YIELD EQUATIONS AND INDICES FOR

TROPICAL FRESHWATER FISH POPULATIONS

by

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ABSTRACT

Simple algebraic relationships and yield equations that require the minimum of data are developed so as to enable quick and reliable assessments of relative rate of harvesting tropical freshwater fish populations.

The age of a fish at the inflexion point is inversely related to the growth rate (K) and directly related to the natural logarithm of the weight length exponent (b).

Algebraic relationships between the exponent of anabolism (m) and the weight length exponent are developed.

Equations for estimating total mortality from age and length distributions in catch samples are given. Total mortality for both continuous and discrete recruitment are considered. The probability density function and the discrete probability function for a negative exponential are given.

The effect of a number of variables on trawl catches is studied and some multiple regression equations which might be used to assess the relative degree of exploitation are presented.

The parameters which have been recognized as vital to yield prediction are: the growth rate (K), the weight length exponent (b), the maximum length to which a fish grows (L∞) and the natural and total mortality rates.

It is shown that one can replace age with a length expression in yield models and still have reliable yield predictions. It is also shown that a model with a few very relevant parameters, has almost the same predictive power as a model requiring more parameters.

TABLE OF CONTENTS

# LIST OF TABLES

LIST OF FIGURES

# ACKNOWLEDGEMENT

# INTRODUCTION

The current trend in the study of fish population dynamics is towards a detailed analysis of variables affecting yield and the construction of theoretical models which describe the interrelations of these variables. Unfortunately, attempts to attain realistic models introduce complexities that require more and more basic data. The collection and analyses of these data take much time. Moreover, it is necessary to have many long sampling periods to reduce the effect of annual variability on estimation. In the circumstances of rapid development of some African freshwater fisheries, it may obviously be difficult to meet the data requirement of modern management models.

Additionally, management of natural populations of fish in tropical freshwater is made difficult by:

(a) lack of readily detectable growth rings on skeletal structures,

(b) variability in growth rates,

(c) absence of definite spawning periods,

(d) limited catch statistics.

It is therefore desirable to consider the functional relationships among the population variables that influence yield. This might enable development of some simple and useful approximations that give reliable indications of the relative degree of exploitation.

1

The purpose of this study is to focus on the most relevant population parameters and to develop simple analytical methods and theoretical models that require the minimum of data so as to enable quick and reliable assessments of relative rates of exploitation of tropical freshwater fish populations.

In this thesis, consideration is first given to the separate processes of growth, fecundity, mortality and some simple algebraic relationsips are developed which could be used in management.

Throughout, *Tilapia* has been used as an example to test the validity and usefulness of the findings. Additionally, a few references are made to *Bagrus docmac* and *Haplochromis* spp.

A separate section is devoted to the recent data on catches of *Tilapia* in Lake Victoria. The analysis of the catches by multiple regression methods provide useful information on the abundance and distribution of *Tilapia* species and indicates the variables related to high catches. This type of analysis could be used in managing other fish species in tropical freshwater.

Lastly, consideration is given to yield equations and some simplifications which might lead to quick, easy and yet reliable estimation of fish yields.

# ESTIMATION OF GROWTH CHARACTERISTICS
## WITH PARTICULAR REFERENCE TO
## *TILAPIA* IN EAST AFRICA

## Variability of Growth Rate

The estimation of growth rates of tropical fish poses several problems. The absence of seasonal environmental fluctuations means that growth at each age and the age of maturity cannot easily be determined by reading annual rings on scales or other skeletal structures. This difficulty has to now limited the use of yield models which are based on age, in the management of tropical freshwater fisheries. In some cases rings have been observed on bony parts of some tropical fish, sometimes the rings are apparently a result of spawning and other times as a result of drought and starvation (Garrod 1959 and Lowe 1956).

Species of *Tilapia* show considerable variability in growth (Lowe 1956). In order to understand the growth processes, extensive and intensive studies must be carried out to determine the growth rate, the maximum length and weight attained by these fish in various waters and the length, weight and age of maturity. Even within a single lake, one observes differences in growth rate and size of maturity and this is exemplified by *Tilapia esculenta* in Lake Victoria. Garrod (1959) used the scale method to determine the age of *Tilapia esculenta*, a mouth brooder with two spawning seasons.

