppm for *S. mossambicus* and 0.2 ppm for *S. aureus*. Tilapias are able to tolerate a pH range of 5 to 11. *S. aureus* tolerates a maximum of 2.4 mg/l un-ionized ammonia but after exposure to sublethal concentrations can raise this limit to 3.4 mg/l.

Introduction

Fish of the genera *Tilapia* and *Sarotherodon* are native to Africa and Israel, the northern limit of their distribution. The tropical origin of tilapias is clearly expressed in their ecological physiology, especially in their temperature preference during their reproductive period.

Tilapias become inactive at water temperatures below 16°C, which is the minimal temperature for normal growth. Reproduction occurs above 22°C. Their adaptation to stable ambient temperature regimes has limited their natural distribution to tropical areas.

In recent years tilapias have been distributed all over the world where temperatures are suitable for their growth and reproduction. In many parts of the world tilapias have been introduced for vegetation control, pond culture and recreational fishing. They have become established in numerous lakes in Florida, California and Texas where winter temperatures are not limiting.

They also occur in other regions of the U.S.A. in water bodies which are warmed above normal ambient temperature during the winter by geothermal water sources or artificial heating in conjunction with the operation of power plants. Some tilapias have excellent aquaculture potential because of their fast growth, herbivorous or omnivorous feeding habits, high food conversion efficiency, high tolerance to low water quality, ease of spawning, ease of handling, resistance to disease and parasites and good consumer acceptance.

Temperature

One of the problems of using tilapia for pond culture is their inability, in general, to survive water temperatures below 10°C for more than a few days. The influence of temperature on survival and growth has been studied through field observations, laboratory investigations and a few physiological experiments designed specifically to determine thermal effects. There is a large variation in the reports of thermal tolerance in tilapias, stemming from a lack of standardized methods. Other variations in results might be attributed to differences in: 1) acclimation time, 2) water quality such as total dissolved oxygen (DO), total dissolved solids and salinity, 3) age, size, sex and health of the fish, and 4) duration of the drop in temperature.

Activity and feeding of tilapias become reduced below 20°C and feeding stops completely around 16°C. Although tilapias may be able to resist short-term exposure (a few hours) to temperatures of 7 to 10°C, death can occur (in some species) at temperatures as high as 12°C after long-term exposure.

Some tilapias are more tolerant to low temperatures than others. *Tilapia sparrmanii* is a hardy fish, capable of withstanding much lower temperatures than those tolerated by other species. The lowest water temperature tolerance recorded for this species was 7°C in Zambia (Maar et al. 1966) and the same temperature was recorded in South Africa (Hofstede 1955). *T. rendalli* was able to survive a temperature of 11°C in Zambia (Sklower 1955).

Of the mouthbrooding fish, *Sarotherodon aureus* seems to be the most resistant to low temperature. Yashouv (1960) found that at temperatures below 10°C, *S. aureus* (reported as *T. nilotica*) ceases all motion, while at 6 to 7°C it loses its ability to maintain body position. However, when exposed to low temperatures for only a few hours the fish recovers. Sarig (1969) found that local *S. aureus* in Israel was able to tolerate temperatures of 8.0 to 8.5°C. *S. vulcani*, which was introduced to Israel from Lake Rudolf, dies at temperatures of 11 to 13°C. On the other hand, its hybrid with *S. aureus* had a lower temperature tolerance limit of 8.0 to 9.0°C. Denzer (1968) recorded a temperature of 11°C as the lower lethal limit of *S. niloticus*. Chervinski and Lahav (1976) showed that the hybrids between *S. niloticus* ♀ x *S. aureus* ♂ and *S. vulcani* ♀ x *S. aureus* ♂ have temperature limits similar to *S. aureus*. Similar experiments conducted by Lee (1979) showed that *S. aureus* is more tolerant to low temperature (6.7°C) (criteria, 50% of the fish lost equilibrium) than *S. hornorum* (10.0°C) and *S. niloticus* (7.8°C). The crosses between *S. niloticus* ♀ x *S. aureus* ♂ and *S. hornorum* ♀ x *S. aureus* ♂ were similar to *S. aureus* in their low temperature tolerance.

Another factor that affects low temperature tolerance of tilapias is the thermal history (acclimation) before exposure to low temperature. Chervinski and Lahav (1976) found that *S. aureus* acclimated to 28°C for two weeks began to die at 11°C while those acclimated to 18°C (for two weeks) began to die only at 9°C.

S. mossambicus is killed between 8 and 10°C (Chimits 1957). The minimum temperature at which the fish ceases to feed is 15.6°C and 100% mortality occurs at 8.3 to 9.4°C (Kelly 1956). Lower temperature tolerance (5.5°C) was reported for *S. mossambicus* in Hanoi, Viet Nam (Li et al. 1961). The influence of salinity on the lower temperature tolerance limits of *S. mossambicus* was investigated by Allanson et al. (1971). They found that *S. mossambicus* tolerated 11°C in 5‰ saline water but when in freshwater it could not survive at that temperature. It was suggested by Allanson et al. (1971) that the ability of *S. mossambicus* to withstand low temperature is correlated with the maintenance of high plasma sodium and chloride concentrations.

In contrast to their limited low temperature tolerance, tilapias are very tolerant to high water temperatures. *S. alcalicus grahami*, which lives in the hot springs of Lake Magadi, Kenya, tolerated temperatures up to 42°C (Coe 1966). A similar resistance to high temperatures (up to 42°C) was found in *S. shiranus chilwae* (Morgan 1972). Gleastine (1974) reported a low level of mortality at 41°C for *S. aureus*.The upper lethal limit for *S. niloticus* was also determined to be 42°C (Denzer 1968), while the upper median lethal temperature was 38.2°C for *S. mossambicus* (Allanson and Noble 1964).

Experiments conducted by Beamish (1970), using *S. niloticus*, showed that the temperature preferendum was 30°C when the fish was acclimated to temperatures between 15 and 30°C. A lower preferendum of 28°C was found when the fish was acclimated to 35°C.

Salinity

It is assumed that tilapias evolved from a marine ancestor and that their penetration to fresh water is secondary (Myers 1938; Steinitz 1954). This may account for marked euryhalinity of certain species (Chervinski 1961a).

S. aureus is able to survive direct transfer from freshwater to 60 to 70% sea water (20.2 to 25.0‰ salinity) and through gradual adaptation is able to withstand up to 150% sea water (Lotan 1960). The growth and survival of *S. aureus* and *S. galilaeus* in brackishwater have been studied in small-scale experiments in aquaria, concrete tanks and earth ponds (Chervinski 1961a, 1961b, 1961c, 1966). The growth of *S. aureus* in seawater ponds investigated by Chervinski and Yashouv (1971) was found not to differ significantly from that in freshwater. Good growth of F_1 hybrid offspring of the cross *S. niloticus* ♀ x *S. aureus* ♂ in brackishwater ponds was found by Fishelson and Popper (1968) and Loya and Fishelson (1969).

S. mossambicus is euryhaline and grows and reproduces in fresh, brackish and seawater. According to Vaas and Hofstede (1952) reproduction does not occur in salinities between 30 and 40‰. However, Hora and Pillay (1962) found that reproduction occurred in seawater up to a salinity of 35‰. Recent

observations by Popper and Lichatowich (1975) showed that in seawater ponds in Fiji, *S. mossambicus* is able to reproduce at salinities of 49‰. Fry of *S. mossambicus* were found to live and be in good healthy condition at salinities of 69‰ (Potts et al. 1967). These differences may be attributed to different races of *S. mossambicus*.

Tilapia zillii was found to reproduce in Lake Qarun (Egypt) in salinities between 10 to 26‰ (El Zarka et al. 1970a). *T. zillii* was found in the Red Sea at salinities of 42.7‰ (Bayoumi 1969) and in the hypersaline Bardawil Lagoon at salinities of 41 to 45‰ (Chervinski 1972).

Neither *S. aureus* nor *T. zillii* reproduces in sea water. In addition no nest building occurs and the gonadosomatic index dropped in *S. aureus* (Chervinski and Yashouv 1971; Chervinski and Zorn 1974). This fact can be used to control wild spawning of these species. The high tolerance of *S. aureus*, *S. mossambicus*, *S. galilaeus* and *T. zillii* for seawater was attributed by Morgan (1972) to their natural habitat in estuaries and the lower reaches of rivers.

Other Water Quality Parameters

DISSOLVED OXYGEN

Due to their tolerance to poor water quality, tilapias are found in habitats which most other fish genera are unable to inhabit. Even under conditions of heavy feeding, fertilization and manuring no mortality occurs.

The lowest short-term DO limit recorded for a tilapia is 0.1 ppm DO for *S. mossambicus* (Maruyama 1958) and *S. niloticus* (Magid and Babiker 1975). *S. niloticus* ♀ x *S. hornorum* ♂ hybrids tolerate 0.3 ppm DO (Lovshin et al. 1974). Experiments conducted at Texas A&M University using fresh chicken manure to fertilize ponds at a rate of 2,760 hens per hectare of pond water showed DO's at dawn: 0.4 to 0.8 ppm. A correlation was found between the low DO measurements at dawn and reduced growth in *S. aureus* (McGeachin pers. comm.).

Studies by Job (1969a, 1969b) showed that the respiration of *S. mossambicus* was independent of DO at temperatures between 15 and 30° C until the partial pressure of oxygen dropped to 50 mm Hg, equivalent to 32% saturation. Below this level the metabolic rate became dependent on available oxygen. Similar results were shown by Rappaport et al. (1976) who found that the growth of tilapia and carp is reduced below 25% oxygen saturation. Mortality occurs when oxygen remains below 20% saturation for more than 2 to 3 days.

It seems that tilapias are able to tolerate DO's as low as 1 ppm. Below this level they may utilize atmospheric oxygen. Stickney et al. (1977) reported that *S. aureus* reared in ponds receiving swine wastes experienced heavy mortality when the pond surface became covered with duckweed, possibly because its ability to utilize atmospheric oxygen was restricted. A well-known phenomenon in harvesting tilapia ponds is the fact that tilapias can survive for several days in small mud puddles with little ill effect.

pH

Most pH values associated with tilapia growth come from pond observations. Swingle (1961) summarized the relationship between pH and fish culture. He found that the lethal acidic limit is approximately pH 4 and the alkaline limit is pH 11. Huet (1971) recommended pH 7 to 8 for culture. Bardach et al. (1972) stated that tilapias did not grow in the acid waters of West Congo. *S. alcalicus grahami* in Lake Magadi, Kenya was found to tolerate pH 5 to 11 without any adverse effect. Lovshin et al. (1977) reported a pH range in culture ponds in Brazil from a minimum of pH 7.7 in the morning to over pH 10 in the afternoon. Experiments conducted at the Aquaculture Research Center of Texas A&M University, showed that *S. aureus* tolerated a pH range of 7.5 to 10.2 in tanks receiving chicken manure (McGeachin pers. comm.). Also in ponds receiving chicken manure (100 kg/ha/day of dry matter) the pH ranged between 7.2 and 9.3 at 11:00 A.M. (Burns and Stickney 1980).

AMMONIA

Fish excrete most of their nitrogenous waste through the gills in the form of ammonia. Excreted ammonia exists in water in equilibrium between the un-ionized NH_3 (toxic to fish) and ammonium ions NH_4^+ which are not toxic. The toxicity of un-ionized ammonia depends on the DO. When the DO is low un-ionized ammonia is toxic at a lower concentration. The toxicity of NH_3 also decreases with increasing CO_2; this depresses the pH which shifts the NH_3/NH_4^+ equilibrium.

The influence of un-ionized NH_3 on *S. aureus* was investigated by Redner and Stickney (1979). The 48-hour median lethal concentration (LC_{50}) was 2.4 ppm. When fish were acclimated to sublethal concentrations (0.43 to 0.53 ppm) for 35 days, a concentration as high as 3.4 mg/l caused no mortality within 48 hours. This pattern is important when heavy feeding, fertilization and manuring are being applied in intensive pond culture. The maximum total ammonia tolerated by *S. aureus* in experimental ponds receiving fresh chicken manure from 2,760 hens per hectare was 11 ppm at pH 8 and 27°C. The amount of the un-ionized ammonia present was 0.75 ppm (McGeachin pers. comm.). Burns and Stickney (1980) reported the total ammonia level recorded with 4,000 hens per hectare to be 2.4 ppm, which appears low.

Table 1. Salinity tolerance of *Sarotherodon* and *Tilapia* species.

Salinity (‰)	Comments	Source
	S. aureus	
6	Grew and reproduced in brackishwater ponds	Chervinski (1966)
10	Growth was nearly equal to that in freshwater ponds; greater mortalities in brackishwater	"
18.9	Reproduced in brackishwater	Chervinski (1961b)
20-25	Survived direct transfer from freshwater	Lotan (1960)
36.6-44.6	Grew well; failed to reproduce	Chervinski and Yashouv (1971)
53.5	Able to survive through gradual adaptation	Lotan (1960)
	S. galilaeus	
10-26	Thrived and bred naturally	El-Zarka et al. (1970a)
19.5	Thrived and grew after direct transfer from freshwater	Chervinski (1961c)
	S. mossambicus	
30	Grew well and reproduced in ponds	Chimits (1957)
30-40	No reproduction	Vaas and Hofstede (1952)
35	Reproduced	Hora and Pillay (1962)
49	Reproduced	Popper and Lichatowich (1975)
	T. zillii	
11-29	Thrived and reproduced; survived better than *S. aureus* and *S. niloticus*	El-Zarka et al. (1970a)
23.4-27.3	Maximum salinity tolerated after direct transfer from freshwater	Chervinski and Hering (1973)
39	Was able to tolerate this through gradual adaptation	"
38.8-43.7	Acclimated to this salinity; Grew better than *S. aureus;* Did not reproduce	Chervinski and Zorn (1974)
42.8	Found in the Red Sea	Bayoumi (1969)
41-45	Found in the hypersaline Bardawil Lagoon	Chervinski and Hering (1973)

Table 2. Lower temperature limits (°C) recorded for *Sarotherodon* species.

Temperature (°C)	Comments	Source
	S. aureus	
5	Survived in ponds when temperature dropped for a short time	Yashouv (1960)
6-7	Survived in ponds when temperature dropped for a short time	Chervinski (unpublished)
8	Survived this temperature for a short time in laboratory	Yashouv (1960)
8-8.5	Died under experimental conditions	Sarig (1969)
9	Began to die: previously acclimated at 18°C for two weeks	Chervinski and Lahav (1976)
11	Began to die: previously acclimated at 28°C for two weeks	"
11	Higher survival when kept in 5‰ salinity than in fresh water (0.4‰)	"
5.6	Died: previously acclimated to 21°C for 2 days. (Drop in temperature 0.8°C/1 hour)	Lee (1979)
	S. galilaeus	
8	Survived in laboratory when exposed to this temperature for a short time. Lost equilibrium when exposed to 7.5°C for a short time.	Yashouv (1960)
	S. mossambicus	
5.5		Li et al. (1961)
8-10	Tolerated	Chimits (1957)
8.3-9.4	Total mortality	Kelly (1956)
9-12	Did not survive these temperatures in fresh water; at 11°C, disorientation; survived 11°C in 5‰ salinity	Allanson et al. (1971)
	S. niloticus	
6.7	Determined experimentally	Lee (1979)
11	Determined experimentally	Denzer (1968); Chervinski and Lahav (1976)

Discussion

LOVSHIN: My experience of tilapias is that they do much better in waters with a high pH. At pH 5 to 6 or below, they become sick and lethargic and do not grow very well. Tilapias are found in the Zaire Congo Basin anyway, where the pH of some tributaries can get down to around 5; tilapias can live in waters of low pH, and I would like to

know if anyone has any information on tilapias in low pH waters. My observations suggest that the sarotherodons are alkaline water fish and if we attempt to raise them in acid waters they will not respond well, quite apart from the low productivity. Are there tilapias which do well and spawn in low pH situations? [Tilapias are generally absent from most of the central basin of the Congo, the forested part (Trewavas, pers. comm.), but Dubois (1959) reported *T. congica* living in Lake Tumba, Zaïre, where the pH is 4.5 to 5.0 (see Philippart, this volume)].

LOWE-McCONNELL: I do not think they get into very low pH, but I have pH's for *S. niloticus*. Some of the lagoons have pH's around 9.

ROBERTS: We keep our experimental populations in Scotland in tap water at pH's of 6.4 to 6.8.

HEPHER: What about high pH's? For example, 10.2 was mentioned. What is the source of this high pH? Is it caused by a fluctuation in the bi-carbonate cycle or by deposits of sodium carbonate? A pH as high as 10.2 may affect tilapias.

CHERVINSKI: In fact we are talking about fluctuations of pH.

HEPHER: That is all right. Most fish will tolerate those levels. The main question is, can you construct tilapia ponds in a swampy area which has acid soils?

LOWE-McCONNELL: Dr. Prowse at Malacca had tilapia in ponds at very low pH's; I think around 2 to 4 or something of that order. If you look in the Malacca reports, you will find all the data. These were acid lands which were of little use for anything else but to grow fish. He was liming them. I don't know what the pH was after he limed them.

CAULTON: I would like to comment on an unusual aspect of environmental adaptation shown by *S. mossambicus*. I have been informed by a reliable source of three reports of live *S. mossambicus* being dug out of apparently dry river beds in Zimbabwe. These reports have never been scientifically verified, but I am quite happy with their reliability. In all instances, no surface water was present yet the fish survived in the damp subsurface moisture as deep as 50 cm below the surface. The fish have obviously adapted to a severely modified microenvironment and appear to remain alive under extremely adverse conditions. All attempts at recreating these conditions in the laboratory have, however, resulted in total mortality.

CHERVINSKI: It is known by fish culturists that when you drain ponds, tilapias can withstand very low oxygen levels in the mud. After one or two days, when you put the water back again, they will revive.

HEPHER: But that is not dry.

CHERVINSKI: No, but still the oxygen is still very low, and it may be that tilapias are able to use atmospheric oxygen. We see them in ponds going up to the surface and swallowing air. We have done some small experiments and showed that when tilapias cannot reach the surface, there is a lot of mortality.

ROBERTS: I would like to comment on the pH tolerances. In Mombasa, Haller has stocks of *Sarotherodon alcalicus grahami*. They will not survive in any pH below 9 and live at pH 10 or 12 without any difficulty. Also, I cannot agree with Dr. Chervinski that levels of CO_2 are unimportant. We have a very considerable problem in several places where high CO_2 water supplies cause nephrocalcinosis.

CHERVINSKI: I agree that CO_2 can be very important, but in the work I was discussing, lowered O_2 is more important. The fish can avoid high CO_2 waters.

GUERRERO: I would like to give some information about tilapia culture in the Philip-

pines where people are working a great deal in brackishwater. At salinities between 15 and 30‰, *S. niloticus* do not reproduce. They seem to grow better at 15‰.

HEPHER: But *S. mossambicus* will spawn in seawater.

CHERVINSKI: *Tilapia zillii, S. aureus* and *S. niloticus* are all very salt tolerant.

TREWAVAS: It is interesting that *T. zillii* can tolerate high salinities in, for example. Lake Qarun (Egypt), but appears unable to do so in West Africa where it is replaced by *T. guineensis.*

MIRES: North of Eilat in Israel, hybridization between *S. niloticus* females and *S. aureus* males is very difficult in salinities of 20‰ and above.

AVTALION: Is there any evidence that environmental parameters can affect the sex ratio of the progeny?

MIRES: Not to my knowledge. Temperature, at least, appears to have no influence.

HENDERSON: I would be suspicious of drawing any general conclusions from the effects of varying salinity on reproduction. There are so many physiological factors involved.

PULLIN: I was interested to hear you talk about oxygen tolerance. I believe you said that when a culturist who subjected his fish to low oxygen conditions such as early morning dissolved oxygen (DO) of around 0.1 ppm the fish suffered growth depression, and could not make this up even if the oxygen levels went back to normal during the day. We sometimes get DO's as low or lower than this for several hours in manured ponds in the Philippines.

CHERVINSKI: With experiments conducted with *Sarotherodon aureus* it has been shown that there is a correlation between low oxygen in the early morning and growth.

PULLIN: Twenty-four hour records of oxygen levels are essential in experimental work.

MORIARTY: The important point to consider here is, I think, the interaction between temperature and oxygen. As the temperature goes up, the fish are going to have a higher oxygen demand and be much more stressed. We did have a fish kill some time ago in Lake George, Uganda, but it was in the center of the lake where the plankton densities were highest, not around the edges. It happened at night. The tilapias could have come to the surface and breathed air. None of the air breathing species died. In Lake George, the temperatures are very high. The lethal stress was therefore the high temperature and the high oxygen demand when the oxygen levels are already low.

CAULTON: I would like to make one point which is not often considered. The oxygen stored in the swimbladder can, in *S. mossambicus*, sustain metabolism for some time. My estimates are that a fish of 400 g may survive for as long as 30 minutes using this oxygen at 25°C. Obviously, the greater the depth that the fish is found in, the greater the volume of oxygen available. Similarly, the lower the temperature and the larger the fish, the longer the supply could last.

LOVSHIN: I used to think that tilapias utilized atmospheric oxygen a lot but now I doubt it. I think rather that they come up to the surface film where the dissolved oxygen is high and flush their gills with this water to get enough oxygen to survive. If they do not have access to the surface or are crowded in cages, they die very quickly at low DO's. I think I have read somewhere that tilapia have the ability to lower their metabolism

when DO's go down to a certain level. I have seen this in the basic studies we have carried out in Brazil. The fish have the appearance of being dead, but they are not, and the amount of oxygen in the surface layers is enough to keep them going as long as they have contact with it.