Related to the spawning behavior of mouth brooding, there is
a cessation of growth resulting in ring formation. On the basis of
this observation, Garrod (1959) determined 12 "ring years" for *Tilapia*
*esculenta*. In terms of actual years *Tilapia esculenta* lives for 6 years.

Other methods may be employed in growth studies. Rings on
skeletal structures are made more readily detectable by heating but
this has not been done for *Tilapia*. Lowe-McConnell (1956) obtained
some indications of growth rate by analysing length frequency distributions.
The main limitation of this method is that a number of fish species
spawn all the year round so that there is considerable overlap of size
ranges of different ages. The adult and young *Tilapia* live in different
habitats and therefore sampling in one locality will give length frequen-
cies that are truncated.

Growth rates can also be determined by conducting mark and
recapture experiments but this has not yet been done for *Tilapia*.

Management of *Tilapia* and other tropical fish species, is
possible even without direct determination of age, provided we can estimate
the von Bertalanffy growth equation parameters. The maximum length
($L\infty$), maximum weight ($W\infty$), the rate at which a fish approaches its asymp-
totic size (K) and the weight length exponent (b), have to be determined
if we are to understand the growth of fish species. With the above
parameters plus a few simplifying assumptions a number of useful relation-
ships can be established.

Ursin (1967) reports that Putter in 1920 first realized the
truism that food absorbed is the difference between food ingested and

that ejected and advanced a metabolic growth model. The rate of intake
of food is surface dependent whereas the rate of breakdown is weight
dependent because it occurs in all parts of the body, viz:

$$\frac{dw}{dt} = HW^{2/3} - kw \qquad (1.1)$$

where w is the weight, t is the time, H is the coefficient of anabolism
and k is the coefficient of catabolism.

Putter's work was continued by von Bertalanffy (1934, 1938)
who regarded an organism as a reacting chemical system. The processes
of anabolism and catabolism control the weight of an organism. The rate
of change of weight of an organism dw/dt is expressed in terms of exponents
m and n of the body weight.

$$\frac{dw}{dt} = HW^m - kw^n \qquad (1.2)$$

where m is the exponent relating anabolism to weight and n is the exponent
relating catabolism to weight.

The equation given by von Bertalanffy (1934) describes the
rate of change of length with time and is the equivalent of equation
(1.1) when expressed in terms of length and asymptotic length:-

$$\frac{dl}{dt} = K(L\infty - l) \qquad (1.3)$$

where l is the length of a fish at time t and $L\infty$ is the asymptotic length
and K is the rate at which a fish approaches its maximum length.

When integrated (1.3) gives the von Bertalanffy growth equation:

$$l_t = L\infty (1 - e^{-K(t - t_0)}) \qquad (1.4)$$

where $t_0$ is the time at which the length of a fish is theoretically zero.

Other workers have investigated the von Bertalanffy growth equation and have made several developments (Beverton and Holt 1957, Taylor 1959 and 1962, Paloheimo and Dickie 1965 and 1966.) Ursin (1967) looked at the processes of anabolism and catabolism and also examined the exponents m and n in equation (1.2). He outlined ways in which m and n could be measured.

## The Point of Inflexion on the Growth Curve

Rational exploitation of a fishery requires knowledge of the weight and age of a fish at the inflexion point. At the point of inflexion a fish has maximum change in weight dw/dt. In some species of fish the maximum growth increment is attained before sexual maturity. Exploitation of such a fish species requires catching the fish at a size or age beyond the point of inflexion so that there will be sufficient individuals of sufficient age to reproduce. For those fish populations with a high natural mortality rate, this could mean loss of biomass. The stunted population of *Tilapia nilotica* in Lake Albert exemplifies this case. This *Tilapia* population has a natural mortality of 3.37 and sexual maturation is attained at 10 to 12 cm. (Iles, MS.). The maximum biomass occurs at about 8 to 9 cm. In contrast, the population of *Tilapia nilotica* in Lake Albert (open water) and *Tilapia esculenta* in Lake Victoria attain maturity prior to the size and age corresponding to the point of inflexion. Therefore maximum yield can be obtained by catching the fish at the

size corresponding to the point of inflexion.