Reproductive Physiology in Cichlid Fishes, with Particular Reference to *Tilapia* and *Sarotherodon*

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Works dealing with the external and internal factors which regulate reproductive efficiency in *Tilapia* and *Sarotherodon* are reviewed. Gametogenesis, although presenting the same general features as in most other teleosts is characterized by a low production of gametes related to the high efficiency of parental care: in substrate-spawners *(Tilapia)* the number of small sticky eggs is approximately related to the cube of body length, whereas in mouth-brooders *(Sarotherodon)*, eggs are bigger, not sticky, and their number is related to the square of body length.

Both groups seem to exhibit a capacity for precocious sexual maturation, the reason for which is not clear. There is also unlimited successive breeding through whole populations in equatorial areas and an increased tendency for seasonal breeding with increasing latitude, with maximum activity during maximum temperature and light intensity. When temperatures exhibit seasonal variations of large magnitude, low temperature (15 to 22°C) inhibits reproduction during part of the year. Social factors have been shown to enhance spawning frequency and might also influence sexual precocity through mechanisms which need further work.

Despite some attempts, specific tilapia gonadotropins have not yet been satisfactorily purified; the ubiquity of specific prolactins in controlling both osmoregulation and parental care behavior must be confirmed, and their possible inhibitory action on gametogenesis need investigation. The precise nature of steroids which mediate the pituitary action during different phases of the reproductive cycle also needs more research.

Introduction

The efficiency of reproduction in *Tilapia* and *Sarotherodon* has paradoxical consequences: on one hand, this aptitude which allows easy and rapid propagation in various tropical and subtropical environments, partially explains the economic interest in these species for fish culture; on the other hand this reproductive efficiency can be a source of problems because

uncontrolled multiplication within a limited environment in situations of food competition is liable to produce dwarf fish populations, of little value.

The behavioral patterns which occur after spawning and which characterize substrate-spawners *(Tilapia)* and mouthbrooders *(Sarotherodon)* have been described and discussed by numerous authors (Lowe-McConnell 1959; Perrone and Zaret 1979). Whatever the role of each sex in brood care, which differs among species, this care provides an efficient protection for eggs and fry against predators, and contributes greatly to the reproductive efficiency of these species. However, the physiological mechanisms which control parental care behaviour are poorly understood.

Another aspect of the reproductive efficiency of tilapias is precocious sexual maturation which can occur as early as 3 months in some species (McBay 1961; Arrignon 1969) and depends probably, in addition to genetic factors, on environmental factors like temperature (Hyder 1970a; Siddiqui 1979a), food availability, social factors, etc. Precise data based on experimentation are generally lacking.

As soon as sexual maturity is attained, and provided temperature is suitable, most cichlid females are able to undergo successive breeding cycles, producing new broods at 4 to 6 week intervals. This usually results in a continuous production of fry throughout a population, with the exception of certain environments subject to substantial seasonal variations (Moreau 1979). But the relative asynchrony between the sexual cycles of individual females can be a problem when mass production of homogenous fry is required for intensive fish farming.

Thus, for practical reasons dictated by fish farming conditions, it would often be advantageous either to inhibit or delay sexual maturation, or in some cases to favor synchronous spawning and breeding for mass production of fry.

This paper reviews the external and internal factors which seem to be involved in the control of different stages of the reproductive cycles of cichlids, to suggest practical means for artificial control. As literature in the field of cichlid reproductive physiology is scattered, references will be made, when necessary, to the present state of knowledge in other teleosts. For more detailed information concerning reproductive physiology and endocrinology in fish, see recent reviews by Dodd (1975), Fontaine (1976), Jalabert (1976), Olivereau (1977), Callard et al. (1978), Peter (1978), Billard et al. (1978) and Breton et al. (1980).

General Characteristics of Gametogenesis

Sexual differentiation of the gonad into a juvenile testis or ovary with a characteristic morphology occurs very early in *Tilapia* (Yoshikawa and Oguri 1978) and in *Sarotherodon* (Nakamura and Takahashi 1973), around 15 to 30 days after fertilization (at 23 to 25°C). Sexual maturity can be then completed after a few months.

Gametogenesis in cichlids appears to present the same general features as in most other teleosts and lower vertebrates, whether in males or in females (Barr 1968; Hoar 1969). Thus some stages in the following de-

scription are taken from noncichlids. All the available information suggests that this is valid (Dadzie 1969; Hyder 1970a, 1970b; Polder 1971; Von Kraft and Peters 1963; Hodgkiss and Man 1978; Babiker and Ibrahim 1979; Moreau 1979b).

In males, the testis possesses a stock of undifferentiated gonial cells (type A) which originates from the primordial germ cells of the embryo through mitotic divisions. Active spermatogenesis begins with the isolation of type A spermatogonia, each one surrounded by a few somatic cells, followed by successive synchronous mitotic divisions of spermatogonia (type B), while surrounding somatic cells divide to form a continuous layer of cells, called "Sertoli cells". This process results in numerous cysts of cells throughout the testis. After an unknown number of spermatogonial mitotic divisions, meiosis occurs synchronously for each cyst, each spermatogonium then producing four spermatids which will differentiate into spermatozoa (spermiogenesis). Cyst evolution occurs along testicular lobules which are separated from each other by fibroblast cells and interstitial tissue. The latter is particularly well developed in cichlids in comparison with some other teleosts. Spermiation occurs when spermatozoa are released from cysts after separation of the Sertoli cells, first into the lobules and then into the vas deferens.

In female teleosts, the ovaries contain a stock of undifferentiated oogonia which seems to be renewed by mitotic divisions throughout life unlike higher vertebrates. For example, unilateral ovariectomy stimulates oogonial mitosis in the remnant ovary of *Sarotherodon aureus* (Dadzie and Hyder 1976). Some oogonia begin a meiotic division but remain at arrested prophase (primary oocytes). Each primary oocyte increases in size and is progressively surrounded by layers of somatic cells: inner granulosa cells which form a monolayer directly in contact with the thickening outer oocyte envelope (the zona radiata, i.e., the future chorion) and an outer theca, made of several layers of fibroblasts penetrated by capillaries. The theca forms the external cellular envelope of the ovarian follicle. The morphology of ovarian follicles in *Tilapia* and *Sarotherodon* has been well described by Von Kraft and Peters (1963).

Oocyte growth can be divided into two main phases: first, the previtellogenic phase when size increases (up to 0.6 to 0.9 mm diameter in *S. niloticus*) which is considered to be the result of synthesis occurring mainly within the oocytes (endogenous vitellogenesis) and second, the vitellogenic phase which results from the rapid accumulation, after minor biochemical modifications, of "vitellogenin": a lipophosphoprotein which is synthesized in the liver, released into the blood and incorporated into the oocytes by micropinocytosis (exogenous vitellogenesis or yolk deposition). At the end of vitellogenesis, meiosis resumes: a general process called oocyte maturation, characterized by completion of the first meiotic division, with first polar body emission, which is accompanied by important changes in the gross morphology of yolk and cytoplasm just before ovulation (expulsion of mature secondary oocyte from the follicle). Oocyte maturation ends only after sperm penetration with the second meiotic division and second polar body emission.

In contrast to the spherical shape of the mature egg in most teleosts, *Tilapia* and *Sarotherodon* eggs are ovoid. In substrate-spawners *(Tilapia)*, ovulation is accompanied by the production of sticky material (probably mucopolysaccharides), which seems to be secreted by the granulosa, from light microscope evidence (Von Kraft and Peters 1953) and electron microscope observations (Nicholls and Maple 1972). This sticky substance is deposited around special threads emerging from the zona radiata of oocytes (Von Kraft and Peters 1963), and glues all the eggs into one mass which sticks to the substrate. In mouthbrooders *(Sarotherodon)* eggs are usually not embedded in these sticky threads, with the exception of *S. galilaeus* which leaves the eggs some minutes on the substrate before commencing mouthbrooding (Fishelson 1966b).

As discussed by Perrone and Zaret (1979), egg size and fecundity in fish are strongly related to parental care patterns. In *Tilapia* and *Sarotherodon*, whose behavior provides a high level of parental care, production of gametes is rather low. In males, testis weight is very low compared to that of other teleosts without parental care (Peters 1971), whereas in females the number of eggs per spawning is of the order of hundreds in *Sarotherodon*, and a few thousand in *Tilapia* (Peters 1963): very different from the millions of pelagic eggs produced by some species without parental care. In tilapias, as in other teleosts, fecundity, egg size and egg weight usually increase with female size: egg production increases approximatively in relation to the square of body length in *Sarotherodon* and in relation to the cube of the length in *Tilapia zillii* as discussed by Welcomme (1967b).

The temporal patterns and rhythmicity of gametogenesis have been much studied in *Tilapia* and *Sarotherodon*. Individual females spawn successively, either during a defined breeding season or year-round, with a few weeks interval between spawnings (Moreau 1979): this requires either rapid or continuous gametogenesis. In both sexes successive waves of gametogenesis have been demonstrated (Von Kraft and Peters 1963; Peters 1963; Dadzie 1969; Moreau 1971, 1979; Hyder 1970a; Bruton and Boltt 1975; Siddiqui 1977b, 1979a; Babiker and Ibrahim 1979).

In females some doubt remains as to the stage from which a new wave of oocytes develops to prepare for the next spawning. Some authors (Von Kraft and Peters 1963; Peters 1963; Hyder 1970a) have reported that the next wave of oocytes is already in the process of active vitellogenesis in spent fish just after spawning, but some other evidence suggests that each new batch arises from a stock of previtellogenic oocytes (Silverman 1978a, 1978b; Moreau 1979). This dubious point may be due to imprecisions in the exact definition of active vitellogenesis (or exogenous vitellogenesis, i.e., under pituitary control), to differences in species, and to enviromental differences. For example, Moreau (1979) showed that the mean interval which separates the last two successive waves of oocytes in *Tilapia rendalli* is different in two different lakes. This point, however, would need more precise observation and experimentation to understand the underlying endocrinological mechanisms (see below), particularly in species where the female exhibits brood care behavior after spawning, during which ovarian growth might be inhibited.

In males, spermatogenesis is reported to occur continuously, the testis containing cysts at all different stages, in both *Sarotherodon* (Dadzie 1969; Hyder 1970a, 1970b; Moreau 1979) and *Tilapia* (Moreau 1979), but quantification reveals that substantial variations can occur in the intensity of spermatogenesis in marginal temperature conditions (Moreau 1979). Methods of quantification (Billard et al. 1974) should be used more extensively to assess spermatogenetic continuity. As in the case of females, this would allow investigation of the occurrence of any post-spawning inhibition in species where the male exhibits brood care behavior.

The Role of Environmental Factors in the Regulation of Reproductive Activity

In most teleosts, spawning periods appear to be adjusted to (and by) environmental factors (photoperiod, temperature, salinity, rainfall, etc.) so that they are suitable for rearing offspring (de Vlaming 1974). Fish of temperate zones, where photoperiod and temperature variations are of great magnitude, spawn during a limited period of the year, and only once in most cases. In equatorial and tropical regions, where these variations are more limited, temperature is rarely a limiting factor, but considerable environmental changes can occur which might inhibit or favor offspring survival, favoring related adaptations (for example rainfall and cloud cover during the rainy season).

Tilapia and *Sarotherodon* species are abundant in both equatorial regions and subtropical regions as well as the mediterranean and have even been introduced into environments which can be considered as marginal, for at least a part of the year, especially with respect to low temperature tolerance. This is the case in lakes at high altitude in Madagascar (Moreau 1971, 1979). Here the low temperatures encountered are very different from those in the original habitats of tilapias and the response in breeding patterns may be considered as the limit of a tendency. *Sarotherodon* and *Tilapia* extend their breeding seasons for as long as temperature is favorable. During the cold season spermatogenesis is greatly retarded but all its developmental stages remain present in the testis. In females, on the contrary, exogenous vitellogenesis seems to be completely inhibited by low temperatures and all yolk-laden oocytes disappear.

In more appropriate environmental conditions, such as equatorial lakes and ponds, *S. niloticus* was found to breed throughout the year, though the number of breeding fish was slightly higher during the wet season (Lowe (McConnell) 1958). In areas distant from the equator, the same species exhibits a well defined breeding season, spawning mainly during the warmest and most sunny season (Lowe (McConnell) 1958). Among *Tilapia*, *T. zillii* in equatorial lakes shows no reproductive seasonality and individual fish spawn successively year-round (Siddiqui 1979a). On the other hand, the same species in northern areas presents a definite seasonal breeding, spawning during the period of maximum water temperature and maximum light (Ben Tuvia 1959; Fishelson 1966a, 1966b; Siddiqui 1977b).

However, the assumption that no reproductive seasonality occurs in equatorial areas might even be questioned in regard to the precision and the validity of the method of appreciation, if we consider the contradictions between Hyder (1969, 1970a) and Siddiqui (1977b) concerning *S. leucostictus* in the same equatorial lake: the first studies show a seasonal variation in breeding activity, while the latter denies this finding and concludes that breeding is non-seasonal.

It seems therefore that *Tilapia* and *Sarotherodon* have a capacity for unlimited successive breeding (at least when the whole population is considered) in equatorial regions and an increased tendency for seasonality with increasing latitude, with maximum reproductive activity during periods of maximum temperature and day light. The effects of seasonal rainfall cannot, however, be excluded (Aronson 1957; Lowe (McConnell) 1958; Lowe-McConnell 1959; Hyder 1969, 1970a; Marshall 1979a, 1979b; Moreau 1979) but these remain controversial, probably because of differences between species.

It remains difficult to assess which are the key factors to stimulate, inhibit, or exert any regulation on the various stages of the breeding cycles of *Tilapia* and *Sarotherodon.* This uncertainty is due in part to the absence of any experimental study to dissociate the role of separate environmental factors, and also part to the imprecise methods which have been used to determine the different parameters relative to the intensity of reproductive activity.

The Role of Social Factors in the Regulation of Reproductive Activity

Social interactions are known to influence some parameters of reproduction, particularly the timing of first sexual maturation, spawning frequency and fecundity. In cichlids, spawning frequency is increased by different sensory stimulations coming from conspecific fishes, e.g., visual stimuli, sound production, lateral line contacts and probably chemical communication (Aronson 1945, 1951; Polder 1971; Marshall 1972; Chien 1973).

In some *Sarotherodon* species the female is able to spawn regularly even when isolated, but shows increased interspawning intervals compared to non-isolated females (Aronson 1945; Marshall 1972; Silverman 1978a, 1979b). In *S. mossambicus* Silverman (1978a, 1978b) was able to dissociate the effects of different levels of social contact on separate parameters of the interspawning interval. He distinguished between unlimited contact (several fish in the same aquarium), medium contact (adjacent aquaria each containing one fish so that each fish can see into the other tank) and low contact (visually isolated fish in different aquaria) and showed that visual stimuli hastened mainly ovulation with little influence on oogenesis but that other non-visual stimuli (e.g., tactile or chemical) in unlimited-contact females were able, in addition, to advance yolk deposition by about 7 days. Males and females were shown to be equally effective as stimulus animals. This may reflect some "general conspecific effect" related to gregariousness of *S. mossambicus*, a species where "presence" within a social group is important, according to Silverman. He suggested that regular spawning in isolation

would most likely occur in species where males with ripe gonads are continuously available waiting for new females to encounter their nests. Although very interesting, these experiments concerning *S. mossambicus* should be performed on other species, and efforts should be made to look for the existence of pheromone-like substances which have been shown in other fish (Solomon 1977).

The Role of Internal Factors in the Regulation of Reproductive Activity

Numerous organs, endocrine glands, and hormones are involved, directly or indirectly, in the regulation of reproduction in fish as in other vertebrates (Fontaine 1976; Olivereau 1977). This complex control system is directed by the nervous system which integrates external stimuli together with ontogenetic and physiological constraints, and exerts its control mainly through the hypothalamo-pituitary-gonad axis. The following section will deal essentially with the functional modalities of this axis. Points which are still very controversial in other teleosts, and which have not even been studied in cichlids to our knowledge will be omitted: for example, the role of the pineal organ.

The Role of the Pituitary

Many works reviewed by Pickford and Atz (1957) have demonstrated how important the role of the pituitary is in the control of reproduction in fish. This role was confirmed in cichlids *(Sarotherodon spilurus)* by means of chemical hypophysectomy using methallibure and replacement therapy (Hyder 1972; Hyder et al. 1974; Hyder et al. 1979). Methallibure, which was shown to inhibit gonadotropin secretion by the pituitary in fish (Breton et al. 1973) as it is known to do in mammals, induces an effective gonadal regression in both male and female *S. spilurus* after 4 to 5 weeks of treatment with daily doses of 1 mg/l of aquarium water (Hyder 1972). This treatment results in an extensive resorption of yolk-laden oocytes and a complete inhibition of vitellogenesis in females and in the complete inhibition of two steps of spermatogenesis in males: the step between spermatogonia and spermatocytes (meiosis) and final spermiation. A similar effect was confirmed by Lanzing (1978).

The present state of knowledge of teleost fish reproduction tends to support the hypothesis that two different pituitary gonadotropins are involved in the control of gametogenesis. One purified at first from carp, *Cyprinus carpio* (Burzawa-Gerard 1971), trout, *Salmo gairdneri* (Breton et al. 1976) and in salmon of the genus *Oncorhynchus* (Donaldson et al. 1972) is characterized by its control over final intrafollicular oocyte maturation (Jalabert et al. 1974) and its effect upon spermatogenesis (Billard et al. 1970). A second kind of gonadotropin which seems necessary for vitellogenesis was recently purified from carp and salmon pituitaries (Idler and Bun Ng 1979).

In cichlids, some attempts have been made to purify and characterize pituitary gonadotropins. Farmer and Papkoff (1977) obtained two preparations from *S. mossambicus* which exhibited some biochemical characteristics similar to luteinizing hormone (LH) and follicular stimulating hormone (FSH) from higher vertebrates. The first preparation stimulated testosterone production in isolated rat testis Leydig cells, an assay which is considered highly sensitive and specific for mammalian LH. Neither of the two preparations was assayed for its activity on *Sarotherodon* gonads. More recently, Hyder et al. (1979) observed enhanced gonadotropic activity (as judged by testis stimulation in methallibure-treated *S. spilurus*) after chromatographic separation of a glycoprotein fraction from *S. niloticus*. The fraction was the same as that known to contain FSH when the same biochemical procedure is applied to pituitary preparations from higher vertebrates. Results are thus still confusing, and more work remains to be done in order to find specific bioassays for the gonadotropins of cichlids.

Another pituitary hormone, characterized as a "prolactin-like" hormone, is believed to play an interesting role in the reproductive physiology of cichlids, in relation to the regulation of breeding activity and parental care Blüm and Fiedler (1964) found that injection of ovine prolactin induced behavioral and histiotropic effects in *Symphysodon aequifasciata axelrodi*. The behavioral reactions were of fanning movements with the pectoral fins orientated to a distinct reference point (normally associated with parental care towards the brood) and suppression of feeding and fighting tendencies. The histiotropic effect was an increase in mucous cell production on the body surface which normally serves to nourish the young in that species (Hildemann 1959), thus exhibiting a curious analogy with the secretion of crop-milk in pigeons and milk production in mammals.

In other cichlids, e.g., *Pterophyllum scalare*, *Aequidens latifrons*, *Cichlasoma severum* and *Astronotus ocellatus* (Blüm and Fiedler 1965) ovine prolactin induces similar effects, including increase in mucous cell production although to a lesser extent than in *Symphysodon* and here this is not related to nursing of the young in that species. It is possible that mucus secretion can be related to the osmoregulatory properties of prolactin in fish (Blüm 1973; Bern 1975). Isolation and purification of *Sarotherodon* prolactin was successively reported by Blüm (1973) using behavioral and histiotropic effects in *Symphysodon* and by Farmer et al. (1977) using specific assays for osmoregulation. Considering the pleiotropic action of prolactin, isolating the same molecule through different kinds of bioassays is not surprising, but a comparison of different preparations using the same tests would be of interest in assessing the reality of this pleiotropic role for the same hormone. Among the alleged multiple actions of prolactin in fish, one could be of interest for *Tilapia* and *Sarotherodon* culture if its mechanism could be elucidated: the inhibition of gonad development (Blüm 1976). In natural conditions, gonadal development after spawning might be inhibited during parental care, which is precisely the period when prolactin is supposed to be acting. In addition, some antagonism between prolactin and gonadotropins was found to occur regarding spawning behavior (Blüm and Fiedler 1965).

THE ROLE OF THE GONADS

In addition to the central role of gametogenesis the gonads possess complex endocrine properties which, under pituitary control, contribute to the regulation of reproductive cycles by direct action on gamete differentiation, by controlling the activity of different organs and tissues involved in reproduction (such as the liver, fat and bone mineral stores) and also by controlling the development of secondary sexual characteristics. Finally the endocrine secretions of the gonads participate in the regulation of pituitary activity (a feed-back mechanism) and also act on the central nervous system, allowing different kinds of behavioral patterns to occur during the successive periods of the sexual cycles.

Sexual steroids are the main hormones produced by the gonads, but other compounds, the occurrence of which have not been investigated in cichlids, must certainly be secreted (Breton et al. 1980). Steroids are generally considered to be produced by specialized cells presenting histochemical and morphological features common to all vertebrates (Hoar and Nagahama 1978).

In males these cells form a typical interstitial tissue which has been characterized as steroidogenic by demonstration of 3β-hydroxy-steroidogenase (Yaron 1966) and from ultrastructural evidence (Nicholls and Graham 1972). They exhibit increased activity (number, size, lipid concentration) during spermatogenetic progression, with maximum activity during spermiation, when there is also rapid development of sexual coloration, nest building activity and territoriality (Hyder 1970b), and when the testis contains high levels of testosterone (Hyder and Kirschner 1969). The fact that interstitial tissue activity is under pituitary control can be demonstrated by several methods. Treatment with human chorionic gonadotropin (HCG), which exhibits gonadotropic activity in some fishes, induces both stimulation of interstitial tissue and an increase in the testosterone content of the testes (Hyder et al. 1970). Conversely, methallibure inhibition of pituitary gonadotropin secretion lowers interstitial cell activity, an effect which can be overcome by administration of HCG or *Sarotherodon* pituitary extracts (Hyder 1972; Hyder et al. 1974). But testosterone is probably neither the only nor the main steroid mediator produced in the gonad, as testosterone propionate administered to methallibure-treated *Sarotherodon* failed to restore spermatogenesis, producing only some spermiation at high doses (Hyder et al. 1974). As a range of androgenic steroids has already been found in fish, like 11-ketotestosterone in female *S. aureus* (Eckstein 1970), further studies would be of great interest in attempting to identify the major active steroids in *Tilapia* and *Sarotherodon*, and to understand their action on the different steps of spermatogenesis, sexual behavior and secondary sexual characteristics: for example, the genital tassel of male *S. macrochir* which seems to be an important signal in the spawning behavior of that species (Wickler 1965, 1966b).

In female cichlids both histochemistry (Livni 1971; Yaron 1971) and ultrastructural morphology (Nicholls and Maple 1972) show that most ovarian steroidogenesis is probably located in two kinds of follicular cells: the granulosa cells (although the ultrastructural evidence is here somewhat equivocal) and special theca cells, located mainly close to capillaries.

Estradiol-17-β (E2) seems to be of general occurrence in fish. It is mainly involved in the control of vitellogenin synthesis in the liver and of mobilization of mineral and fat stores (Olivereau and Olivereau 1979; Mugiya 1978). This seems to be true also in *S. aureus* where estradiol-17β was identified in the ovary by Katz et al. (1971). Later a positive correlation was found between plasma E2 concentration and ovarian weight, i.e., the stage of vitellogenesis (Yaron et al. 1977; Terkatin-Shimony and Yaron 1978). In the same species, some ovarian steroidogenic pathways were investigated by Eckstein (1970) and Eckstein and Katz (1971), leading to the identification of new steroid metabolites like 11-ketotestosterone and 11-hydroxytestosterone among others which are more classical (testosterone and progesterone). Their exact function, although related to sexual activity (Katz and Eckstein 1974) is unknown. Deoxycorticosterone, a corticosteroid which can be synthesized either in the interrenal tissue or in the teleost ovary (Colombo et al. 1973) was found to increase 38-fold in the blood of *S. aureus* between a sexual resting phase at 18 to 20°C and sexual activity at 30°C. As this steroid is assumed to be one of those mediating gonadotropin action on final maturation and ovulation in catfish, *Heteropneustes fossilis* (Sundararaj and Goswami 1977), it is tempting to propose a similar model for final maturation control in *Sarotherodon*. However, the state of "sexual activity" (stage of ovarian development) at which the blood of female *Sarotherodon* was collected by Katz and Eckstein (1974) was not known precisely and further work is needed to find out which steroids mediate pituitary gonadotropin control over final oocyte maturation and their mechanism: for reviews on this problem in other teleosts, see Jalabert (1976) and Sundararaj and Goswami (1977).

Prolactin also has some control over ovarian steroidegenesis as can be inferred from the observation of Blüm and Weber (1968) that ovine prolactin greatly stimulates the activity of 3β-steroid dehydrogenase in ovaries of the cichlid *Aequidens pulcher*. This observation suggests that inhibition of ovarian growth by prolactin is mediated through steroid action. An understanding of the precise mechanism for this action would be of great interest.

Regulation of Pituitary Activity

As in higher vertebrates, gonadotropin secretion by the pituitary appears to be regulated by the nervous system through the hypothalamus which secretes a releasing factor first indicated in fish *(Cyprinus carpio)* by Breton et al. (1971) and Breton and Weil (1973). This factor is probably not very different from mammalian luteinizing hormone-releasing hormone (LH-RH) (Breton et al. 1972, 1975a) at least as far as the biologically active part of the molecule is concerned. Recent studies show that LH-RH's from lower vertebrates, including *S. mossambicus*, differ from those of higher verte-

brates both in immunological and biochemical characteristics (King and Millar 1979). Other experimental data in fish support the hypothesis that factors inhibiting pituitary gonadotropin secretion could be present in the fish hypothalamus (Peter 1978).

Ovarian endocrine secretions, particularly some steroids, seem to be able to exert positive or negative feed-back action upon the activity of the hypothalamo-pituitary complex in fish (Billard and Peter 1977; Breton et al. 1975b; Billard 1978; Jalabert et al. 1980) as they do in mammals.

A better understanding of all these controls over pituitary activity could provide practical means to manipulate some aspects of reproduction in cultured fish.

Conclusion

Some *Tilapia* and *Sarotherodon* species are well-suited for experimental work in reproductive physiology. They perform gametogenesis and regular spawning in aquaria, where external factors (light, photoperiod, temperature) can be easily controlled and they are of a convenient size for endocrinological studies involving blood sampling on living cannulated fish at different stages of the sexual cycle. Experimental data are rather scarce, however, making it very difficult to propose any techniques immediately applicable in tilapia culture. Thus, experimental research is still greatly needed to determine the respective roles of internal and external factors on first sexual maturation in the different steps of gametogenesis and on spawning frequency. Concerning the role of hormones, important results may come from work on other groups of fish and other vertebrates, concerning, for example, the hypothalamic regulation of gonadotropin secretion and non-specific means to control this activity. The development of specific methods to manipulate reproduction in tilapias requires better knowledge of their specific protein and steroid hormones involved in the control of sexual differentiation, gametogenesis and sexual and brooding behavior.

Discussion

NASH: I agree with you on the importance of egg quality. For example, salmon hatcheries tend to discard the first and last eggs available in a spawning season as they are invariably of poorer quality than those taken in the middle. Do you recommend for describing oogenesis in tilapias your six-part scale or Yamazaki's five-part scale? In your six-part scale, stages 3, 4 and 5 appear to be stages IIIa, IIIb and IIIc of the five-part scale. I assume that your stage 6 is atresia?

JALABERT: The important point is that we find oocytes at all stages in just about every fish in the population.

HEPHER: In temperate regions, it is found that vitellogenesis in fish is affected very much by day length. You haven't mentioned this at all. Is this because tilapias are from the tropical regions where there is little change in day length?

JALABERT: Some people say that there is a daylength effect even in equatorial regions, others say there is none. In tilapias, there is no clear evidence for such an effect and it

would need very precise criteria to assess small variations in the intensity of gametogenesis to investigate this. I remember for instance the contradictions between Hyder (1970a) and Siddiqui (1977b) concerning the seasonality of *S. leucostictus*. Such contradictions probably indicate the lack of precise criteria.

HEPHER: The works I know show that, for fish in general, day length affects vitellogenesis more than the other stages of oogenesis, but since you didn't mention this effect at all, may I assume that it does not exist in tilapias?

JALABERT: I don't know. We have to make controlled environment experiments to investigate this. The same is true for the effects of salinity on reproduction and growth. The evidence seems to be that in tilapias, responses to environmental changes are very variable indeed and may differ even within the same species. We conducted some recent experiments with trout to try to select for early and late reproduction to spread availability of eggs. We observed a shift in the timing of reproduction after only one generation. For tilapias, therefore, we can expect different responses for different species and strains.

NASH: We cannot generalize about reactions to environmental stimuli with subtropical and tropical fish. In mullet it is the light stimulus that triggers oogenesis and then the temperature takes control. And, although you cannot suppress development completely, you can delay it by temperature control even after triggering by light. There are groups of fish for which the opposite is the case. The temperature acts as the trigger and the light control acts as the monitor.

MORIARTY: I would like to ask a question from the point of view of the fish culturist. Is it going to be of any practical benefit to have a much more detailed knowledge of the reproductive hormones of these fish, or do you think that this is so complex that we would be better advised to study environmental and social factors?

JALABERT: Although the practical applications are not evident now, we do need more work on the reproductive hormones of fish and on their modes of action, in order to understand how environmental and social factors interact to modulate sexual activity. I believe that management decisions could be more efficient if based on such basic knowledge. But, from a strategical point of view, I feel that some fundamental questions are closer to application than some others; for example, are pheromones important in tilapia reproduction?

GUERRERO: In one experiment you described the separation of the two sexes of tilapia. You say that there was no pheromone action because the fish still spawned.

JALABERT: In this experiment the isolated females spawned anyway, or, more exactly, released their eggs, but the interval between successive spawnings was increased. When fish were together, this interval was reduced. We cannot rule out pheromones here, among the other factors. On the other hand, spawning in artificial environments can be affected by many stress factors which are not necessarily specific.

Feeding, Digestion and Growth—Qualitative Considerations

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Tilapias feed as herbivores and detritivores. Food particle size is reduced in the pharyngeal mill which facilitates peristaltic mixing and increases surface area for exposure to digestive fluids in the gut. Gastric acid secreted to pH values < 2.0 lyses cell walls and cell membranes of bacteria and algae. Subsequent intestinal digestion occurs gradually as the food passes down the extremely long intestine. In addition to microorganisms, detritus is digested and is a major nutritional resource for detritivorous tilapias. Whole diet assimilation efficiencies are lower for tilapias than for carnivorous fishes. Food quality appears to limit the growth of tilapias in natural populations. The limited data available indicate that within a given water body, tilapias select precisely the food that will maximize growth. The combined abilities for cell wall lysis and selective feeding suggest that tilapias hold considerable promise for low technology, protein efficient aquaculture.

Introduction

Animal growth rate is determined through the combined effects of food quantity and food quality. The quantity of food consumed is regulated through appetite to satisfy the animal's energy requirements (Rozin and Mayer 1961, 1964). Limited food availability that does not allow full appetite satisfaction results in growth rates below the maximum potential. Food quality depends on the composition of the diet, and the extent to which the components are digested and assimilated. Quality is rarely a limiting factor in the growth of carnivores since their diet is consistently of very high quality, but the quality of diets consumed by herbivores and detritivores is extremely variable and plays a major role in control of growth at these trophic levels. This contribution reviews recent scientific research on aspects of the diet, digestion, assimilation and growth of the tilapias (family Cichlidae; genera *Tilapia* and *Sarotherodon)*, which are herbivorous and detritivorous, to assess our current understanding of how food quality influences the growth of these animals in natural populations.

The Feeding Apparatus and Digestive Tract in Tilapias

It is important to begin with consideration of the feeding apparatus and digestive tract since these structures limit the range of potential food items that can be consumed and digested efficiently. Compared to the haplochromis cichlids, the feeding apparatus of tilapias is simple and unspecialized (Fryer and Iles 1972). The jaw teeth are small unicuspid, bicuspid or tricuspid structures that occur in one to five rows (Plate 1). In those species for which descriptions are available, the jaw teeth are flattened distally to form blades that appear to be useful as scrapers (Fryer and Iles 1972; Lanzing and Higginbotham 1976). Neither the gill rakers nor the buccal cavity appears to be specialized for feeding, but considerable specialization is evident in the dentition of the pharyngeal bones (Plate 2). These teeth range from fine, thin, hooked structures on the pharyngeal bones of *Sarotherodon esculentus*, a phytoplankton consumer, to the coarse, robust structures on the pharyngeal bones of *T. rendalli*, a macrophyte consumer (Caulton 1976). Mechanical and myological details of the cichlid pharyngeal apparatus are described by Fryer and Iles (1972) and Liem (1973).

The role of the pharyngeal apparatus is to prepare food for digestion. In many species this is done by breaking or cutting the food into smaller sized units. In *S. esculentus*, filamentous and large colonial phytoplankton may be broken into smaller units. In *S. mossambicus* and *S. melanotheron*, detrital aggregate is broken into finer fragments (Bowen 1976a; Pauly 1976) and in *T. sparrmanii* long filamentous periphyton is shredded to short segments of uniform length. The advantages of reduced particle size include a greatly increased surface to volume ratio that facilitates enzyme-substrate interaction, and reduced resistance to peristaltic mixing. In addition, mechanical disruption of macrophyte cell walls by the pharyngeal apparatus in *T. rendalli* increases the efficiency with which this food is digested (Caulton 1976).

The esophagus is short with a small diameter and leads to a small sac-like stomach. Some investigators have questioned the identification of this latter structure (Kamal Pasha 1964; Man and Hodgkiss 1977b) but its separation from the intestine by a sphincter, the low pH of the fluid it contains (Moriarty 1973; Bowen 1976b; Caulton 1976) and the pH optima of proteases extracted from its mucosa (Fish 1960; Nagase 1964; Moriarty 1973) all attest to its gastric function. Immediately behind the pyloric sphincter, the intestine receives a common bile duct. The first, short intestinal segment is thin-walled and of greater diameter than the remainder. Perhaps the most striking feature of the digestive tract of tilapias is the exceptional length of the intestine. Quantitative data for *T. rendalli*, *S. melanotheron* and *S. mossambicus* show that the ratio of intestinal length to fish standard length is between 7:1 and 10:1 (Caulton 1976; Pauly 1976; Bowen, unpublished). Other non-quantitative observations reported in the literature suggest these ratios are representative of the tilapias as a group. By comparison, Fryer and Iles (1972, p. 41) report that only three of 106 cichlids collected from Lake Tanganyika and its affluents had gut length: total length ratios greater than 6:1 and these three may have been tilapias. The intestine ends in an anal sphincter.

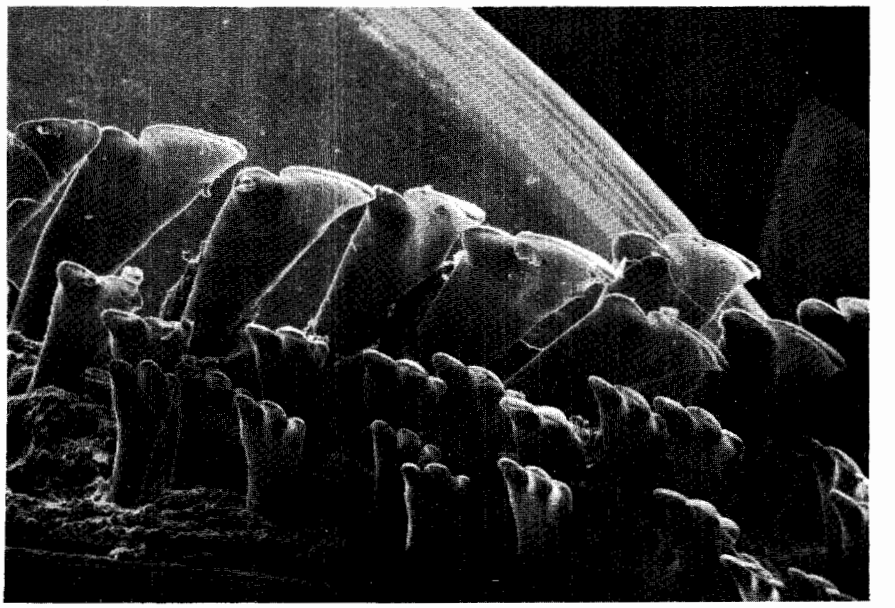

Plate 1. Jaw teeth of an 8 cm standard length *Sarotherodon mossambicus* from Lake Valencia, Venezuela.

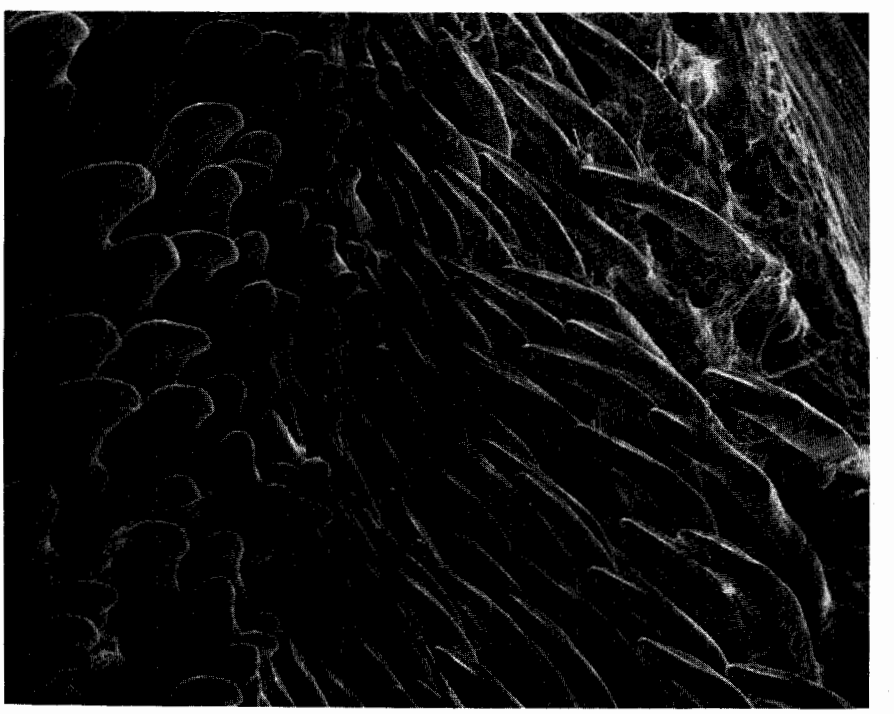

Plate 2. Teeth on the lower pharyngeal bone of an 8 cm standard length *Sarotherodon mossambicus* from Lake Valencia, Venezuela.

The Diet of Tilapias

In common with early developmental stages of nearly all fishes, the larvae, fry and early juvenile tilapias feed on small invertebrates, especially Crustacea (Le Roux 1956). The transition from an invertebrate diet to the typical adult diet is usually abrupt (Bowen 1976a; Moriarty et al. 1973) but in some cases it may occur gradually over the period of a year or more (Whitfield and Blaber 1978).

The diets of adult tilapias have been reported for more than 17 species sampled on three continents and a number of island systems (Table 1). Practically every aquatic animal, vegetable and mineral small enough to pass through the esophagus has been found in the guts of these fish. Some of this variety must be attributed to items that are occasionally abundant in the diet but are rare or absent most of the time and have no long-term significance in the fish's nutrition. For example, Bruton found that *S. mossambicus* in Lake Sibaya fed intensively on formicids for the few days when these were abundant at the lake surface during an annual swarming period, but they did not occur in the diet at other times of the year (Bruton pers. comm.). To describe the characteristic diet of a tilapia species, it is necessary to identify those food items that are consistently present in the diet over long periods of time.

Table 1. Diets reported for adult tilapias in natural habitats.

Species	Diet	Authority
Sarotherodon shiranus	macrophytes, algae, zooplankton	Bourn 1974
S. pangani	periphyton	Denny et al. 1978
S. jipe	periphyton	Denny et al. 1978
S. esculentus	phytoplankton	Denny et al. 1978; Fish 1951, 1955
T. rendalli	macrophytes, attached periphyton	Caulton 1976, 1977b; Denny et al. 1978
S. mossambicus	macrophytes, benthic algae, phytoplankton, periphyton, zooplankton, fish larvae, fish eggs, detritus	Bowen 1979, 1980b; Man and Hodgkiss 1977b; Munro 1967; Naik 1973; Weatherley and Cogger 1977
S. aureus	phytoplankton, zooplankton	Fish 1955; Spataru and Zorn 1976, 1978
S. niloticus	phytoplankton	Moriarty and Moriarty 1973a
T. kottae	phytoplankton, detritus, invertebrates	Corbet et al. 1973
T. mariae	phytoplankton, invertebrates	Corbet et al. 1973
S. galilaeus	phytoplankton	Corbet et al. 1973; Spataru and Zorn 1978
T. zillii	macrophytes, benthic invertebrates	Abdel-Malek 1972; Buddington 1979
T. guineensis	algae, detritus, sand, invertebrates	Fagade 1971
S. melanotheron	algae, detritus, sand, invertebrates	Fagade 1971
S. variabilis	algae	Fish 1955
S. leucostictus	phytoplankton, detritus	Moriarty et al. 1973
T. sparrmanii	periphyton	Bowen unpublished

The characteristic diet of adult tilapias is plant matter and/or detritus of plant origin. Blue-green and green algae, diatoms, macrophytes and amorphous detritus are all common constituents of adult tilapia diets (Plate 3). Bacteria are also present and may be very important for some species. Although tilapias collect their diets from such diverse substrata as macrophytes, lake bottoms, rock surfaces and from suspension, it is the uniformity of their diets that is especially noteworthy. Comparisons of diet composition for tilapias reveal extensive overlap. Tilapias that feed on macrophytes also ingest the attached algae, bacteria and detritus. This attached material is likely to be an important component of the diet. Although quantitative data are lacking for macrophytes consumed by tilapias per se, the dry weight of attached material was found in one study to exceed 25% of the total supporting macrophyte dry weight (Bowen 1980a) and could comprise an even greater percentage of the weight of leaves actually consumed by tilapias. Tilapias that feed on epiphytes also frequently ingest some of the supporting macrophyte (Munro 1967). Deposit feeders that feed in the littoral zone ingest a mixture of algae, detritus and bacteria that is essentially indistinguishable from the material attached to macrophytes. Deposit feeders that feed in deeper water ingest a mixture of sedimented phytoplankton and detritus essentially indistinguishable from the diets of suspension feeders. These various sources provide diets that are so similar that tilapias may switch from one source to another with little change in diet composition (Moriarty et al. 1973; Bowen, unpublished). Thus, despite the diversity of food resources exploited by tilapias, their diets are qualitatively very similar mixtures of algae, bacteria and detritus with or without macrophytes.