If we take equation (1.2) and take a second derivative, the derivative equals zero at the point of inflexion.

$$\frac{dw}{dt} = Hw^m - kw^n$$

$$\frac{d^2w}{dt^2} = mHw^{m-1} - nkw^{n-1} = 0$$

so that

$$mHw^{m-1} = nkw^{n-1} \tag{1.5}$$

which with rearrangement gives the equation

$$w^{(n-m)} = \frac{mH}{nk} \tag{1.6}$$

Let the weight at the inflexion be $W_I$. Then

$$W_I^{(n-m)} = \frac{mH}{nk}$$

$$W_I = \left(\frac{mH}{nk}\right)^{\frac{1}{n-m}} \tag{1.7}$$

When a fish attains the maximum weight ($W\infty$), $dw/dt = 0$. Therefore

$$\frac{dw}{dt} = Hw^m - kw^n = 0$$

$$Hw^m = kw^n$$

and

$$\frac{H}{k} = w^{(n-m)}$$

$$\left(\frac{H}{k}\right)^{\frac{1}{(n-m)}} = w$$

where w is the maximum weight (W∞). Therefore the weight of a fish at the point of inflexion is given by

$$W_I = \left(\frac{m}{n}\right)^{\frac{1}{(n-m)}} \cdot W\infty \tag{1.8}$$

The parameters m and n are difficult to measure and therefore we cannot readily estimate the weight at the point of inflexion (1.8).

A generalized growth equation in terms of weight is

$$W_t = W\infty \, (1 - e^{-K \, (t - t_0)})^b \tag{1.9}$$

where b is the weight length exponent. If we take $W_t$ to be the weight of a fish at the inflexion point, the significance of b in (1.9) is very evident. The weight of a fish is related to length by the equation

$$W = qL^b \tag{1.10}$$

where q is the constant of proportionality. Many fish have b = 3.0 and therefore show isometric growth. However there are other fish for which b is not 3.0 and which change in shape with increase in length.

Paulik and Gales (1964) have discussed the consequences of assuming isometric growth, on the shape of yield curves. We are aware that the value of b for known fish species ranges from 2.5 to 3.5.

The first derivative of equation (1.9) is

$$\frac{dW_t}{dt} = b \, W\infty \left[ (1 - e^{-K(t - t_0)})^{b - 1} \cdot Ke^{-K(t - t_0)} \right]$$

and the second derivative is

$$\frac{d^2W_t}{dt^2} = bW\infty \left[ (1 - e^{-K(t - t_0)})^{b - 1} \cdot (-K^2 e^{-K(t - t_0)}) \right.$$

$$\left. + (b - 1) \cdot (1 - e^{-K(t - t_0)})^{b - 2} \cdot (K^2 e^{-2K(t - t_0)}) \right]$$

Factoring leads to

$$\left[ bW\infty \, e^{-K(t - t_0)} \right] \cdot \left[ (1-e^{-K(t - t_0)}) \right]^{b - 2} \cdot \left[ - K^2(1 - e^{-K(t - t_0)}) + \right.$$

$$\left. K^2 \cdot (b - 1) \cdot (e^{-K(t - t_0)}) \right] = 0 \tag{1.11}$$

The above equation has 3 square bracketed terms multiplying each other and any of them being zero could make the whole equation zero. Taking the first square bracketed expression, the parameters b and $W\infty$ could not be zero at the point of inflexion. For the first square bracketed term to be zero, it will be necessary that

$$e^{-K(t - t_0)} = 0$$

which is true when $t = \infty$. However, the age of a fish at the point of inflexion cannot be infinity.

If the second bracketed expression is equal to zero, we have

$$1 - e^{-K(t - t_0)} = 0$$

which is true when $t = t_0$. The value of $t = t_0$ is imaginary because a fish cannot reach a point of maximum dw/dt at time $t_0$.