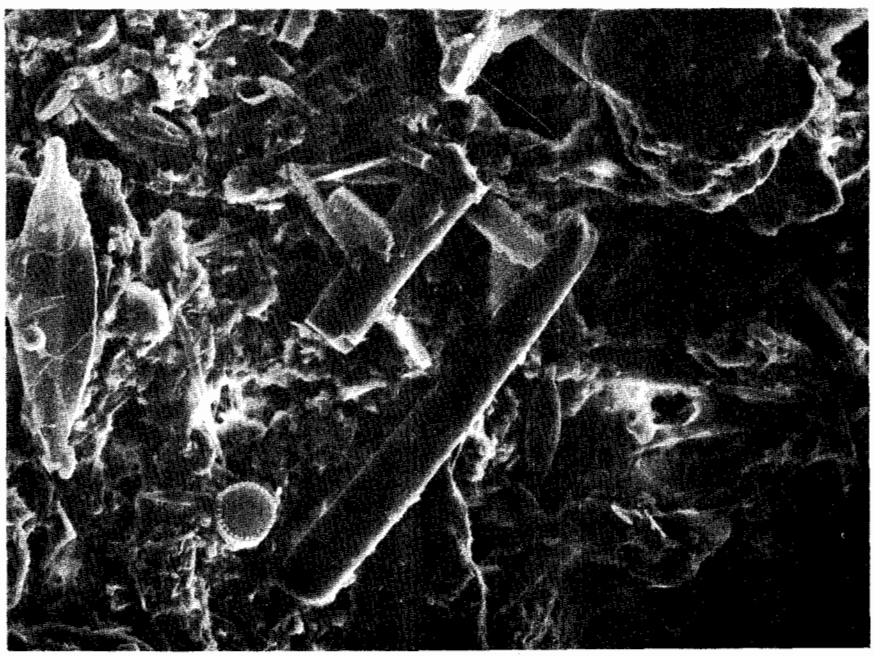

Plate 3. Scanning electron micrograph of typical stomach contents from *Sarotherodon mossambicus* in Lake Valencia, Venezuela.

The role of animal found in the diets of tilapias is, at present, an enigma. In some studies, animal remains are rare or absent from gut contents even when hundreds of specimens were examined. In most cases animal remains are present in low numbers and investigators have concluded these were ingested incidentally, either as whole invertebrates or as fragments of dead invertebrates, while the fish fed on other more typical foods. But in some cases, invertebrates clearly make up a significant proportion of the diet and are probably ingested intentionally (Abdel-Malek 1972; Spataru and Zorn 1978; Whitfield and Blaber 1978). Inclusion of invertebrates in the diet may be an important variable in the feeding strategy of tilapias, but until more quantitative data are available to describe circumstances under which animal prey are selected and the significance of such selection for nutrition, this aspect of the diet will remain an enigma.

The Process of Digestion in Tilapias

Digestion in tilapias is a two-step process with distinct gastric and intestinal components. The mechanism for gastric digestion found in tilapias appears to be unique among animals. In other animals, the pH of fluids in an actively digesting stomach ranges from about 2.0 to 2.2 (Barrington 1957). This is the pH at which vertebrate gastric digestive enzymes, including those of tilapias (Fish 1960; Nagase 1964; Moriarty 1973) show maximum activity. In contrast, the pH of stomach fluid in actively digesting tilapias is frequently as low as 1.25 (Moriarty 1973; Bowen 1976; Caulton 1976) and values as low as 1.0 have been recorded (Payne 1978). Moriarty (1973) was the first to describe the role of gastric acid in digestion by tilapias. He studied the population of *S. niloticus* in Lake George, Uganda, which feeds on phytoplankton dominated by colonial and filamentous blue-green species. As the algae pass from the esophagus they may travel either of two routes through the stomach. Peristaltic movement carries the food in a posterior direction along the ventral wall, up the posterior wall and back along the top to the pyloric sphincter. Algae that travel this route are exposed to progressively lower pH as HCl is secreted by the gastric mucosa. Exposure to acid at pH 1.8 or lower decomposes the algal chlorophyll to phaeophytin and thus a gradual change in color from green to brown is seen as the algae move along the gut wall. Some algae take a shorter route passing across the anterior of the stomach from the esophagus directly to the pyloric sphincter and are not exposed to acid concentrations below pH 2.0. These cells remain green. Moriarty demonstrated that acid not only decomposes chlorophyll but actually lyses blue-green cell walls. This makes subsequent intestinal digestion possible by providing intestinal enzymes access to the algal cytoplasm. Following Moriarty's discovery, it was found that the same mechanism allows *S. mossambicus* to digest bacteria associated with detritus in its diet (Bowen 1976a). These observations are significant since vertebrates lack gastric enzymes capable of attacking the prokaryotic cell wall. Development of a special mechanism for lysis of blue-green algae and bacteria allows the tilapias special access to a relatively protein-rich (about 50%) food resource for which there is little, if any, vertebrate competition.

Gastric acid is similarly important in digestion of some eukaryotic cells. The efficiency of diatom digestion increases with lower pH to pH 2.5 (Bowen 1976b). Tilapias that consume macrophytes also have low gastric pH when feeding and there is some indication that gastric acid may facilitate digestion of their food as well (Caulton 1976).

Details of gastric digestion have been studied for *S. mossambicus* in Lake Valencia, Venezuela (Bowen 1981). Comparison of food and stomach contents for juveniles fed periphytic detrital aggregate (PDA) in aquarium experiments showed that gastric acid decomposed much of the mineral component of the diet (Table 2). In effect, this increased the concentration of organic matter available for the fishes' nutrition by a factor of 1.5. Measurable protein values increased by a factor of 1.6. Although a small fraction of this increase may be gastric enzymes, *in vitro* simulation of gastric acidification showed most of the increase was due to the effect of acid in facilitating protein extraction for subsequent assay (Table 3). Experimental data indicate that about 20% of the dietary carbohydrate is decomposed by gastric acid.

Table 2. Results of aquarium experiments to assess effects of gastric digestion on periphytic detrital aggregate ingested by *Sarotherodon mossambicus*. Samples for which the coefficient of variation (CV) is not given were pooled. Total organic values are % of sample weight; protein and carbohydrate values are % of organic weight.

Food Component	Experiment number	Food intake (%)	Stomach contents (%)	CV (%)	Stomach (%) / food (%)
Total Organic	1	35.7	55.8	12.7	1.56
	2	32.1	61.2	12.4	1.91
	3	43.7	64.9	4.1	1.49
	4	56.1	62.8		1.11
	5	44.7	56.4		1.26
	6	40.2	53.4		1.33
	7	38.3	63.1		1.65
					$\bar{x}$ = 1.47
Protein	4	1.42	1.97		1.39
	5	1.79	3.35		1.87
	6	0.84	1.19		1.42
	7	1.19	2.00		1.68
					$\bar{x}$ = 1.59
Carbohydrate*	4	17.4	14.2		0.82
	5	16.7	13.1		0.79
	6	18.5	14.0		0.76
					$\bar{x}$ = 0.79

*Mean of three determinations

Table 3. Effect of gastric acid on the food of *Sarotherodon mossambicus* in Lake Valencia, Venezuela simulated *in vitro* ([a]% sample weight, [b]% organic weight).

pH	Organic[a]	Protein[b]	Carbohydrate[b]	Carbonate[a]
7.0	41.0	1.52	11.8	11.9
3.0	47.6	2.57	10.6	11.0
2.5	48.5	2.63	10.6	10.1
2.0	49.7	2.47	10.1	9.5
1.5	49.9	2.79	9.8	9.8

The importance of gastric enzymes in digestion by tilapias is not clear and may vary with species or with diet for a single species. Although a protease with pH optimum around 2.1 is present in the gastric mucosa of *S. mossambicus* (Fish 1960; Bowen 1976a) and *S. niloticus* (Moriarty 1973), it has not been detected in the gastric fluids (Moriarty 1973; Bowen 1976a). This enzyme has a greatly reduced reaction rate at pH values below 1.5, and it is possible that it is not secreted when gastric acid is used to lyse cells.

Secretion of gastric acid stops at the end of the daily feeding period and stomach fluids return to pH 5 to 7. In *S. mossambicus* (Bowen 1976b) and *S. niloticus* (Moriarty 1973) the stomach is completely empty during this resting phase but in *T. rendalli* a small amount of food remains (Caulton 1976). At the start of the next day's feeding, acid secretion begins only as the stomach is filled with the result that the first food to pass into the intestine is not exposed to strong acid. In those species whose diet is rich in chlorophyll, the food ingested at the start of a feeding period remains green and undigested as it moves along the length of the intestine (Moriarty 1973; Caulton 1976). Similarly the first diatoms to be ingested by *S. mossambicus* remain undigested (Bowen 1976b). This explains why early workers who compared stomach and posterior intestine samples sometimes reported that algae were not digested.

The second step in the digestive process occurs in the intestine. The common bile duct which opens into the intestine on the back of the pyloric sphincter adds bile salts that maintain the pH between 6.8 and 8.8 (Fish 1960; Nagase 1964). Trypsin, chymotrypsin, amylase and esterase activity have all been identified in intestinal fluid (Fish 1960; Nagase 1964; Moriarty 1973).

Details of intestinal digestion have been studied for *S. mossambicus* in Lake Valencia, Venezuela. Contents of digestive tracts removed from freshly caught specimens were divided into five subsamples: stomach contents, and the contents of the first, second, third and fourth quarters of the intestine. Each subsample was analyzed for organic matter, carbohydrate, protein and total amino acids (Bowen 1980b, 1981). Values from these analyses were expressed in units of weight per weight of hydrolysis resistant sample ash (HRA). This indigenous component of the diet is used as an undigested reference compound relative to which digestion and assimilation are measured (Conover 1966; Bowen 1981). The results show total organic matter and carbohydrate are digested rapidly in the first and second quarters of the intestine with no evidence of digestion in the third and fourth quarters

(Figure 1). Digestion of protein is complete in the first quarter. This component of the diet is thought to be microbial protein present in living cells and protein that may be associated with detritus. The results indicate that microbial cells lysed in the stomach are digested immediately in the intestine while those not lysed are not digested at any point. Very different results were obtained for total amino acids (Figure 2). This class of compounds is comprised of amino acids bound into the complex chemical milieu of the detritus in addition to amino acids that make up microbial proteins. Whether detrital amino acids are single amino acids, oligopeptides or polypeptides is not yet known. As a group, the total amino acids are digested gradually as food passes down the intestine and maximum digestion is not achieved until the end of the digestive tract.

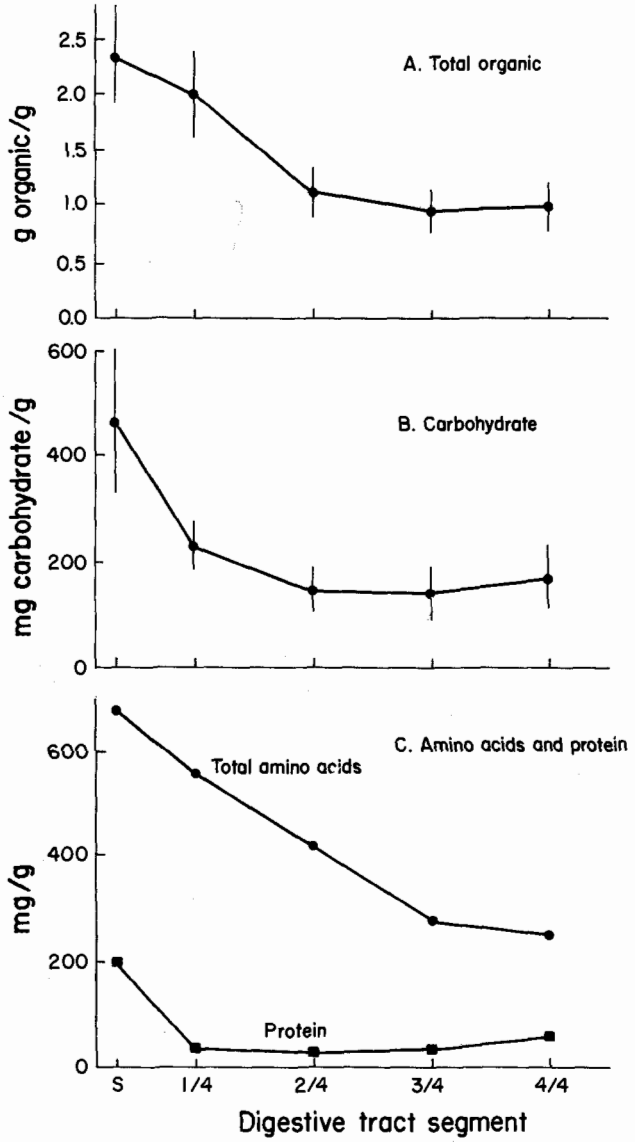

Figure 1. Comparisons of samples from the stomach (S) and the four quarters of the digestive tract of *Sarotherodon mossambicus* from Lake Valencia, Venezuela, to show the course of digestion. Means ± 95% confidence limits, n = 55 (after Bowen 1980).

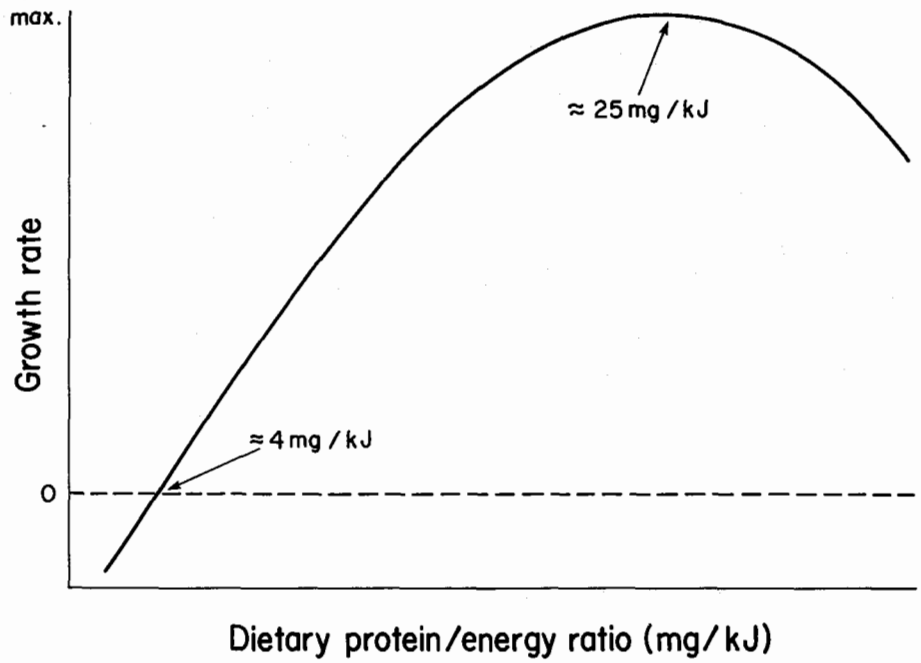

Figure 2. Graphic description of the relationship between dietary protein/energy ratios and growth rate in *Sarotherodon mossambicus*.

Assimilation of Digested Food

Digestion breaks macromolecules in the diet into progressively smaller subunits. Assimilation occurs when these subunits are small enough to pass through the gut wall. Because assimilation is the point in the nutritional process at which energy and materials gathered from the habitat are actually incorporated into and become an integrated part of the consumer, a measure of assimilation is the single most valuable quantitative descriptor of the diet.

Assimilation is usually quantified in terms of assimilation efficiency (AE): (amount assimilated ÷ amount ingested) x 100. AE's of tilapia feeding on various diets have been determined by two techniques. The mass-balance technique estimates the amount assimilated as amount ingested minus the amount defecated. A disadvantage of this approach is that precise estimates of ingestion and defecation are often difficult to obtain. In addition, this approach can only be used under controlled experimental conditions that necessarily differ from the natural feeding habitat. Since secretion of gastric acid is very sensitive to disturbance (Fish 1960; Moriarty 1973), efficiency of assimilation can be altered by experimental conditions. Nonetheless, the mass-balance technique has produced valuable results when used with fish acclimated to laboratory conditions and precise quantification that is possible using ^{14}C-labeled algae.

The second technique for determination of AE uses some refractile compound in the diet as an undigested reference. Some workers have added a reference compound such as Cr_2O_3 (Furukawa and Tsukahara 1966; Bowen

1978), while others have utilized refractile indigenous components such as cellulose for macrophyte grazers (Buddington 1979; Buddington 1980) and ash or HRA for detritivores (Bowen 1979, 1980b, 1981). AE is calculated by comparison of food:reference, and feces:reference ratios using the formula developed by Conover (1966). The advantage of the refractile reference technique is that it may be applied to analysis of tilapias taken directly from their feeding habitat. Since it appears there is no assimilation through the stomach, samples of stomach contents and posterior intestinal contents from freshly caught specimens may be compared for the purpose of estimating AE. This means determinations may be made for fish feeding under totally natural conditions and all handling effects are eliminated.

The few data available for assimilation efficiency of tilapia feeding on natural diets are summarized in Table 4. Two important generalizations can be drawn. Firstly, AE values are high for blue-green algae and diatoms, but are low for green algae and macrophytes. This is not surprising since the gastric acid that lyses blue-green cell walls and denatures diatom cell membranes would not be expected to have a direct effect on the cellulose cell walls of green algae and higher plants. Secondly, whole-diet AE estimates for these four tilapias are low in comparison to the average of 85% for a variety of carnivorous species (Winberg 1956). Again, this is not surprising when we consider that macrophytes and detritus contain abundant refractile compounds including cellulose and lignin that are not vulnerable to vertebrate digestive enzymes. A similarly low AE is reported for *Ctenopharyngodon idella*, a cyprinid macrophyte grazer (Hickling 1966). The low total AE for *S. niloticus* fed suspended matter > 100 μm filtered from Lake George appears to be the result of the long time interval between the start of feeding and the point at which digestion reaches peak efficiency in this species (Moriarty 1973).

Another interesting aspect of the data in Table 4 is that protein and lipid are assimilated much more efficiently than total organic matter or food energy. This same result was reported for tilapia fed pelleted algae that had been dried and ground to a powder such that all natural impediments to enzyme-substrate interaction had been removed (Kirilenko et al. 1975). Thus, the efficiency with which macromolecular groups are digested is related not to selective disruption of cell walls or membranes, but rather to basic characteristics of the digestive process itself.

Food Quality and Growth

The food quality of a given diet is directly proportional to its ability to support growth. The dietary component most important in limiting the growth of herbivorous and detritivorous fishes is protein. There are 10 to 13 amino acids that are essential for building new tissues (Cowey and Sargent 1972). These amino acids cannot be synthesized by fish and must be obtained from the diet. Carnivorous fish consume prey that may be > 80% protein by dry weight, but the diets of tilapias range from about 50% to < 1% protein. Values below 15% are most common (Boyd and Goodyear 1971; Caulton 1978a; Bowen 1979, 1980a, 1980b).

Table 4. Assimilation efficiency (AE%) estimates for tilapias feeding on natural diets.

Species	Experimental diet	Component of diet	AE%	Technique	Reference
Sarotherodon niloticus (phytoplankton grazer)	*Microcystis*	^{14}C	70	mass balance	Moriarty and Moriarty 1973a, b
	Anabaena	^{14}C	75		
	Nitzschia	^{14}C	79		
	Chlorella	^{14}C	49		
	Lake George suspended matter > 100 μm	total C	43		
Tilapia zillii (macrophyte grazer)	*Najas guadalupensis*	dry weight	29	reference (cellulose)	Buddington 1979
		organic matter	32		
		non-cellulose organic matter	56		
		protein	75		
		lipid	76		
		energy	45		
Sarotherodon mossambicus (detritivore)	Benthic detrital aggregate	organic matter	38	reference (ash)	Bowen 1979
		protein	46		
		carbohydrate	35		
		energy	42		
	Periphytic detrital aggregate	organic matter	63	reference (HRA)	S. Bowen 1981
		carbohydrate	63		
		protein	77		Bowen 1980b
		detrital amino acids	64		Bowen 1980b
Tilapia rendalli (macrophyte grazer)	*Ceratophyllum demersum* (aplical segments only)	dry weight	53-60	mass balance	Caulton 1978
		protein	80		
		energy	48-58		

To describe food quality, protein levels are frequently expressed as mg assimilable protein per kJ assimilable food energy. This reflects the fact that appetite controls protein intake indirectly through its response to food energy levels, and consequently the amount of protein assimilated depends on the amount associated with assimilable food energy (Harper 1967; Russell-Hunter 1970). A minimum of 4 mg protein per kJ is required for maintenance (Figure 2). Growth increases with increasing protein levels up to a maximum of about 25 mg/kJ. Protein at higher levels is in excess of the animal's ability to utilize it anabolically and thus growth decreases presumably as a result of the energetic cost of protein catabolism.