Taking the third square bracketed expression, the possibilities are for $K^2$ to be zero or for b to equal 1 and hence (b - 1) = 0 or

$$1 - e^{-K(t - t_o)} = 0$$

If $K^2$ is zero, there would be no deceleration of growth. A value of b = 1 implies growth in weight is directly proportional to growth in length which could only occur with a fish which grew in one dimension. It follows then that some rearrangement of (1.11) must produce an expression equalling zero.

After factoring and simplifying the third bracketed expression, we have

$$- (1 - e^{-K(t - t_o)}) + (b - 1) \cdot e^{-K(t - t_o)} = 0$$

which gives

$$- 1 + e^{-K(t - t_o)} + be^{-K(t - t_o)} - e^{-K(t - t_o)} = 0$$

which may be further simplified to

$$- 1 + be^{-K(t - t_o)} = 0$$

Therefore

$$be^{-K(t - t_o)} = 1$$

and

$$e^{-K(t - t_o)} = \frac{1}{b} \qquad (1.12)$$

If we take natural logarithms

$$- K (t - t_o) = - \ln b$$

$$K (t - t_0) = \ln b$$

and

$$t = \frac{1}{K} \ln b + t_0 \qquad (1.13)$$

where t is the age of a fish at the point of inflexion.

Equation (1.13) thus describes the necessary interrelation between the age at the point of inflexion, the growth rate (K) and the weight length exponent (b) if equation (1.1) is to be satisfied.

It has been reported that for most tropical fish, particularly the family cichlidae, the parameter $t_0$ is almost zero (Iles MS.). This would mean that the age of a fish at the inflexion point is determined by K and b. The parameters K and b can be estimated for the important commercial fish species in the tropics. If we know the age of a fish at the inflexion we can use equation (1.9) to determine the weight of maximum dw/dt. Equation (1.13) indicates that the age of a fish at the inflexion point increases as the weight length exponent increases. Thus fish which are relatively heavy for their length reach the inflexion point at a relatively older age, than those fish with low values of b. Fish which have a high K attain maximum growth increments at a very low age. For example the stunted *Tilapia nilotica* in Lake Albert Uganda, with K = 2.77 and b = 3.33, has the age at the inflexion of 0.43 years. But *Tilapia nilotica* (with normal growth) in the same Lake, has a growth rate (K) of 0.5 and b of 3.34 and the age at the inflexion point of about 2.4 years. The estimated ages when replaced into the growth equation lead to estimates of weight at inflexion.

The age at inflexion on the growth curve has been calculated for values of b where $(2.5 \leq b \leq 3.5)$ and for K values between 0.1 and 0.6 (Table 1). Figure 1 gives isopleths of age at the inflexion point against b and k.

The importance of a simple deterministic expression (1.13) for age in terms of b and K relies on two factors: (1) b and K can be estimated easily for many fish species, (2) the age at the inflexion point and the age of maturity are very close to each other for many fish species. Beverton (1963) investigated the age of maturity of clupeid and engraulid fish. Fish with high K mature at an earlier age than fish with low K. Therefore the parameters K and b are important in determining the size and age at which a fish is best caught to obtain maximum yield.

TABLE 1 - Estimated age at the point of inflexion for various values of K and b assuming $t_o$ is zero.