Protein-energy ratios have been used to assess food quality in two studies of the feeding of *S. mossambicus*. One study was conducted at Lake Sibaya, South Africa (Bowen 1979). The Lake Sibaya population was especially interesting because its juveniles grew well and were in good condition but the adults were stunted and showed extensive marasmás indicative of malnutrition (Bruton and Allanson 1974; Bruton and Boltt 1975). Although both juveniles and adults fed on benthic detrital aggregate, they collected their food from different parts of the lake. Juveniles fed near shore, frequently at depths less than 30 cm, while adults fed in water 3 to 5 m deep. Analyses of samples from the lake bottom showed that protein-energy ratios were high in shallow, near-shore waters, but dropped rapidly with increasing depth. Analyses of stomach contents confirmed that juvenile diets contained considerably more protein that adult diets. When the protein/energy criterion was applied, these results showed that juveniles have enough protein in their diets to produce good growth, but the adult diet lacks adequate protein for maintenance and the observed malnutrition would be expected (Figure 3). Reasons why

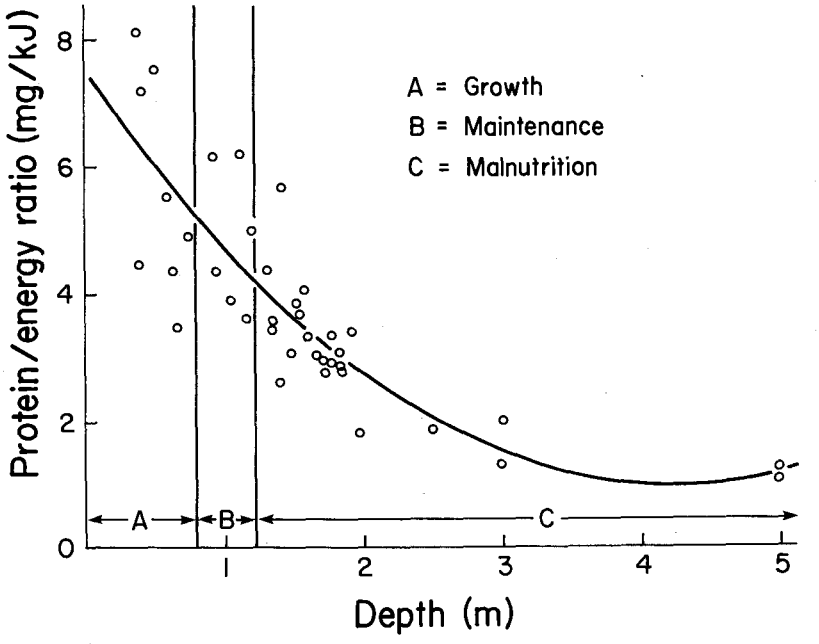

Figure 3. Relationship between protein/energy ratios and depth for benthic detrital aggregate consumed by *Sarotherodon mossambicus* in Lake Sibaya, South Africa, showing expected nutritional significance of feeding at different depths. Curve fitted by parabolic regression (after Bowen 1979).

adults do not feed in the shallows are discussed elsewhere (Bowen 1976b; Bruton 1979). With regard to the food quality problem, the important findings of the Lake Sibaya study are: 1) food quality varies significantly between and according to a predictable pattern and 2) juvenile *S. mossambicus* risk the perils of the near-shore shallows (predators, heavy-wave action) to utilize selectively food of the highest available quality.

Similar results were obtained in a study of *S. mossambicus* adults in Lake Valencia, Venezuela (Bowen 1980a, 1980b, 1981). These fish fed on periphytic detrital aggregate attached to *Potamogeton* spp. The protein content of this food resource varied from site to site and was directly proportional to the slope of the littoral zone bottom. Adult *S. mossambicus* fed selectively in the steeply sloped littoral zone (Figure 4). Some difficulty arose in interpretation of these results because assimilated protein:assimilated energy ratios indicated that protein levels were too low to support growth, but the fish were in excellent condition and reached a large maximum size. Further study revealed that in addition to protein, the diet contained detrital amino acids bound into the amorphous detritus. Detrital amino acids were most abundant in the steeply sloped littoral zone where the fish feed (Figure 5) and were assimilated with an efficiency of 64%. With this source of amino acids taken into consideration, adult *S. mossambicus* in Lake Valencia assimilated the equivalent of 14.4 mg of protein per kJ of assimilated food energy: an amount expected to produce good growth. As with the Lake Sibaya study, these results show *S. mossambicus* in Lake Valencia selected high quality food that maximized growth.

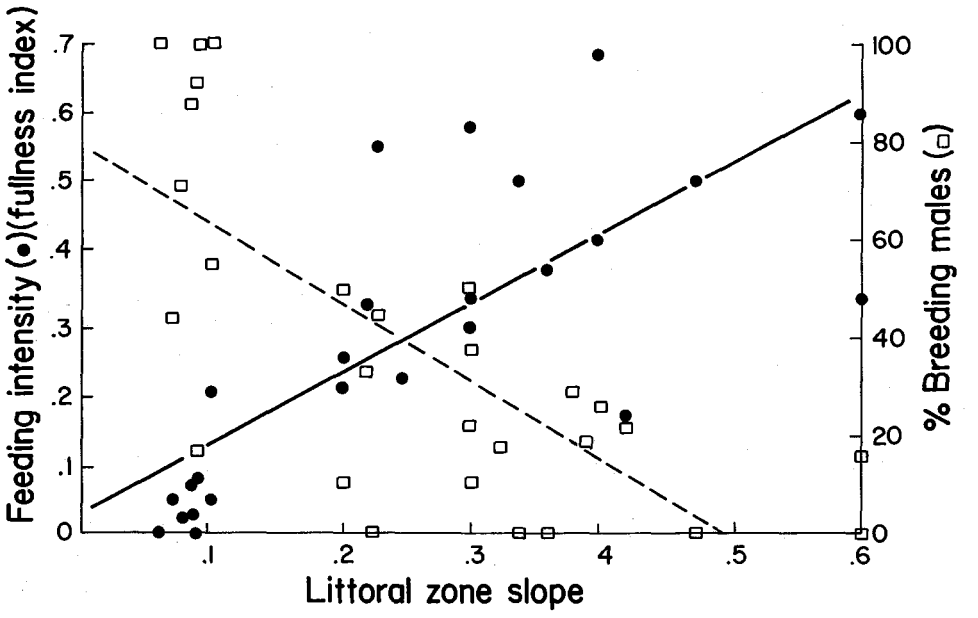

Figure 4. Habitat partitioning by male and female *Sarotherodon mossambicus* in Lake Valencia, Venezuela. Males in breeding coloration build nests and defend territories in the gently sloped littoral while females and non-breeding males feed in steeply sloped littoral where food quality is highest. Lines fitted by least-squares. (Reproduced by permission of the Ecological Society of America.)

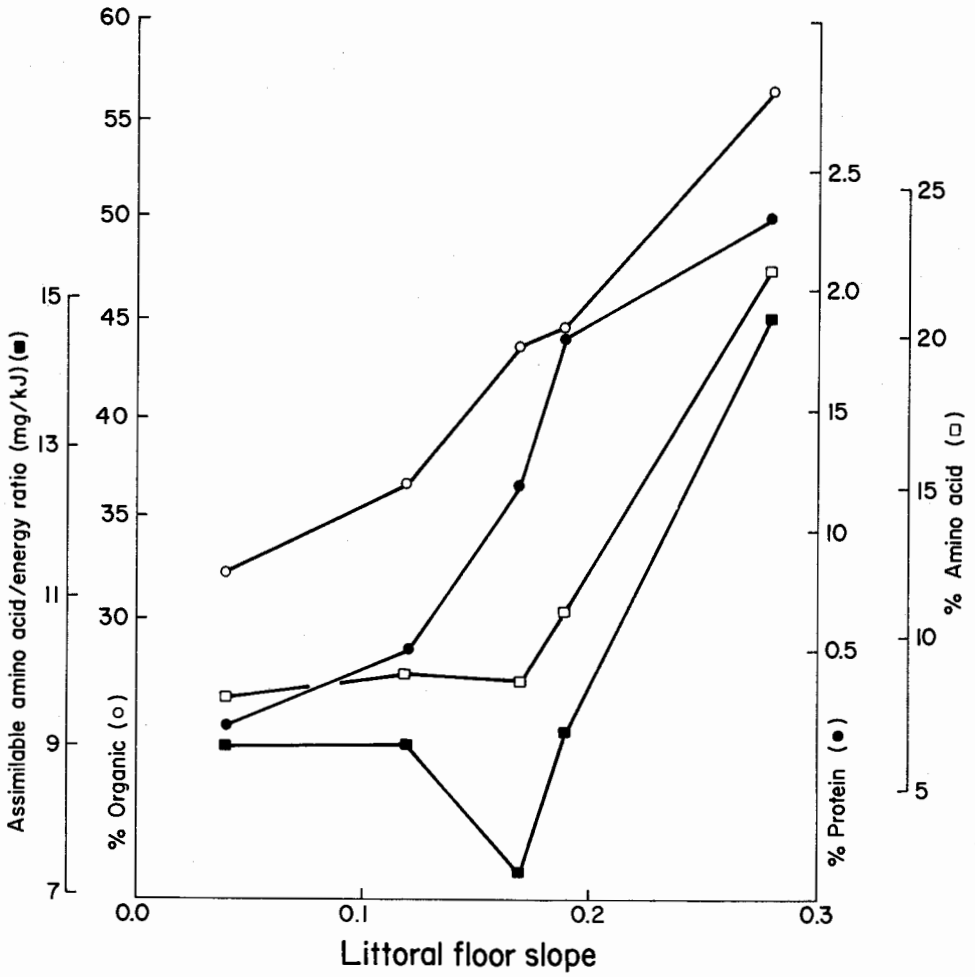

Figure 5. Relationship between organic content, protein content, total amino acid content and assimilable amino acid/energy ratios in the diet and slope of the littoral floor in Lake Valencia, Venezuela. Adult *S. mossambicus* feed selectively in the steeply sloped areas. (Reproduced by permission of the American Association for the Advancement of Science.)

In view of the abundance of detrital energy and the limited availability of protein-rich detrital food, both the Lake Sibaya and the Lake Valencia populations provide excellent examples of the way in which "ecosystems function to expend readily available energy to minimize the constraints imposed by limiting nutrients" (Reichle et al. 1975).

Summary and Conclusions

The characteristic diet of adult tilapias is a mixture of algae, detritus, bacteria, and, in some cases, macrophytes. Tilapias possess morphological and physiological adaptations for utilization of this diet. Pharyngeal teeth break food components into smaller units for easier peristaltic mixing and increased exposure to digestive enzymes. Gastric acid secreted to an unusually low pH, frequently below pH 1.5, lyses prokaryotic cell walls and denatures prokaryotic and eukaryotic cell membranes to expose the cytoplasm therein to intestinal enzymes. The extreme length of the intestine is essential for efficient digestion and assimilation of some components of the diet.

Food quality, quantified in terms of mg assimilable protein / kJ assimilable food energy, is potentially a limiting factor in the growth of tilapias. Studies of the detritivorous *S. mossambicus* show that the quality of available food resources varies widely, and that the fish utilize selectively the resource that produces maximum growth. Future studies of tilapia that feed on macrophytes and suspended matter are also likely to reveal selective feeding for growth maximization.

These trophic abilities of tilapia make them ideally suited for aquaculture. Since they feed at the base of the food chain, they are energetically very efficient and ecosystem carrying capacity should be high for these organisms. Their uncommon ability to exploit prokaryotic algae and bacteria as sources of protein makes them unusually protein efficient since they do not rely on invertebrate intermediates. In addition, the ability to utilize prokaryotic protein may open new doors to cost-efficient aquaculture. A principal economic obstacle in culture of fish is the cost of protein in culture diets (Weatherley and Cogger 1977). It is likely that bacteria and blue-green algae can be grown either directly in culture ponds or in adjacent facilities using locally available agricultural waste products and low-technology manipulations (Schroeder 1978). The protein/energy criterion could be used to optimize the quality of the food produced. Although systematic evaluation of this approach has not yet been attempted, what we have learned about the feeding of tilapias in natural systems suggests that it is a very promising possibility for the future.

Acknowledgments

I am grateful to Dr. D.J.W. Moriarty for helpful discussion of the manuscript. Plates 1 and 2 were produced by the Electron Microscopy Unit, Rhodes University, Grahamstown, South Africa.

Discussion

LOVSHIN: Dr. Bowen, I have one question, just a yes or no will do. Did you study the density of fish per unit area or the predator populations within the two lakes? Was there some sort of control on the effects of tilapia density between the two lakes, because I think your results could be affected tremendously by differences in density.

BOWEN: In Lake Sibaya the densities of all fish were very low and there were a lot of predators for tilapia. In Lake Valencia the tilapias were very dense, but still in very good condition. (See Caulton, this volume, for further discussion—Editors.)

Feeding, Metabolism and Growth of Tilapias: Some Quantitative Considerations

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Tilapias are strongly thermophilic with an eccritic thermal range varying from 30°C to 36°C depending on species. Natural populations of tilapias often show a diel movement which mirrors the diel thermal fluctuation of shallow inshore waters of lakes, pans or inundated river flood plains. The movement of young tilapias is shoreward, toward warm water, during the day and away from the shore during the night as the shallows cool rapidly. Metabolic energy demand, being a function of both temperature and mass, is strongly influenced by the thermophilic behavior of tilapias living in natural waters. Tilapias that feed on aquatic macrophytes demonstrate that food intake is related to both body mass and environmental temperature. Assimilation efficiency increases with increasing temperature. The cost of food processing is a function of both food quality and quantity but is also influenced by environmental temperature. The increased net gain in assimilated energy at high temperatures may be almost offset by the increased cost of food processing at comparable temperatures.

When considering these factors and formulating a simple energy budget it is clear that high daytime temperatures coupled with lower nighttime temperatures lead to an optimal use of energy resources and results in increased growth potential. Aquaculturists should take note of such physiological optima and with careful design of ponds and water management could create a diel temperature variation resulting in enhanced growth potential and decreased food conversion ratios.

Introduction

Rapid growth rates, good productivity per unit volume of water and economic, efficient food conversion make the tilapias a suitable fish for the needs of the modern aquaculturist. This group of fish made an early appearance in the field of aquaculture, but the rather premature enthusiasm waned somewhat when many of the earlier trials failed to come up to expectations. Today, however, significant advances have been made in the basic understanding of the biology of these fish, and controlled production is becoming increasingly successful. Notwithstanding this recent upsurge in the importance of these fish to aquaculture, there still remains a paucity of information which would contribute to our understanding of their physiological and

related environmental requirements. The principal environmental factor influencing physiology, i.e., temperature, will be the theme of this paper which is structured to include some aspects of feeding, metabolism and growth and to demonstrate the inter-relationships of these functions through the influence of temperature in the development of a simple energy budget.

Historically, the spread of tilapias from the hot equatorial inland lakes and rivers of Africa immediately suggests that these fish are well adapted to the prevailing climatic conditions of these areas. Just how well these fish have adapted to their environment may be of importance in our attempts to domesticate these fish. The survival of tilapias is generally limited to waters with temperatures warmer than 10°C to 12°C, although under exceptional circumstances (e.g., in areas of increased saline content such as estuaries - Allanson and Noble 1964), thermal tolerance of lower temperature may be marginally increased. It is not perhaps the tolerance to temperature that is important to most wild populations, but rather the effect that temperature, by its influence on the physiology, may have on growth.

Temperature and Metabolism

It is generally accepted that tilapias cease growing significantly at temperatures below about 20°C, but at the same time constant warm temperatures may not, by themselves, be adequate for optimal growth. Figure 1 illustrates the distribution of two species when subjected experimentally to a thermal gradient in a horizontal test tank. In each instance, the fish respond positively to the warm water, orientate rapidly and swim actively toward water which is only marginally cooler than their upper lethal temperature tolerance.

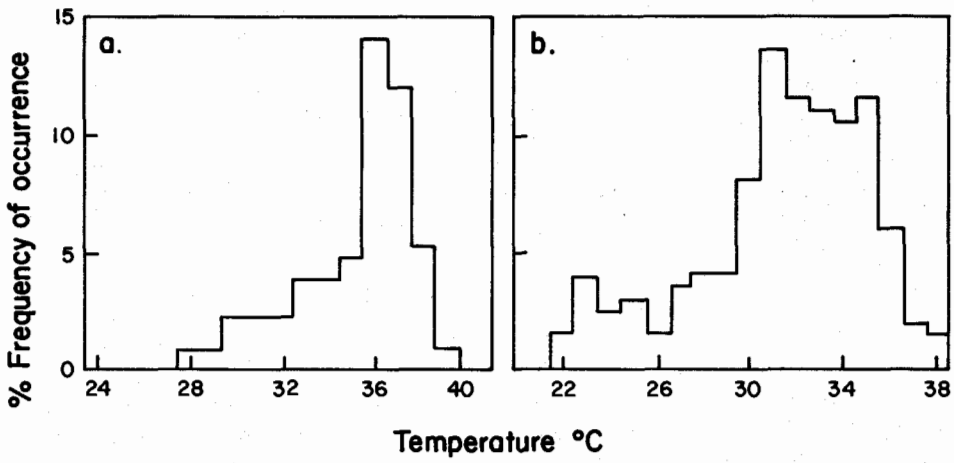

Figure 1. Temperature 'selection' by juvenile a) *Tilapia rendalli* and b) *Sarotherodon niloticus* in a thermal gradient test tank (after Caulton 1979).

Such an intense behavioral response to temperature clearly indicates that these fish are strongly thermophilic and in some instances, this response is so strong that individuals briefly enter water warmer than that in which they could normally survive. The eccritic temperatures demonstrated by the species tested (*Sarotherodon mossambicus*, *S. niloticus*, *S. macrochir* and *Tilapia rendalli*) varied between 30°C and 36°C. Temperatures of this

magnitude may initially appear extraordinarily high, but they are not uncommon in the shallow marginal waters of tropical and equatorial lakes, lagoons and river pools of Africa. These high, temperatures, however, are generally not stable throughout the day but, due to the shallowness of the water, are subject to diel oscillations often in excess of 15°C per day. It has been noted by many authors (e.g. Welcomme 1964; Donnelly 1969; Fryer and Iles 1972; Bruton and Boltt 1975; Caulton 1975) that a variety of tilapias react to such temperature oscillations by moving inshore during the day and offshore at night. A graphical example of such a movement by juvenile *T. rendalli* is illustrated in Figure 2.

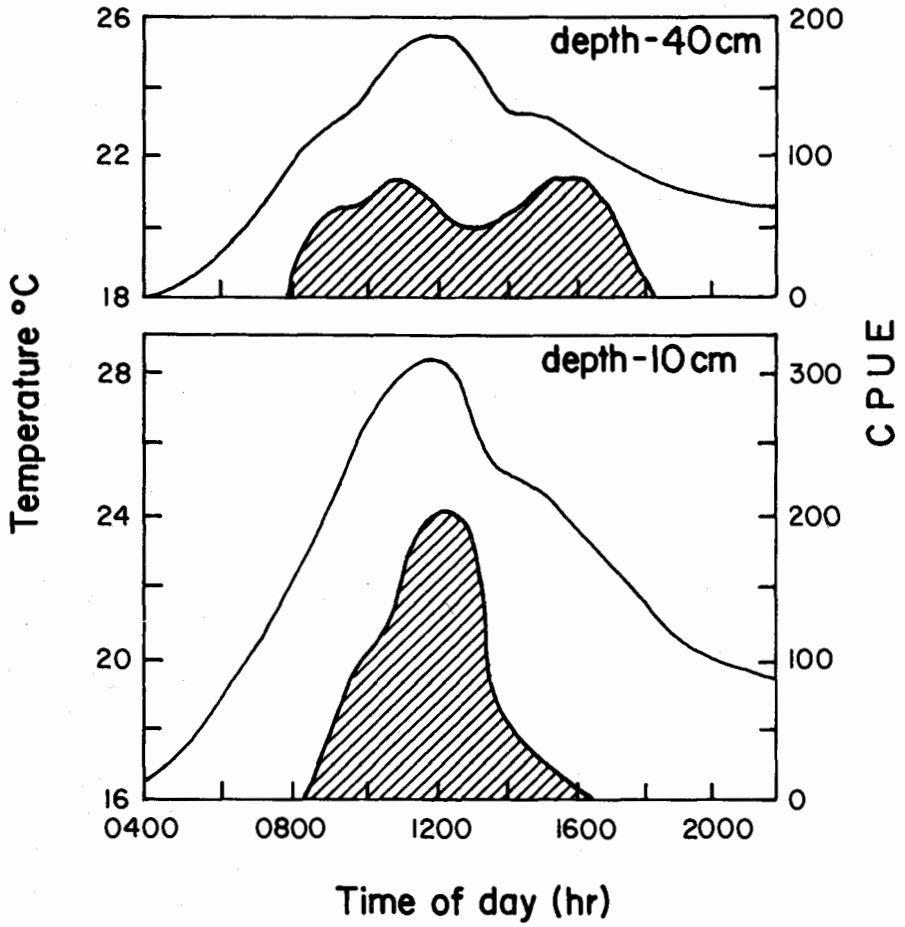

Figure 2. The daily inshore (10 cm depth)/offshore (40 cm depth) movement of young *Tilapia rendalli* in Lake McIlwaine, Zimbabwe. (1.10.74). Catch per unit effort (CPUE) is given as the number of fish caught over a 15 min time period using a 2 m cast net. The numbers of fish caught are shown by the cross hatch areas. Upper lines show the change in temperature (after Caulton 1975a).

With the knowledge that tilapias are strongly thermophilic, it may not be surprising that such daily inshore/offshore movements do occur. In the example illustrated, the movement of young *T. rendalli* (up to 10 cm SL) can be followed from the deep (> 1.5 m) homothermal water, where they stay overnight, into water 40 cm deep, beginning at 8:00 A.M. or when the temperature at this depth exceeds that of the homothermal waters. The

inshore movement of juvenile fish continues throughout the morning and eventually large schools of juveniles are found in shallow warm water at midday. A reverse movement is noted in the late afternoon when the fish, again responding to temperature, leave the now cooling margins to return to the relatively warmer, homothermal deeper waters.

Such diel movements are commonly encountered in shallow gradient shoreline areas, while fish habitually favoring deeper open waters may occasionally show a less spectacular but nevertheless visible vertical movement for a similar reason. These patterns of diel movement can however be easily disrupted; for example, during periods of even moderate winds the wave wash along the shore is sufficient to restrict movement into very shallow water. Similarly, during exceptionally warm periods, or in areas where excessive shoreline vegetation assists in insulating the warm daytime water in the shallow margins, a nocturnal presence of juveniles is not uncommon. When in areas of food paucity, fish often have to remain in the shallows at night in order to feed. The presence of predators in deep water is also a strong factor which will seriously disrupt any set daily pattern of movement although avian predation along the margins during the day does not seem to influence the movements very strongly.