| b | K | | | | | |
|---|---|---|---|---|---|---|
| | .1 | .2 | .3 | .4 | .5 | .6 |
| 2.5 | 9.16 | 4.58 | 3.05 | 2.29 | 1.83 | 1.53 |
| 2.6 | 9.56 | 4.78 | 3.19 | 2.38 | 1.91 | 1.59 |
| 2.7 | 9.93 | 4.97 | 3.31 | 2.48 | 1.99 | 1.65 |
| 2.8 | 10.29 | 5.15 | 3.43 | 2.57 | 2.06 | 1.72 |
| 2.9 | 10.65 | 5.32 | 3.55 | 2.66 | 2.13 | 1.78 |
| 3.0 | 10.99 | 5.49 | 3.66 | 2.74 | 2.20 | 1.83 |
| 3.1 | 11.31 | 5.66 | 3.77 | 2.83 | 2.26 | 1.89 |
| 3.2 | 11.63 | 5.82 | 3.87 | 2.91 | 2.33 | 1.94 |
| 3.3 | 11.94 | 5.97 | 3.98 | 2.99 | 2.39 | 1.99 |
| 3.4 | 12.23 | 6.11 | 4.07 | 3.05 | 2.44 | 2.03 |
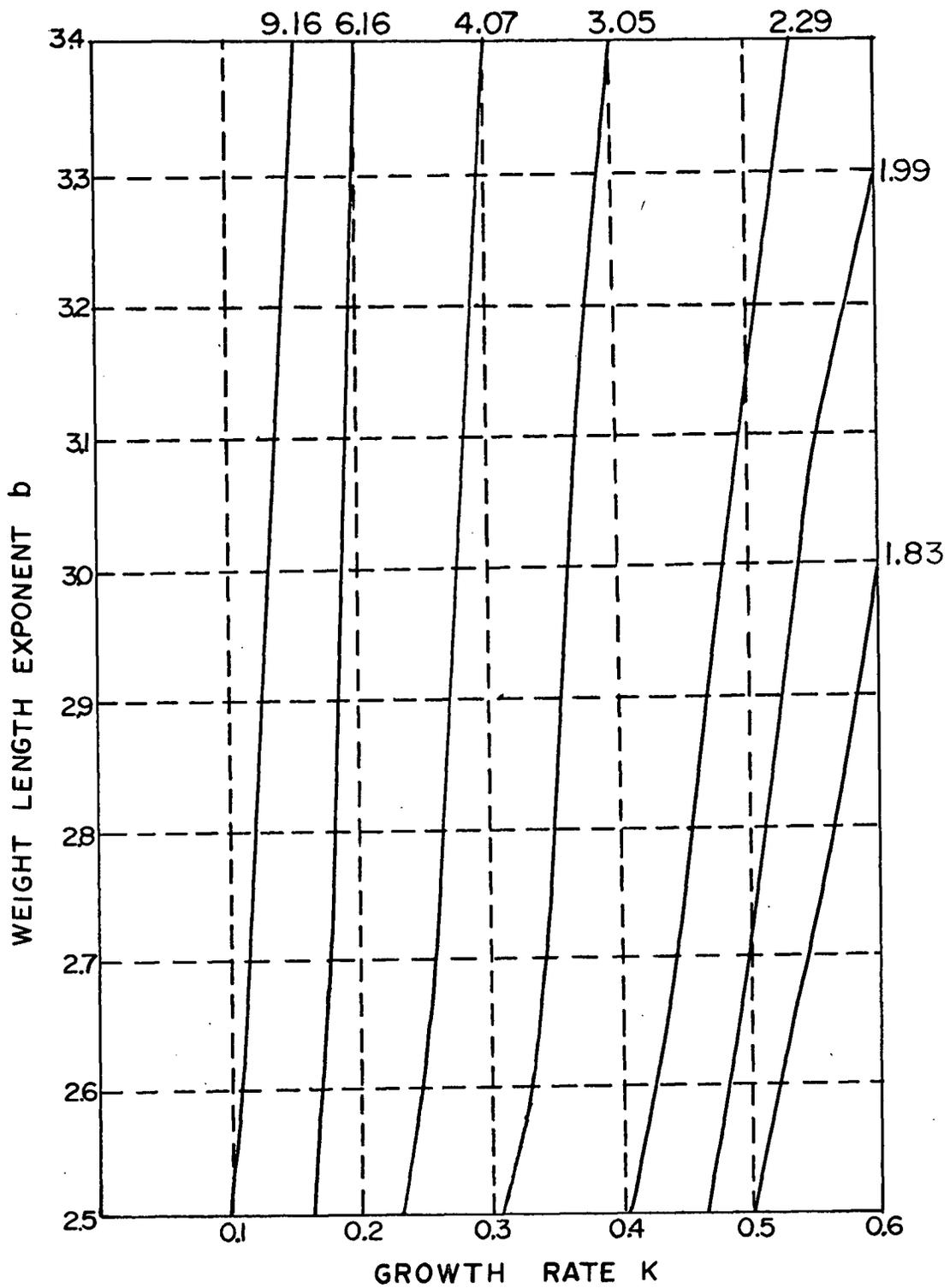
Figure 1 - Contours of age at the inflexion point for various values of K and b. Age is given in years.