Notwithstanding the possibility of such numerous disruptions, many young tilapias are often subjected to a daily thermal variance of between 10°C and 15°C and, since fish are poikilothermic, such thermal variations will understandably have an important bearing on almost all of the animals' physiological functions. Of these functions, metabolism would be expected to be most markedly affected. In broad theoretical terms, metabolic energy demands are expected to approximately double with every 10°C rise in body temperature. Thus a tilapia moving into the warm shallows during the day must expend considerably more energy than it would during the night in the relatively cooler deeper water. It may be expected that as a consequence of this fluctuating energy demand, fish living under these conditions of thermal fluctuation would show unnecessarily high expenditure of energy during the day, which could otherwise have contributed to either storage or growth.

To investigate this, it is necessary first to look in some detail at the effect temperature has on metabolism. Metabolism, as a function of aerobic respiration, can be quantitatively equated to the uptake of molecular oxygen which in turn is a simple measure that can be obtained in the laboratory. Many extrinsic variables can modify the basic metabolic rate or oxygen consumption of a fish in nature, but, suppressing most of the variables, with the exception of temperature, relationships demonstrating the influence that temperature has on metabolism can be investigated. Obviously, a laboratory test animal out of its natural environment is subjected to a number of unnatural stresses which are capable of either increasing or suppressing normal oxygen consumption but, in general, laboratory acclimated juvenile tilapias are reasonably suited to respirometry and show few visible signs of the stress so often encountered in the apparently more nervous cyprinids and other fish.

Using a simple continuous flow, continuous recording respirometer as described by Caulton (1975a), a satisfactory measure of routine metabolism in both *T. rendalli* and *S. mossambicus* has been obtained. Routine metabolism

by definition can be described as the energy required by an unfed fish exhibiting spontaneous rather than directed movement. Such a measure of metabolism is particularly suited to tilapias, since movement even in their natural habitat is very seldom vigorously directed but can more often be described as spontaneous fin generated movements. Obviously, exceptions do occur, e.g., during intense feeding activity, migrations or predator avoidance. This suggestion is borne out to a certain extent by the fact that schools of juvenile *S. mossambicus* in a large communal respirometer all displaying normal swimming, schooling behavior and feeding movements (into sterile sand) showed an increased metabolic demand 25% greater than that required by the same fish at night, when they were almost stationary, or that obtained from the summation of individual oxygen requirements in a normal single chamber respirometer. This contrasts markedly with generally faster moving, continuously swimming fish species, especially predators, which may require at least twice as much energy during normal active periods than during inactive periods.

The conversion for equating oxygen consumption to the amount of metabolic energy liberated by herbivorous tilapias was calculated as 13.68 J/mg O_2 (Caulton 1977a), and thus with the availability of such a conversion factor, it is possible to obtain more quantitatively meaningful information from respirometry. The routine metabolic energy demand by *S. mossambicus* can be satisfactorily described by the equation:

$$R_r = 0.0086\ t^{2.0783}\ M^{0.652}$$

where R_r is the energy of metabolism expressed in J/hr, 't' the temperature in °C and M the fresh mass of the fish in grams (restricted to fish less than 150 g, the maximum size used in the trials). The full details of the derivation of this formula are given in Caulton (1978c).

A similar relationship between temperature and metabolism, but for a single size range of fish, is shown graphically in Figure 3, where the metabolism

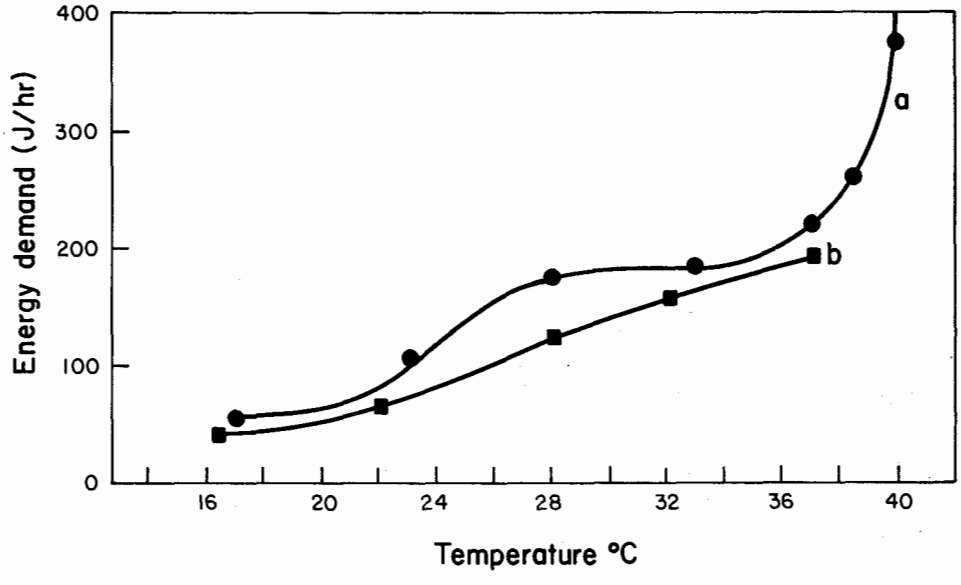

Figure 3. The influence of temperature on metabolic energy demand in a) *Tilapia rendalli* and b) *Sarotherodon mossambicus* (modified after Caulton 1977a, 1978c).

of *T. rendalli* and *S. mossambicus* is compared. Unlike *S. mossambicus*, *T. rendalli* shows an unexpected three-phase energy demand in which the distinctive plateau phase, extending from approximately 28°C to 37°C, is an unusual characteristic. Over this temperature range the metabolic demand of *S. mossambicus* increases by 62% whereas the metabolic energy demand by *T. rendalli* over the same temperature range increases by only 22%. Similarly structured, unusual metabolic curves have been reported for other fish species (Schmein-Engberding 1953; Sullivan 1954; Job 1969a, 1969b and Fry 1971 for *S. mossambicus*). Denzer (1968) reports a similar function in *S. niloticus*. Exactly how important, or in fact how real, such thermal homeostasis is, is difficult to determine and respirometry technique (static versus flowing systems) must be considered when appraising results. Obviously any function that can appreciably depress an expected rise in energy demand must also benefit the overall energy balance in consequence.

The metabolic energy required to sustain routine maintenance by a 50 g *T. rendalli* at, for example, 28°C is approximately 175 J/hr (Figure 3) but to appreciate this requirement in terms of the utilization of storage tissue, it may be pertinent to consider which catabolic fuels are responsible for the supply of energy. Glycogen or the major carbohydrate fraction is an energy source usually stored in the liver but, in *T. rendalli* at least, is not of great significance as a sustained catabolic energy source. A 50 g *T. rendalli* in good condition has a maximum glycogen content of 0.46% by mass (about 230 mg) and of this amount 144 mg are stored in the liver while the remainder is present in the muscle. On starvation approximately 100 mg of glycogen is utilized within the first few days, thereafter the level remains relatively constant even to the state of near death from starvation. This 100 mg could supply sufficient energy to maintain a 50 g fish at 28°C for less than 12 hours and thus cannot be classified as of great importance as a storage fuel to a starving fish, which is thus reliant mainly on lipids and protein as a source of catabolic energy. The importance of condition is immediately evident and a close relationship does exist between condition and the type of catabolic fuel mobilized during routine maintenance. The mobilization of lipids is always associated with some protein mobilization (and vice versa) and follows a pattern closely linked with condition.

Condition in the present context is described as a morphometric interpretation of a fish's plumpness as compared to the population mean. As such, condition is an extremely useful measure of assessing the physiological state of a fish and more cognizance of this measure should be taken by the fish farmer. The classical measurement of relative condition as described by Le Cren (1951) using the formula $Kn = 100\ W/L^b$ where Kn is the relative condition, W the fresh mass in grams, L the standard length in cm and 'b' the length/mass regression exponent, provides an adequate quantitative assessment of condition if the basic measurements are made carefully. In *T. rendalli* close relationships do exist between condition and the proportionate mobilization of fat/protein during metabolism but extreme care must be exercised when interpreting these relationships (see Caulton and Bursell, 1977, for a discussion of these problems, especially the use of percentages when measuring or interpreting results).

The mass of all major body constituents, with the exception of the inorganic compounds, must, by definition, decrease with a decline in condition, but it is the relative pattern of decline of each constituent that is important. The lipid content (predominantly the triglyceride groups) declines rapidly with decreasing condition (Figure 4) indicating a preferential mobilization of triglyceride lipids during routine catabolism in fish of good condition. When compared with protein mobilization, the initial preferential utilization of storage fats as a catabolic fuel becomes even more evident (Figure 5). Tilapia in good condition derive nearly 3 times as much metabolic energy from fat reserves than from protein while fish in poor condition come to rely almost exclusively on protein as a catabolic fuel when triglyceride lipid has declined to a level which may be critical or almost non-existent (Figure 4). Since lipid is a high energy compound containing 1.7 times more energy per unit mass than protein, it follows that as the fish become more and more reliant on a protein source for catabolism, so the rate of decline in mass or condition accelerates. This may be one of the reasons why a decline in condition so often appears to lag behind an expected decrease due either to a predicted environmental stress or to some expected physiological stress at the end of a period of good growth.

The preferential mobilization of either lipid or protein as the major metabolic energy source has little effect on oxygen consumption since 13.72 J of energy is liberated from lipid for every mg of oxygen utilized while only marginally less energy, 13.39 J, is liberated per mg of oxygen if protein is the prime energy source. Thus, although fish that show rapidly declining condition will be largely utilizing somatic protein as a catabolic fuel, oxygen consumption basically remains a function of the mass of tissue and only in extremely accurate work is the proportionate composition of the fish important.

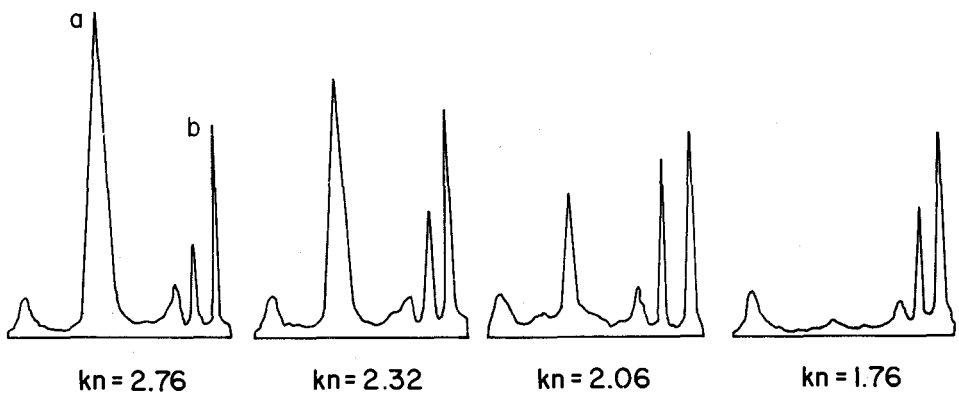

Figure 4. Semi-quantitative analysis of the various lipid fractions from *Tilapia rendalli* of varying condition (a = triglyceride, b = phospholipid, kn = relative condition factor).

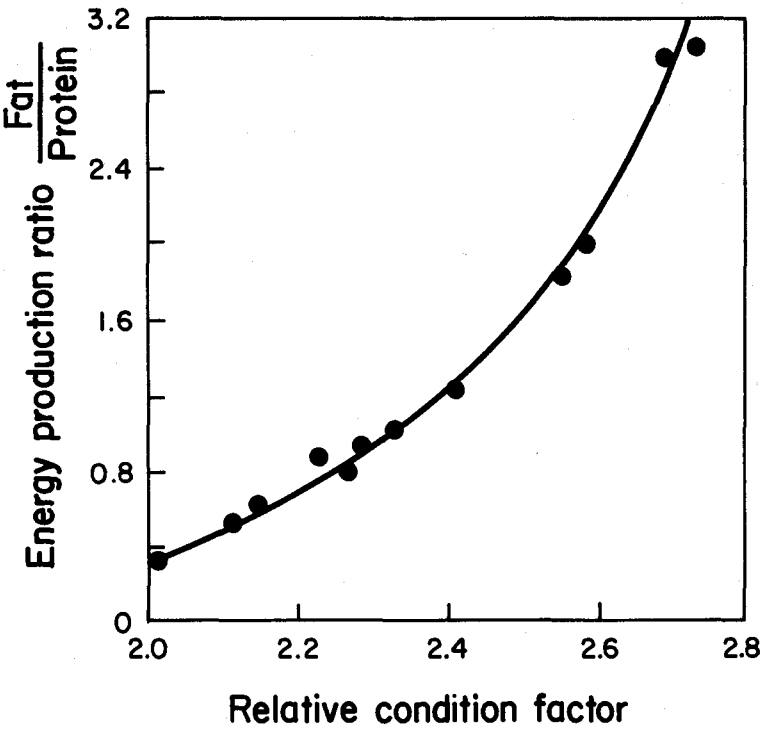

Figure 5. The energy production ratio of fats and proteins during change in relative condition factor for *Tilapia rendalli* (after Caulton 1978b).

The problem of accurately predicting the tissue mass of a live fish prior to respirometry is difficult because the relationship between tissue mass, water content and condition is continually changing. The proportionate relationship between tissue (lipid and/or protein) and water is seldom a simple inverse linear function, as so often suggested, but changes with changing condition. The ratio of water and tissue in *T. rendalli*, for example, is lowest in fish of good condition (Figure 6), highest in medium condition fish and marginally declines in fish of poor condition. This complicating factor will certainly have a small but important effect on oxygen consumption when it is related to the fresh mass of the fish and thus for precise measurement of metabolism, oxygen uptake or the metabolic demand should be related rather to the dry tissue mass or the energy content of the fish and not simply the fresh mass unless the fish are all in a similar condition.

The information already discussed can be correlated and cross-referenced to metabolism: an exercise that gives confidence to some of the results discussed. For example, a morphometrically similar group of young *T. rendalli* with an average mass of 42.63 g and having an average condition of 2.23 were maintained without food for a period of ten days at a constant temperature of 18°C. The average mass loss over this period was measured as 2,020 mg per individual. From our knowledge of oxygen consumption and energy utilization by *T. rendalli* (Figures 3 and 5), it is calculated that over

the trial period 11.7 kJ of energy was released to sustain routine metabolism. From the information given in Figure 5, a fish of condition 2.23 would be expected to derive 43.8% of its energy from fat catabolism and 56.2% of its energy from a protein source. Thus of the 11.7 kJ of energy required for maintenance, 5.1 kJ would be supplied from a lipid source and 6.6 kJ from a protein source. This, in terms of total tissue mass, represents 130 mg. of lipid and 280 mg of protein or a total of 410 mg of tissue. It can be estimated that approximately 1,760 mg. of water associated with the tissue would be simultaneously lost (Figure 6) thus giving a total fresh mass loss of 2.17 g: a reasonable comparison to the measured loss of 2.02 g. Similar comparative estimates for various other temperatures are given in Table 1. The reasonably close values demonstrate that tissue composition as derived from careful condition factor analysis is a useful and fairly accurate predictive method to determine composition for detailed respirometry or to establish the pattern of utilization of catabolic fuels during metabolism without killing the experimental fish.

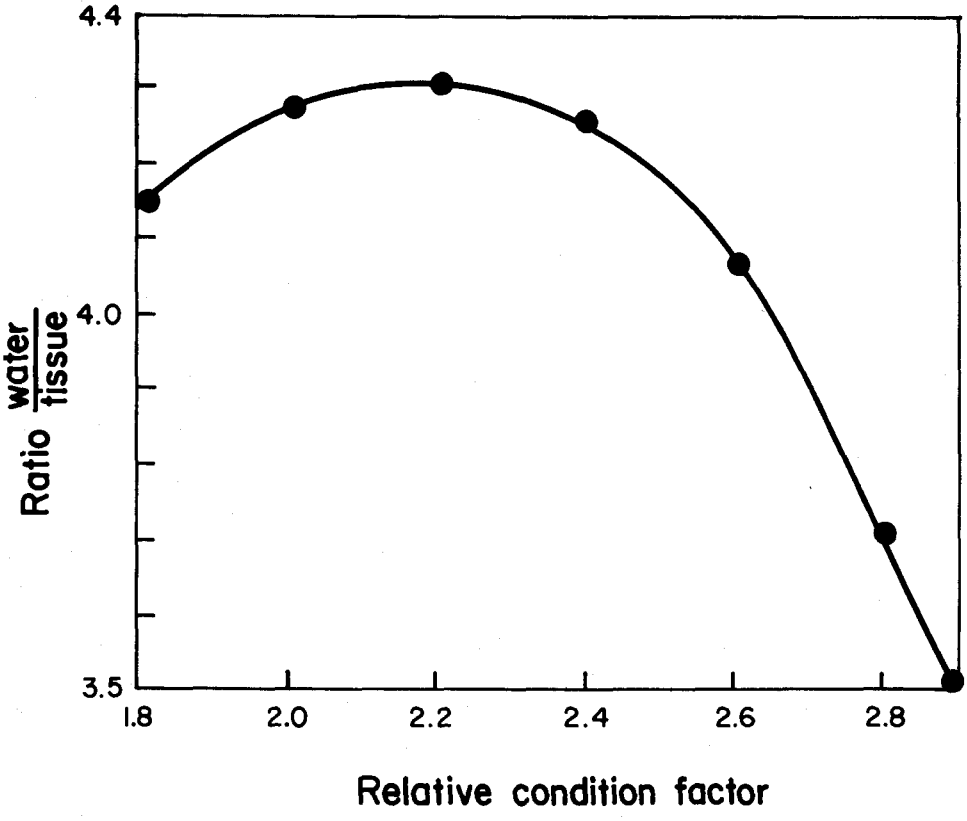

Figure 6. The relationship between water content and tissue content for *Tilapia rendalli* of varying relative condition factor (after Caulton 1978b).

Table 1. Comparison of measured and estimated change in mass during starvation of *Tilapia rendalli* at six experimental temperatures (after Caulton 1977c).

Temperature °C	18	20	21	24	30	34
Time of starvation (d)	10	6.25	6.75	6	12	8
Mean condition factor (kn)	2.23	2.42	2.51	2.68	2.58	2.60
Number of fish	19	19	19	8	14	18
Total measured mass lost (mg)	2020	1260	1940	3282	3641	4196
Estimated mass of tissue used (mg)	409	268	373	607	779	802
Estimated mass of water lost (mg)	1759	1140	1563	2398	3101	3272
Total estimated mass lost (mg)	2168	1408	1936	3005	3880	4074

Feeding and Growth

Sub-adult and adult *T. rendalli* are essentially macrophagous plant feeders in areas of abundant aquatic vegetation, a feature which lends this species most favorably to quantitative feeding experiments. The ubiquitous plant *Ceratophyllum demersum* heads a list of preferred food types eaten by *T. rendalli* when available, and it was for this reason that this plant was chosen for the work to be described. Like almost all species of tilapia, *T. rendalli* generally restricts its feeding to daylight hours (Figure 7) and thus to maintain some level of simulated natural conditions laboratory feeding trials were conducted over the same time period.

C. demersum growing shoots (terminal 1-7 g) were used throughout the trials and the following necessary facts about the plant were established. To convert fresh mass (limited centrifugation to remove surface moisture) of *C. demersum* to dry mass equivalents the following relationship was used:

$D = 0.0839\ W - 0.7845$ ($r = 0.986$, $n = 50$, SE 'b' = 0.003) and for converting dry mass to fresh mass, $W = 11.5941D + 26.7257$ ($r = 0.986$, $n = 50$, SE 'b' = 0.478) where W is the fresh mass and D the dry mass both expressed in milligrams. The average energy value of the dry shoots was determined as 17.9477 kJ g^{-1} ($n = 20$, SE = 0.0236).

Laboratory maintained fish fed to satiation during a prescribed daylight period of 12 hours showed a linear relationship between food consumed and fish mass (Table 2), a feature also reported for wild fish (Moriarty and Moriarty 1973a; Caulton 1977a) but in reality, over the range juvenile to large adult, it may be expected that as growth rates decline so less food per unit mass of fish would be consumed. Using the data presented in Table 2 for consumption rates at various temperatures, the relationship between food consumed and temperature, for a given size fish, is found to be curvilinear showing increasing food intake with increasing temperature (Figure 8). This relationship holds over the range 18°C to 30°C, but between 30°C and 35°C consumption is little affected by temperature, while at temperatures in excess of 35°C, food intake declines and ceases at about 37 or 38°C.

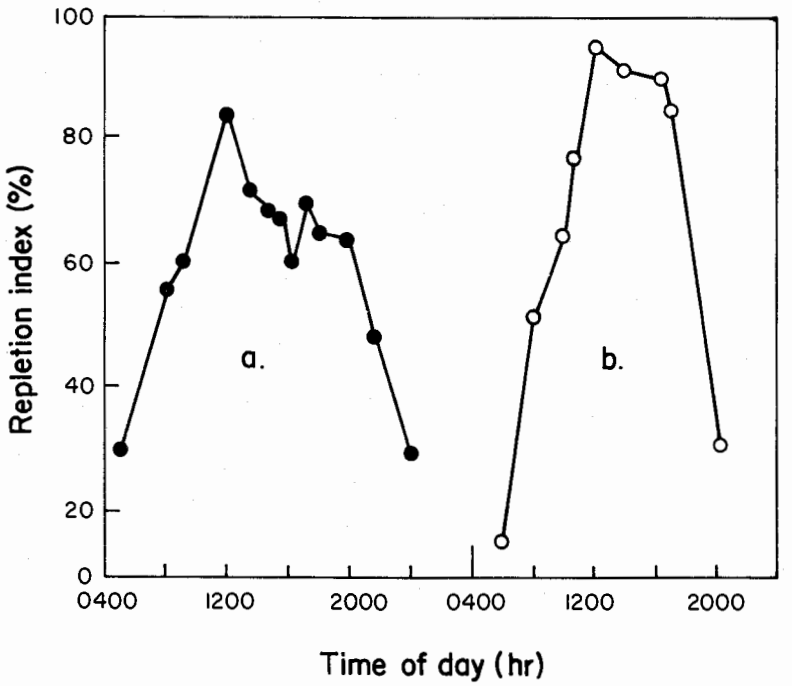

Figure 7. The daily feeding cycle of *Tilapia rendalli* in Lake McIlwaine, Zimbabwe (a, 1.9.75; b, 30.10.75).

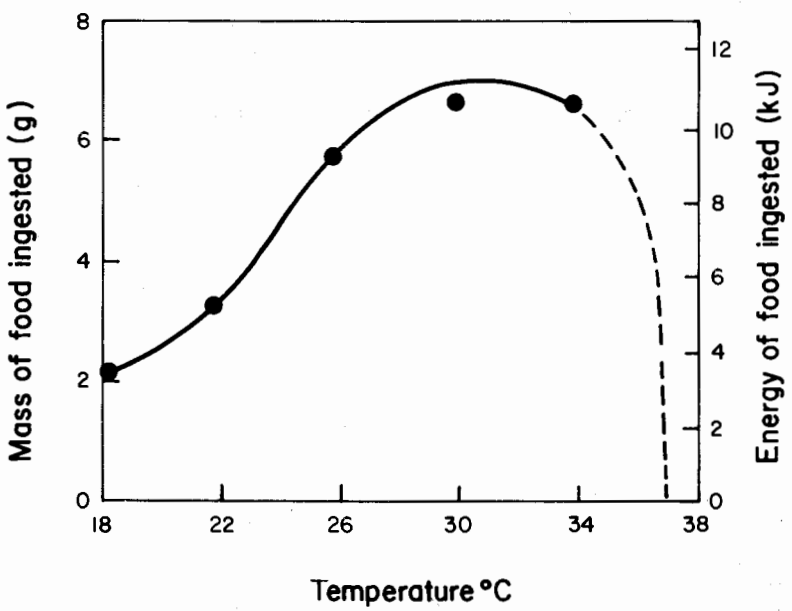

Figure 8. The effect of temperature on the daily food ingestion of laboratory-maintained juvenile (50 g) *Tilapia rendalli*. Dotted line extrapolated to show decline and cessation of feeding above 35°C (see text).

It is well known that many species of fish, especially the tilapias, will regulate their food intake in confined captivity. Thus, it is extremely difficult to relate quantitatively the patterns of food intake shown in Figure 8 and Table 2 to wild populations. Estimates of food ingestion in some wild populations have, however, been calculated using a most useful technique initiated by Moriarty and Moriarty (1973a). This particular technique is suited for use in some algal feeding tilapias, but it is a technique possibly even more suited to macrophagous feeders, such as *T. rendalli* when feeding on *C. demersum*: a food with a characteristic green color. Moriarty and Moriarty (1973a) estimated, for example, that a 200 g *S. niloticus* in Lake George would consume just less than 3 g (dry mass equivalent) of algae per day while a *T. rendalli* of equal proportion in Lake Kariba would consume about 3.3 g (dry mass equivalent) of *Panicum repens* per day (Caulton 1977b). Similarly, a 100 g *T. rendalli* in Lake Kariba would consume about 2.2 g (dry mass) of food per day, yet a laboratory maintained fish of 100 g at 28°C (roughly equal temperatures) consumes 12 g of fresh *C. demersum* per day (Table 2) or an equivalent of 1 g dry mass of food. Thus, it would appear that laboratory satiation is equivalent to about half the daily food intake of wild, free-living fish. A similar observation published by Moriarty and Moriarty (1973b) shows that this function is not restricted to macrophagous tilapias, but is also a feature of phytoplankton-feeding species.

Table 2. Linear regressions describing the amount of *Ceratophyllum demersum* growing shoots ingested by young *Tilapia rendalli* at various temperatures when fed *ad lib* in laboratory. (Feeding period = 12 hours; C is the fresh mass of food ingested and M the mass of the fish) (both measured in grams: after Caulton 1978b).

$C_{18°C} = 0.0667M - 1.061$	(n = 37, r = 0.975, S. E. 'b' = 0.002)
$C_{22°C} = 0.0709M - 0.261$	(n = 28, r = 0.946, S. E. 'b' = 0.001)
$C_{26°C} = 0.1097M + 0.278$	(n = 30, r = 0.974, S. E. 'b' = 0.004)
$C_{30°C} = 0.1169M + 0.683$	(n = 23, r = 0.970, S. E. 'b' = 0.003)
$C_{34°C} = 0.1205M + 0.868$	(n = 19, 5 = 0.986, S. E. 'b' = 0.005)

Quantitative and accurate measurements of the assimilatory potential of *T. rendalli* fed on *C. demersum* in the laboratory are possible (Caulton 1978a). Table 3 summarizes the results obtained for such experiments over a temperature range 18°C to 34°C. A definite relationship between assimilation efficiency and temperature indicates an increased efficiency of assimilation with increasing temperature. A relative increase in efficiency of 18.6% between 18°C and 34°C is a feature that may be expected to have some favorable effect on the energy balance resulting in better growth. Not only is more nutrient mass being extracted from the food at higher temperatures but also more energy per unit mass of food is being assimilated. This feature is reflected in the relative decline in the energy content of the feces with increasing temperature. It is also noted that the inorganic mineral content of

the feces recovered from a given meal of *C. demersum* varies from 4% to 15% less than that consumed, but this removal of minerals snows no relationship to, or definite pattern with, either assimilatory efficiencies, meal size or temperature. In the results presented in this paper cognizance is taken of this fact and the results given are corrected accordingly. A further feature of note is that the relative energy content of the feces is greater (gram for gram, mineral corrected) than the food. This is a common feature, but such differences are often misinterpreted when investigating assimilation.

Table 3. The effect of temperature on assimilation by juvenile *Tilapia rendalli* when fed *ad lib* on *C. demersum* (17.96 kJ/g). (Number of determinations (n) = 28 per temperature).

Temperature °C	Mass (mg) of feces recovered per 1,000 mg dry *C. demersum* consumed	Energy (J) of feces recovered per kJ *C. demersum* consumed	Mean energy (J) assimilated per kJ *C. demersum* consumed	Mean energy (kJ/g) content of feces (2 x SE)	
34	399.2	413.0	587.9	18.6	(0.29)
30	394.6	417.8	582.2	18.9	(0.32)
26	413.5	448.5	551.6	19.42	(0.21)
22	449.8	470.0	530.0	19.34	(0.41)
18	470.5	522.1	477.6	19.92	(0.30)

An assimilation efficiency ranging from 47.8% to 58.7% may be regarded as being very good for a primary macrophagous herbivore. This efficient utilization of food can be attributed largely to successful primary food trituration and efficient pre-assimilatory processing of the food (Caulton 1976). The breakdown of resilient cell wall structures is the key factor and as such, assimilatory capabilities will vary considerably,depending on the species and composition of the plants eaten.

The mechanical trituration of the food, like digestion, absorption and transportation of primary nutrients, also requires an energy input by the fish. Such energy-demanding functions can be collectively termed 'apparent specific dynamic action' (S.D.A.) or the calorigenic cost of food processing. The additional collective energy required for these processes can be measured by feeding fish in a respirometer and measuring the post-feeding increase in oxygen consumption and equating any increase in oxygen uptake to the level of energy input through feeding. The energy costs of feeding *C. demersum* to *T. rendalli* in a respirometer are shown in Figure 9 and Table 4.

From the data presented it is apparent that meal size and processing costs are related in a linear fashion with greater processing costs (relative per unit food consumed) being required to synthesize larger meals. A linear trend of increasing processing costs with increasing meal size may be expected and has been described for a variety of fish (mainly predatory species— Edwards et al. 1972; Hamada and Ida 1973; Beamish 1974), but exponential relationships have also been described for some species (Tandler and Beamish 1979) so there appears to be no standard function to describe this relationship. A second noticeable feature of the results presented in Table 4 is that in *T. rendalli* food processing costs also increase with increasing temperature

irrespective of the amount of ingested energy. As previously shown from results of experiments to determine assimilation efficiency, the amount of energy liberated per unit mass or energy of food ingested increases with increasing temperature thus it may not be surprising that the processing costs of food preparation increase proportionately. The increase in food processing costs with the increasing temperature can, at warm temperatures, seriously deplete the favorable gain in energy due to the greater assimilation efficiency at those temperatures. For example, a fish that consumed 1 kJ of food at 18°C would have available 478 J of post-assimilatory energy from which a further 20 J of energy must be deducted for processing costs leaving approximately 458 J of free energy available for metabolism and growth. Likewise, a fish at 30°C would have 582 J, less a calorigenic cost of 109 J, or 473 J of energy available. The difference in assimilatory efficiency between fish feeding at 18°C and those feeding at 30°C results in a gain of some 104 J, but when the cost of food processing is considered this difference is reduced to an almost insignificant 15 J. This clearly demonstrates just how energy demanding food processing is at higher temperatures. This example also serves to illustrate that digestibility alone, as a comparative measure used to forecast growth potential attributable to various diets, may not always be a suitable measure unless the associated food processing costs are also considered. This is especially important to the users of pelleted rations and fish farmers should not be misled by manufacturers' claims of good digestibility and consequently optimistic growth forecasts, as deduced from digestibility trials alone.

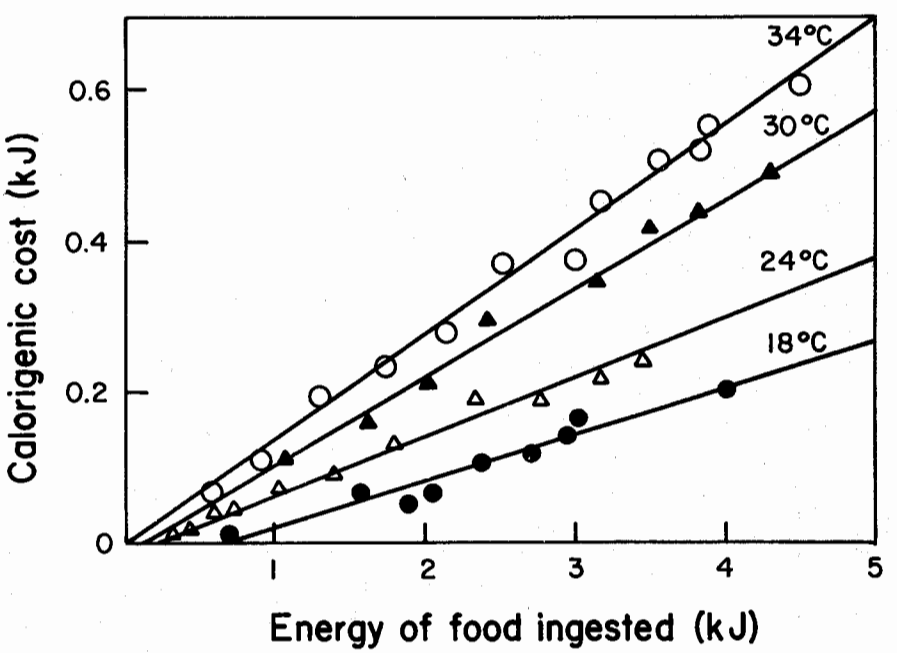

Figure 9. The effect of temperature on the calorigenic cost of food processing shown by *Tilapia rendalli* feeding on *Ceratophyllum demersum* (n = 39, after Caulton 1978a).

Excretory products, predominantly in the form of ammonia, are largely derived as a by-product of protein deamination and as such will reflect the effect of temperature on assimilation. Ammonia has an energy content of 20.4 kJ g^{-1} (Elliott and Davison 1975) and thus by determining the rate of either protein catabolism or protein assimilation, an estimate of the loss of excretory energy can be calculated. Table 5 gives an estimate of the rate of excretory energy loss when *T. rendalli* is feeding on *C. demersum.*

Table 4. Linear regressions describing the effect of temperature on the calorigenic cost of food processing. *Ceratophyllum demersum* by *Tilapia rendalli* (R_s = cost of food processing expressed in joules, C = the energy of *C. demersum* consumed expressed in joules and S. E. 'b' is the standard error of regression slope. (After Caulton 1978b).

Temperature	Regression
18°C	$R_s = 0.063C - 43.41$ (r = 0.94, S. E. 'b' = 0.010)
22°C	$R_s = 0.074C - 26.69$ (r = 0.96, S. E. 'b' = 0.008)
24°C	$R_s = 0.082C - 16.95$ (r = 0.98, S. E. 'b' = 0.006)
26°C	$R_s = 0.094C - 7.99$
30°C	$R_s = 0.119C - 10.10$ (r = 0.99, S. E. 'b' = 0.004)
34°C	$R_s = 0.142C - 10.75$ (r = 0.99, S. E. 'b' = 0.007)

Table 5. An estimate of the expected loss of ammoniacal energy per unit energy of food consumed for *Tilapia rendalli* feeding on *Ceratophyllum demersum.*

Temperature °C	34	30	26	22	18
Joules of NH_4 excreted per joule *C. demersum* consumed	0.028	0.028	0.027	0.026	0.023

The collective data already provided, in various forms of energy gains or losses, can now be integrated to provide some information pertaining to the growth and optimization of productivity by tilapias. For example, a simplified model of physiological growth can be derived from the use of so-called balanced energy equation (Davis and Warren 1971). This equation is derived from the balance between energy inputs and energy outputs and from such an equation one can determine, for example, growth potential as well as some of the ways in which temperature can affect growth. The input of energy in the form of the amount of food energy consumed (C) can be balanced against the various energy losses through egesta (F = feces plus U = excretory products), as heat by routine metabolism (Rr), through the cost of food processing (Rs), by movement (Rm) as well as that energy stored as fat,

protein or glycogen, which together represents the energy of growth or productivity (ΔB). Thus, the basic equation can be given as:

$$C = F + U + Rr + Rs + Rm + \Delta B.$$

or on re-arrangement, growth potential can be derived from:

$$\Delta B = C - (F + U + Rr + Rs + Rm).$$

Substitution of the results given in the appropriate figures and tables into the equation results in the derivation of a simple formula that can describe growth in *T. rendalli*. For example, at 18°C a fish of M grams consuming C joules of *C. demersum* per day would have a daily growth potential of:

$$\Delta B_{18°C} = C - (0.522C + 0.023C + 27.53M + 0.063C - 43.41)$$

or on re-arranging the equation:

$$\Delta B_{18°C} = 0.392C + 43.41 - 27.53M$$

Similar formulae can be derived for the other experimental temperatures and the resultant equations obtained are listed in Table 6. (Energy of movement is not included in these formulae since its omission does not affect the following discussion).

Utilizing the equations an estimate of the food intake required for maintenance, i.e., when $\Delta B = 0$, can be obtained. At 18°C, for example, maintenance energy for a 50 g *T. rendalli* would approximate 3.4 kJ/d (Table 6) which, in terms of *C. demersum* intake, would be equivalent to 189 mg dry mass or 2.2 g of fresh plant material. When compared to the amount of food ingested *ad lib* over a 12-hour laboratory feeding period at 18°C (Table 2, Figure 8), the level of so-called satiation is almost exactly the same as the estimated energy required for maintenance. This similarity in the level of food intake and maintenance energy requirement not only applies to low temperatures but to all the temperatures investigated (Table 7). This phenomenon illustrates the problems associated with attempting to determine growth rates under restricted laboratory conditions, but although field related growth patterns cannot be simulated under restricted conditions, some useful principles concerning growth may still be derived from laboratory work.

T. rendalli fry, like many other tilapia fry, will grow in 80-liter aquaria to about 30 or 40 g, when growth generally decelerates and then almost stops at about 80 g—even under conditions of abundant and nutritious food availability. In aquaria, 10 g *T. rendalli* fry maintained at 18°C showed negligible growth, but a comparable group maintained at 30°C showed a fairly good rate of growth with the latter fry reaching 40 g in six to eight weeks.

At the beginning of this paper, it was suggested that many marginal dwelling tilapias are, in their natural environment, seldom restricted to a

Table 6. Theoretical growth (ΔB) equations to describe the growth potential of young *Tilapia rendalli* at various temperatures. ΔB is expressed in joules per day, C is the energy (J) of food consumed per day and M the fresh mass of the fish, weighing between 40 and 60 g.

$$\Delta B_{18°C} = 0.392C + 43.41 - 27.53M$$

$$\Delta B_{22°C} = 0.428C + 26.69 - 39.66M$$

$$\Delta B_{26°C} = 0.430C + 7.99 - 69.87M$$

$$\Delta B_{30°C} = 0.437C + 10.10 - 88.70M$$

$$\Delta B_{34°C} = 0.422C + 10.75 - 91.34M$$

Table 7. A comparison of the energy required for satiation in the laboratory (see Table 2) and the estimated energy required for maintenance as derived from Table 6 when $\Delta B = 0$, for *Tilapia rendalli* feeding on *Ceratophyllum demersum*.

Temperature °C	Laboratory satiation ($kJ\ d^{-1}$)	Maintenance energy requirement ($kJ\ d^{-1}$)
18	3.43	3.40
22	4.95	4.57
26	8.70	8.11
30	9.84	10.13
34	10.42	10.80

constant temperature but are usually subjected to varying degrees of daily thermal fluctuations. If fry (10 g) restricted in aquaria, were subjected to a thermal oscillation (18°C night, 30°C day), then their growth rate was found to be very similar to that shown by a control group of fry maintained at 30°C. The major difference between the two groups was found, however, in their feeding, with those fry maintained at a constant temperature of 30°C consuming up to *twice* as much food as those fry subjected to daily temperature changes. Both groups of fry grew from a mean standard length of about 6.5 cm to a maximum of 10 cm over a 45 day period. This growth represents an increase from 10 g to about 40 g in mass. Although the two groups showed very similar growth, their food intake was very different. An explanation for this difference can be obtained using the growth equations of Table 6. For example, a 50 g fish maintained at a constant temperature of 30°C and having a growth rate of 1,000 J/d (196 mg fresh mass per day) would be expected to consume:

$$((88.7 \times 50) - 10.1 + 1000) / 0.437 = 12414 \text{ J/d}$$

A similar fish subjected to a 12-hour daytime temperature of 30°C and with a nocturnal non-feeding temperature of 18°C would, in order to grow by the same 1,000 J/d, have to consume:

$$((88.7 \times 50 \times 0.5) - 10.1 + 1000/0.437) + (27.53 \times 50 \times 0.5) = 8028 \text{ J/d}$$

Thus, for individuals from either of the two groups to grow by equal amounts, those fish maintained at a constant temperature require 1.6 times more food than the group subjected to a thermal oscillation of 30°C to 18°C. On testing a variety of combinations in a similar manner, it becomes evident that as the temperature oscillations become less marked, so the ratio between the energy of growth and the energy of food consumed (Δ B/C, Odum's ecological growth efficiency) decreases, resulting in a decline in the efficiency of production.

Estimates of food consumption conducted in (optimal?) *T. rendalli* habitats at Lake Kariba during summer indicate that a 50 g fish consumed an average of 12.6 kJ/d of food, which is equivalent to about 8.2 g/d of fresh food (maximum measured was 10 g/d). Growth estimates obtained from the same wild population by tagging indicate an instantaneous growth capability of 690 mg/d or 3.6 kJ/d. Calculating the ecological growth efficiency (using energy values) of this population, a value of 0.29 is obtained. If the same size fish consumed the same amount of food energy but was maintained at 28°C (mean maximum and minimum of midsummer Kariba temperature oscillation) then growth would be calculated to be 1.3 kJ/d (derived graphically from Table 6) with an ecological growth efficiency of 0.10 or approximately half that calculated for the wild population.

The key factor in this change of growth efficiency is the metabolic energy demand, since, if food is not limiting, the other parameters of the energy balance do not vary in sufficient magnitude to seriously affect the balance at any given temperature. The relationship between food intake and temperature has, in the laboratory, been shown to be strongly temperature related but indications are that in the field, a less marked influence is found, although fish do feed more actively at higher temperatures. This being the case, then, some influence will be reflected in the growth efficiency, but it still remains more likely that metabolism is the governing factor. The pattern of change in metabolic demand with changing temperature may be a complicating factor, but, on the whole, relationships of the type shown for *T. rendalli* or *S. mossambicus* (Figure 3) result in only very subtle variations in the final result. More important is the effect of fish size on metabolism. The smaller the fish the greater the benefit of thermal oscillations may be since the metabolic demand by small fish is greater, per unit mass, than larger fish. Thus, there may well be a limit whereby larger fish no longer benefit from diel migrations to warm shallow water and this, combined with food distribution, may be a reason why juvenile fish are far more abundant in shallow marginal areas of gradient shorelines.

One is able to draw on limited examples from wild populations to support the theory that thermal oscillations are beneficial to the growth of juvenile cichlids. The work of Coe (1966, 1967) showed that the resident population of *S. alcalicus (T. grahami)* in the thermal springs of Lake Magadi (Kenya)

showed stunting and poor growth. These fish were generally located close to the 'eye' of the spring (35°C) at night (response to thermophilia) but during the day fed in the cooler (28°C) periphery—the only source of food. This movement is a complete reversal of the diel migrations previously discussed and it may be expected that as a consequence growth efficiency would be extremely low. Notwithstanding the possibility of poor food quality or abundance or possible problems associated with water quality in this environment, all indications are that the thermal peculiarities of the system are themselves responsible to some degree for the poor growth. These fish do not show any genetic malfunction since on transference to a more 'normal' habitat, growth resumes a normal pattern (Fryer and Iles 1972).