## The Weight Length Exponent and the Exponents of Metabolism.

The weight of a fish at the point of inflexion is given by two equations (1.8) and (1.10)·

$$W_I = \left(\frac{m}{n}\right)^{\frac{1}{n-m}} \cdot W\infty \tag{1.8}$$

and

$$W_t = W\infty \cdot (1 - e^{-K(t-t_0)})^b \tag{1.10}$$

where $W_t$ is the weight at the point of inflexion and therefore equals $W_I$. If equations (1.8) and (1.10) are true, a relationship must exist between the weight length exponent and the exponents of anabolism and catabolism.

We equate the right hand expressions (1.8) and (1.10)

$$\left(\frac{m}{n}\right)^{\frac{1}{n-m}} \cdot W\infty = W\infty (1 - e^{-K(t-t_0)})^b \tag{1.14}$$

Divide by $W\infty$

$$\left(\frac{m}{n}\right)^{\frac{1}{n-m}} = (1 - e^{-K(t-t_0)})^b \tag{1.15}$$

Notice that t in (1.15) is the age of a fish at the inflexion point. We can rearrange the equation (1.15):-

$$1 - e^{-K(t-t_0)} = \left(\frac{m}{n}\right)^{\frac{1}{b(n-m)}}$$

which gives

$$e^{-K(t - t_0)} = 1 - \left(\frac{m}{n}\right)^{\frac{1}{b(n - m)}}$$

$$-K(t - t_0) = \ln\left(1 - \left(\frac{m}{n}\right)^{\frac{1}{b(n - m)}}\right)$$

$$K(t - t_0) = -\ln\left(1 - \left(\frac{m}{n}\right)^{\frac{1}{b(n - m)}}\right)$$

$$t = -\ln\left(1 - \left(\frac{m}{n}\right)^{\frac{1}{b(n - m)}}\right) \cdot \frac{1}{K} + t_0 \qquad (1.16)$$

But both equations (1.13) and (1.16) define the age of a fish at inflexion. We can equate the right hand expressions of these equations

$$\frac{1}{K} \ln b + t_0 = -\ln\left(1 - \left(\frac{m}{n}\right)^{\frac{1}{b(n - m)}}\right) \cdot \frac{1}{K} + t_0$$

Subtract $(t_0)$ from each side and multiply by K

$$\ln b = -\ln\left(1 - \frac{m}{n}^{\frac{1}{b(n - m)}}\right) \qquad (1.17)$$

Rearranging equation (1.17) gives

$$-\ln b = \ln\left(1 - \frac{m}{n}^{\frac{1}{b(n - m)}}\right)$$

$$\frac{1}{b} = 1 - \left(\frac{m}{n}\right)^{\frac{1}{b(n - m)}} \qquad (1.18)$$

von Bertalanffy (1957) dealt with allometric relationships between an animal's metabolic rate and its weight. He claimed that the slope m of the allometric line is either 2/3 for species obeying the surface rule of metabolism, unity for cases where oxygen consumption

is proportional to weight instead of surface area, and that for other
fish species in ranges between .66 to 1.0. Parker and Larkin (1959)
and Ricker (1960) criticize the derivation of the von Bertalanffy growth
equation because of the assumption of the surface law of metabolism.
Taylor (1962) discusses the parameters of the von Bertalanffy equation
and points out factors limiting metabolism. von Bertalanffy argues that
the rate of metabolism is proportional to the $m^{th}$ power of the weight
where m is the exponent of metabolism. But the rate of catabolism is
proportional to weight itself, thus n = 1. Ursin (1967) has pointed out
that the assumption of n being one does not hold for all animals.