Similarly, an early record by van Someren and Whitehead (1959b), who reported that the growth rates of *S. spilurus niger (T. nigra)* in ponds was better in shallow, 30-cm deep ponds than in 60-cm deep ponds, may indicate another example of growth enhancement due to thermal oscillation. Ponds of 30-cm deep would be expected to exhibit a larger diel variation in temperature and tilapia that are restricted to such an environment would be expected to show growth superiority or, at least a better growth efficiency, if food was not limiting. Thus it may not be surprising that the shallow ponds (caused by sedimentation) from which van Someren and Whitehead made the observations showed a good production. My own observations on pond trials tend to confirm this observation but the elimination of the numerous variables in trials of this type is extremely difficult.

A number of documented examples from various African lakes show that tilapias, especially juveniles, have a preference for shallow inshore waters. Recent examples of this distribution preferenda include the tilapias present in Lake Sibaya (Bruton and Boltt 1975), Lake Kariba (Donnelly 1969; Caulton 1977b) and Lake George (Burgis et al. 1973; Moriarty et al. 1973; Gwahaba 1975). In the two former examples food distribution and/or predator pressure may well influence the inshore distribution of young tilapias but in the Lake George example food is more abundant in the deeper areas of the lake yet tilapias are far more abundant in the inshore areas (Gwahaba 1975).

There are obviously a variety of factors contributing to the distribution of tilapia in any particular water body, but indications are that a diel thermal fluctuation may be an important factor to consider. With the exception of the deep rift valley lakes, natural inland waters in Africa are generally composed of shallow river floodplains, seasonal pans, lagoons and marshes as well as large areas of permanent swamp. These areas are sites of tilapia radiation and, prior to the advent of man-made impoundments, constituted the major tilapia habitat. All these areas are subjected to daily temperature fluctuations often in excess of 10°C and thus it stands to reason that the tilapias would have evolved various physiological functions suited to optimizing such conditions.

In concluding this presentation, it is clear that more applied physiological work is urgently required in order to determine the functioning of the various species of tilapia in their natural environment and only after determining the optimum levels of physiological efficiency can we begin to optimize on productivity both in natural water fisheries and in pond culture conditions.

Discussion

NOAKES: A comment more than a question. One of your points is that temperature is very significant for these fish. Their thermal preferanda should therefore change with changing conditions, for example, fed vs. unfed. Is this so?

CAULTON: No, not as far as I know. If you feed the fish in a gradient tank, it makes no difference where the food is, they still go to the same temperature.

NOAKES: Dr. Caulton, you were saying though that different physiological functions have different optima. If this is the case, then it would be reasonable to assume that the fish, when it is undergoing certain physiological functions, would choose the corresponding optimum temperature.

CAULTON: Although this is a reasonable assumption, I do feel that certain physiological optima are sacrificed for others. Certain physiological processes do certainly function most efficiently at a prescribed temperature, yet metabolism, for example, is efficient, in terms of energy saving, at low temperatures yet the overall physiological optimum for a feeding tilapia is at a temperature of about 30°C.

NOAKES: It has been suggested in some temperate regions where there are thermoclines in the summertime that some of the large predator species move above the thermocline in the evenings to feed at a higher temperature where they can move around more efficiently. Then they will go down into colder water where they can digest their food and grow very efficiently.

BOWEN: The thermal preferendum of *Sarotherodon mossambicus* does change with age. It gets lower as the animal gets larger. But even the thermal preferanda of the largest fish are well above any temperatures normally achieved in the natural environment. So, in many cases, they would be expected to migrate back and forth between the thermal gradients along the shores.

HEPHER: Dr. Caulton, what was the average weight of your fish?

CAULTON: We worked with juvenile fish from about 20 to 50 g, but for a lot of the preferenda work, we used fish up to 300 or 400 g. For respirometry work we used a large range of sizes, up to 200 or 300 g. Basically, however, we were concerned with modelling on juvenile fish.

MIRES: Dr. Caulton, from what part of the fish did you take the fat content tissue sample? From muscle?

CAULTON: We used the whole fish.

GUERRERO: Can tilapias get their essential amino acids from blue-green algae and bacterial protein as they can from animal protein?

BOWEN: Yes, it is good quality protein.

MORIARTY: In Lake George, the diet of *Sarotherodon niloticus* consists of about 70% *Microcystis* with a few other blue-greens and diatoms and a few percent bacteria. This was obviously a good food.

GUERRERO: Dr. Bowen, have you studied the amino acid make-up?

BOWEN: Yes I have and it is not significantly different from the amino acid composition of plant proteins in general, including those from macrophytes.

GUERRERO: How does it compare with fish meal?

BOWEN: I have not compared it with fish meal, but I have compared it with the essential amino acid requirements of warmwater fish given in the literature and it is more than adequate to meet these.

MORIARTY: Another point on that of course is that the protein content of microalgae and bacteria is very high compared with that of other plant material. It is around 50 to 60% of the dry weight. This varies of course.

BOWEN: Yes, there are very few storage compounds, such as carbohydrates, in blue-green algae and bacteria and instead of storing energy, these cells continue to reproduce, making more protein.

HENDERSON: You mentioned that there are data for assimilation efficiencies of grass carp feeding on plant protein.

BOWEN: Yes, these are around 50%.

JALABERT: Is there any evidence of feeding rhythms?

MORIARTY: My experience of the Lake George fish is that they feed during daylight hours only. They start feeding at dawn or just before. (Editor's note: Whyte (1975) reported that *Sarotherodon galilaeus multifasciatus* and *Tilapia busumana* in Lake Bosumtwi, Ghana, both feed at night. The water of this lake is very clear.)

JALABERT: Does the efficiency of the food utilization vary according to the time at which it is eaten during the day? For example it has been shown in some fish, particularly catfish, that the efficiency of food utilization is not the same in the morning as in the afternoon.

CAULTON: Yes, we have shown that with the acid secretion cycle in the tilapia. Until you have acid production in the stomach sufficient to lyse the food items, you will not get any release of nutrients. So the first portion of the meal ingested in the morning is hardly digested at all, and there is a large increase in efficiency as the day progresses.

BOWEN: I have actually worked that out by counting the number of empty diatom frustules at different locations in the gut. There is a group of undigested diatoms which is derived from the first part of the daily meal but this is not a very significant portion of the diet and the digestive system becomes efficient very rapidly. So that there is 10% or less of the food that is not fully digested and the remainder is very effectively digested.

NASH: In this detritus, is there any gelatinous material? There seems to be a nice parallel between this freshwater situation and that sometimes found in saline waters. For example, there are some excellent feeding grounds for marine shrimp in Brazil in the Cabo Frio area, and excellent feeding grounds for milkfish in many of the Pacific low atolls where the substrate is a deposit of blue-green algae and detritus, but both are characterized by being very gelatinous. The substrate is similar to the lab-lab prepared in the Philippine milkfish ponds which again has a very high protein level.

BOWEN: Is this gelatinous appearance the result of a large mass of blue-green algae?

NASH: I don't know what it is.

LOVSHIN: There are some blue-greens which form gelatinous masses.

BOWEN: I know that some diatoms secrete gelatinous strands which tend to bind them together into a fine substrate, but I don't know if blue-greens do that.

MORIARTY: Many benthic and planktonic blue-green algae secrete large amounts of slime. Its nutritive value for fish has not been assessed, but it may well be utilized.

COCHE: There is one factor which has not been mentioned from the fish culture point of view. Is the amount of food available affecting growth efficiency? It is well known in fish culture, for instance, that if you feed tilapia *ad libitum* their assimilation efficiency will decrease. That is why the ration becomes so important for a culturist.

HEPHER: There is another point which we should stress more and that is the effect of temperature, particularly at night, on growth rate. I do not know if you hold a fish for long periods at 18°C whether it will grow as well as if you hold it at higher temperatures.

BOWEN: With regard to Dr. Coche's comment, unlike carnivorous and omnivorous animals, the herbivores and detritivores that I am aware of do not in the natural environment ever confront a shortage of food. So quantity to my knowledge is never a limiting factor. It is quality and if I understand Dr. Caulton's contribution correctly, what he has done is to look at how the fish interact with the variables in their environment and try to maximize the amount of food that they are capable of consuming in the absence of any limit on availability. So this does not apply immediately to the culture pond situation where you are trying to maximize the efficiency of food conversion.

LOVSHIN: This is just a comment on the migrations to different temperatures. At Auburn we have a lot of small pool units from which we pick small fry. There are very definite migrations towards the surface when the fish are in small schools. The fry are much easier to collect between 11:00 AM and 2:00 PM when the temperatures are high. There is a very definite time of day when the schools are much more visible and higher up in the water.

CAULTON: Thermal preferanda could be responsible for both a horizontal and a vertical migrations—see text of my paper. In natural tilapia systems, juveniles invariably show a horizontal migration since they are predominantly marginal in habit while adults, present over deeper water, often show a vertical movement. Both environments are affected by daily temperature inversions, hence, the movement of fish.

MORIARTY: Dr. Caulton, did you do any temperature preference studies at night as well as by day?

CAULTON: Yes. The results of these experiments demonstrated that there was no significant difference between day/night thermal preferenda. It also made no difference if the fish were fed or unfed males or females or introduced singly or in shoals.

PULLIN: I would like to comment on the questions raised by Dr. Coche. The amount of food given in a culture situation is obviously very important. I find Dr. Bowen's view that herbivores and detritivores in their natural environment are never likely to encounter shortages of food quantity very significant as some of the detritivores we are trying to grow in fertilized ponds may be encountering a shortage of food. There may well be ways which we can manipulate and improve this kind of culture environment. This may not be as easy as regulating supplemental food, but has anyone any ideas on how detrital feeding can be improved in pond culture?

HENDERSON: The quality of the food is most important because ingestion by the fish is partly related to how much time they spend for the process. If they are processing poor detritus and using a lot of energy and time in the process, they are going to get a lot less benefit than from feeding on blue-greens. But then again, a high quality detritus system may be an improvement.

PULLIN: Yes, and a fertilized pond culture system using organic manures would have a head start over one using inorganic fertilizer.

MORIARTY: The form in which detritus occurs is also important. We have heard mainly about macrophyte feeders and detritus feeders and not very much on the phytoplankton feeders which are also used in pond systems. For the detritus feeders their food must be

in a form which they can pick up easily: if it is more or less soluble or in the form of free swimming bacteria then it may be of little use to the fish. It has to be precipitated in a detrital aggregate or has to be taken up by microorganisms which themselves grow in clumps and form larger aggregates for the fish to ingest. Whether this is in fact detritus *per se*, i.e., non-living material, or whether it is aggregations of living microorganisms is another matter. Detrital foods in ponds must be of the right consistency to be available to fish as well as having the right protein and carbohydrate makeup.

BOWEN: In this regard, it is interesting that a study of manured pond culture of tilapia published recently by Schroeder in Israel looked at microbial production and estimated it. He found that even when he considered that source of nutrition for the tilapia, he could not account for all the production of fish. It remains a great mystery how those fish grew so well, because even if they were cropping 100% of the microbial production, he could not account for all the growth of the fish. He suspects that there must have been a non-living source of nutrients, i.e., organic matter derived from the manure.

MORIARTY: There are a lot of problems in relating microbial production to fish growth.

LOVSHIN: We have talked about various forms of detritus, and I am interested in knowing whether detrital matter has to stay in the water and be worked on by bacteria for some time before it is usable or whether the tilapias can use it fresh, like fresh cut grass?

BOWEN: There are two main categories of organic compounds to consider here with respect to macrophyte material such as palm leaves, grass clippings etc.: structural components that are insoluble in water, and non-structural components which are largely soluble. It is the soluble compounds which are valuable for the nutrition of fish. Cellulose and lignin are not used directly by fish, but soluble proteins, soluble carbohydrates, and lipids, which will go in solution soon after waste plant material is put into the pond will all have a real impact on the fish's nutrition.

LOVSHIN: What type of detrital matter are you talking about here?

BOWEN: I distinguish between morphous detritus and amorphous detritus. Amorphous detritus is the material which has been formed from dissolved organic matter. Its formation is not by fragmentation of leaves, for example, but it is via the dissolved organic components. There are many ways in which you get from dissolved organic to particulate amorphous organic matter. Microbial action is one. Interface reactions either at the air-water interface or the water-mineral interface are others. Simple chemical polymerization in solution is another. UV light also has a physical effect on polymerization. All these factors play a role, but the importance of each of them is not understood. The material which I have found in my studies which plays an important role in the nutrition of *S. mossambicus* is the amorphous organic matter—the amorphous detritus.

LOVSHIN: I think it would be a very important and very interesting line of study to see what material we could throw in the fish pond, or what combinations of materials, to get from these processes the maximum amount of detrital matter which could then be utilized by the fish.

MORIARTY: That is a subject that really does need to be examined in much more detail because detritus is used as such a broad term that in different situations you can have different processes happening.

BOWEN: Schroeder's work shows (or strongly suggests) that an approach to improve detrital feeding would be a very productive one. There is a huge body of literature now on decomposition processes in aquatic environments, which gives some very good ideas of where to begin searching for the manipulation which would simulate detritus formation and give a product that has a high nutritional value.

MORIARTY: Going back to Dr. Chervinski's paper, one thought which occurred to me is that the influence of temperature at the limits of distribution of tilapias, particularly where low temperatures occur, is going to be affected by the surface area and volume of the culture water body. Dr. Caulton's work suggests the use of a shallow pond which will have high temperatures during the day and low temperatures at night, but extreme low temperatures must be avoided. [Editor's note: In Transvaal, dams are stocked with *S. mossambicus*. The fishes survive winter frosts only if they can retire to a part of the dam that is at least 2 m deep (Lombard 1959).] In summarizing the work of Drs. Caulton and Bowen, the quantity and quality of food that tilapias eat need to be considered in relation to environmental factors such as temperature and oxygen. The fish are all considered to be herbivorous, although one group is better termed detritivorous. The origin of detritus is not necessarily from plants, but the role of micro-organisms is obviously very important in the decay of materials such as grass clippings etc. The available protein at the start of decay is not going to be very high and Dr. Bowen's work has shown that it is the total available nitrogen that is important.

Their nitrogen, therefore, has to be in a form that is digestible by proteases, i.e., protein or polypeptides. Amino sugars and amino acids in slime layers may also be utilized, but further work is necessary to study digestibility.

The fish have to use their digestive enzymes to digest detritus. The macrophyte feeders have a very different task. They have thick cell walls to get through and therefore the pharyngeal teeth of the fish are very important. We have said little about the phytoplankton feeders. A lot of the fish that are used for culture feed on blue-green algae which are the most common algae in lakes in the tropics. The work that we did in Lake George showed that the blue-greens were a very nutritious source of food for the fish. The fish had rapid growth rates. The actual assimilation efficiencies were between 30 and 65%: about 45% on average. The maximum assimilation efficiency was 80%. The variability is due to the physiology of digestion and not because there are refractory compounds present in the food. The fish have to secrete gastric acid, and the pH has to fall to about 1.5 for effective digestion to occur. This takes five to six hours—half-way through the daytime feeding period, which accounts for the low assimilation efficiency averaged over a 24-hr period. Even though they assimilate only 45%, our work on the amount that the fish ate per day and their growth rates showed that the amount that they assimilated was more than adequate to support the growth rates obtained and their reproduction. Finally, I would like to stress the importance of Dr. Caulton's work on diurnal migrations between different water masses at different temperatures. Attention to this and to temperature manipulation could be of direct benefit to tilapia culturists.

SESSION 3: CULTURE

Chairman's Overview

H. F. HENDERSON

One of the major difficulties in comparing different culture systems is the lack of an appropriate yardstick for performance. One of the more obvious examples is the expression of the productivity of a system as the biomass per unit of time *per unit area.* In extensive aquaculture in large lacustrine systems, this unit would seem to have the same sort of validity as in comparative studies of the ecology of aquatic ecosystems in general. In pond systems it still seems a useful figure for judging the most economical use of space, but has somewhat doubtful validity in comparing biological efficiencies unless depth is brought into the picture.

As soon as we move into cage and pen systems, however, one hardly bothers to calculate such figures. From the point of view of the culturist, input-output information is of more interest. Unfortunately the commonly quoted feed conversion ratio is not a very satisfactory biological index unless the water content of the feed is taken into consideration. Growth rate and production are of direct interest to both the scientists and the culturists, but are difficult to compare for different lengths of growing season. Dr. Coche gives special attention to these problems, providing several different measures of performance to compare cage culture systems. Recognizing that it may not be very useful to compare the efficiency of the use of space, say, between pond and pen culture, it does nevertheless seem worthwhile to define standard performance criteria for culture systems. These criteria should obviously extend to economic as well as biological factors.

The reviews prepared by Dr. Coche and Drs. Hepher and Pruginin suggest that pen and cage culture of tilapias have advantages for the developing countries while pond culture seems to require rather complex management for success, and may be better suited to the developed countries. It is clear, however, that the main technical and managerial complexities lie in the production of seed rather than in the growout phase, particularly the hybrid seed which seems to be required for profitable production in temperate climates. The question of suitable pond and cage culture systems should also be considered in both high and low technology contexts. Offhand it would seem to me that cage design and construction would offer more problems in developing countries than pond construction. However, inexpensive pre-fabricated cages could conceivably be developed.

Dr. Coche remarks that keeping cage floors well above the bottom of the water body seems to reduce the incidence of disease. He also states, however, that caged fish may be under greater stress than pond fish from crowd-

ing and suggests that they may be more readily attacked by disease and parasites.

Manures and fertilizers seem to be more effectively utilized in pond culture systems. In tropical countries tilapia culture is particularly attractive when it is combined with pig or duck farming. Drs. Hepher and Pruginin point out in their paper that organic manures, by directly stimulating heterotrophic food-chains, are better than inorganic fertilizers for the microphagous tilapias.

Only pond and cage culture systems have been reviewed. It is also valuable to refer to two other systems. One is the very intensive culture of tilapias in tanks and in raceways, systems which are particularly appropriate in utilization of waste thermal waters. The other is extensive culture in small reservoirs, natural lakes and ponds. The highly intensive culture systems pose special problems of providing complete diets as well as removal of wastes from the system. Management of extensive systems, on the other hand, should be of interest in relation to the extent to which cage or pen culture can or should be combined with harvest of the more free-living stocks. This is an important question in, for example, the improvement of the fisheries of the 10,000 or so small reservoirs of Sri Lanka. In small reservoirs, there are some interesting possibilities for the control of reproduction of tilapias through water level control: for example, by exposing nests at critical periods.

Where cage culture has prospered, local administrators have often been unprepared for the resulting legal and environmental problems. Dr. Coche cites several cases in the Philippines where this has happened and I have been told of similar sorts of problems in Polish trout culture. It is, however, not only administrators who have been caught unprepared. There is very little information available on the effects of cage culture in lakes, ponds or bays upon which to base predictions of permissible levels of occupancy. At high levels of occupancy, reduced production in each cage unit becomes obvious to the operators. As in capture fisheries, however, the overutilization of water bodies for cage culture is not likely to be reduced to optimal levels voluntarily. Unfortunately, we know little about predicting permissible levels of occupancy before production begins to drop, nor, to my knowledge, has there been any attempt to define effluent standards for cage culture, analogous to those which have been adopted in some places for pond culture.

Speaking of environmental matters, Dr. Coche also notes that cage culturists and others should take care that inappropriate species are excluded from waters to be used for cage culture. Competition for food between *S. aureus* and wild *S. mossambicus* in cages in Puerto Rico has been cited as an example of this problem. There, the wild *mossambicus* were also thought to be a source of parasites and disease for the cultured *aureus*.

There is a problem not mentioned explicitly in any of the papers, but which will emerge as tilapia culture becomes more intensive and more highly selected strains are used for culture. This is the increased movement of both broodstock and seedstock across national boundaries and the attendant risks of transfer of parasites and disease, and of contamination of stocks with genes of related species. In most countries, there is as yet very little control on either the species, or more importantly, the health of the fish transported.

Roberts and Sommerville note that the diseases of tilapias have not been as well studied as those of other cultured species, both because their culture has only recently been developed to an intensive level where disease problems are more evident, and because diagnostic facilities are, in general, poorly developed in areas where tilapia culture is most common.

Tilapia polyculture systems are discussed in some detail by Hepher and Pruginin, and Coche mentions one instance, in Lake Victoria, of *S. esculentus* and *T. zillii* being cultured together in cages, and two instances of *S. niloticus* being cultured with common carp. It would seem that there is less reason for polyculture in cage systems than in ponds, though others may recognize the availability of distinct niches in cages. In ponds, Hepher and Pruginin suggest that in Israel polyculture is especially advantageous when low to moderate stocking densities of young-of-the-year tilapia are used. At high stocking densities, which are more typical of intensive production systems with hybrid fish, the natural food component is negligible, and hence the feeding synergisms are less important. The use of predators in tilapia culture is perhaps a special case as such use is primarily for controlling recruitment. Hepher and Pruginin suggest that common carp may carry out this latter function to some degree, as well as that of increasing the utilization of natural food.

Dr. Roberts draws attention to the recent demonstration of a biochemical compound in water in which *S. mossambicus* had been intensively cultured, which produces a kind of "shock syndrome" in this and other tilapias. The production of such substances by fish has been frequently referred to elsewhere, but seems not to have been given much attention by culturists. There is some evidence that such substances may be important in spawning behavior.