If we assume that n = 1, we can establish a relationship between
m and b in equation (1.18), i.e.,

$$\frac{1}{b} = 1 - m^{\frac{1}{b\,(1-m)}} \qquad\qquad (1.19)$$

It follows from equation (1.19) that

$$1 - \frac{1}{b} = m^{\frac{1}{b\,(n-m)}} \qquad\qquad (1.20)$$

Raising both sides of the above equation to the power b yields

$$\left(1 - \frac{1}{b}\right)^{b} = m^{\left(\frac{1}{1-m}\right)} \qquad\qquad (1.21)$$

Letting $1 - \frac{1}{b} = x$

we have

$$b = \frac{1}{1-x}$$

We can replace b in equation (1.21) by the appropriate expression, to obtain

$$x^{\frac{1}{1-x}} = m^{\frac{1}{1-m}} \tag{1.22}$$

Equation (1.22) holds if x = m for all real numbers.
But

$$x = 1 - \frac{1}{b} \text{ and also } x = m$$

Therefore from equation (1.21) and 1.22) we can establish the relationship

$$1 - \frac{1}{b} = m \tag{1.23}$$

$$\text{or } 1 = \frac{1}{b} + m$$

$$\text{or } b = \frac{1}{1-m} \tag{1.24}$$

From the relationship above it is evident that fish with isometric growth (b = 3), have m = 0.67 as proposed by von Bertalanffy (1957).

If the exponent of catabolism (n) is one, then it can be deduced from equation (1.23) that fish with b greater than 3 will have m greater than 0.67 and a fish with b less than 3 will have m less than 0.67. Thus a fish with b = 2.5 has m = 0.60 and a fish with b = 3.5 has m = 0.72.

The processes of anabolism change several times during the life span of a fish. But a fish does not change its body shape during

its life span (except for early life history stages and with maturity which are beyond the range of the growth period here considered). Therefore a relationship must exist between b and m. This relationship is expressed by equations (1.23) and (1.24). Changes in the weight length exponent reflect changes in the processes of anabolism.

Hecht (1916) reports that fish and frogs have uniform but indeterminate growth. The body form of a fish is laid down very early in life and this body form is maintained within narrow limits throughout the period of growth. This is in contrast to growth of higher vertebrates in which body form continually changes during the period of growth. However, it must be added that this conclusion applies only to external surfaces for Kellicott (1908) has shown that in a dogfish, the brain and viscera differ in their rates of growth in much the same way as in the higher vertebrates.

When the exponent of catabolism (n) is less than one, the weight length exponent b cannot be expressed explicitly in terms of m and n.

Equation (1.18) is a transcendental equation, i.e.

$$\frac{1}{b} = 1 - \left(\frac{m}{n}\right)^{\frac{1}{b(n-m)}}$$

$$1 - \frac{1}{b} = \left(\frac{m}{n}\right)^{\frac{1}{b(n-m)}}$$

$$1 - \frac{1}{b} - \left(\frac{m}{n}\right)^{\frac{1}{b(n-m)}} = 0 \qquad (1.25)$$

For given values of m and n, we can by iteration processes find values of b which make equation (1.25) zero. If we use Newton's method of solving transcendental equations, the iteration process converges rapidly. However, it is necessary to set the lower and upper limits of b. If b satisfies the inequalities $2.5 \leq b \leq 3.5$, then the values of m range from 0.60 to 0.90 and n ranges from 0.8 to 1.0.

For many fish species, so far studied the weight-length exponent lies within the limits 2.5 to 3.5. Carlander (1969) reports 3 populations of *Coregonus artedi* with b ranging from 3.62 to 3.69. But the values of b are based on samples in which length ranges from 200-230 mm. There are also five populations of *Coregonus artedi* with values of b less than 2.5. But these values of b are based on samples with maximum length of 164-179 mm. Biased sampling may lead to estimates of b outside the range 2.5 to 3.5. The weight length exponent outside the range 2.5 to 3.5 cannot apply over a wide range of length without causing profound changes in body form. There may be a few exceptional fish species with b greater than 3.5 but it is doubtful whether such fish species obey the law of uniform and indeterminate growth.

The exponent of anabolism m cannot be 1 as this would make the value of b tend to infinity (see equation (1.24)). The value of m most probably does not exceed 0.90 for $0.8 \leq n \leq 1$. However some evidence is needed to verify this proposition.
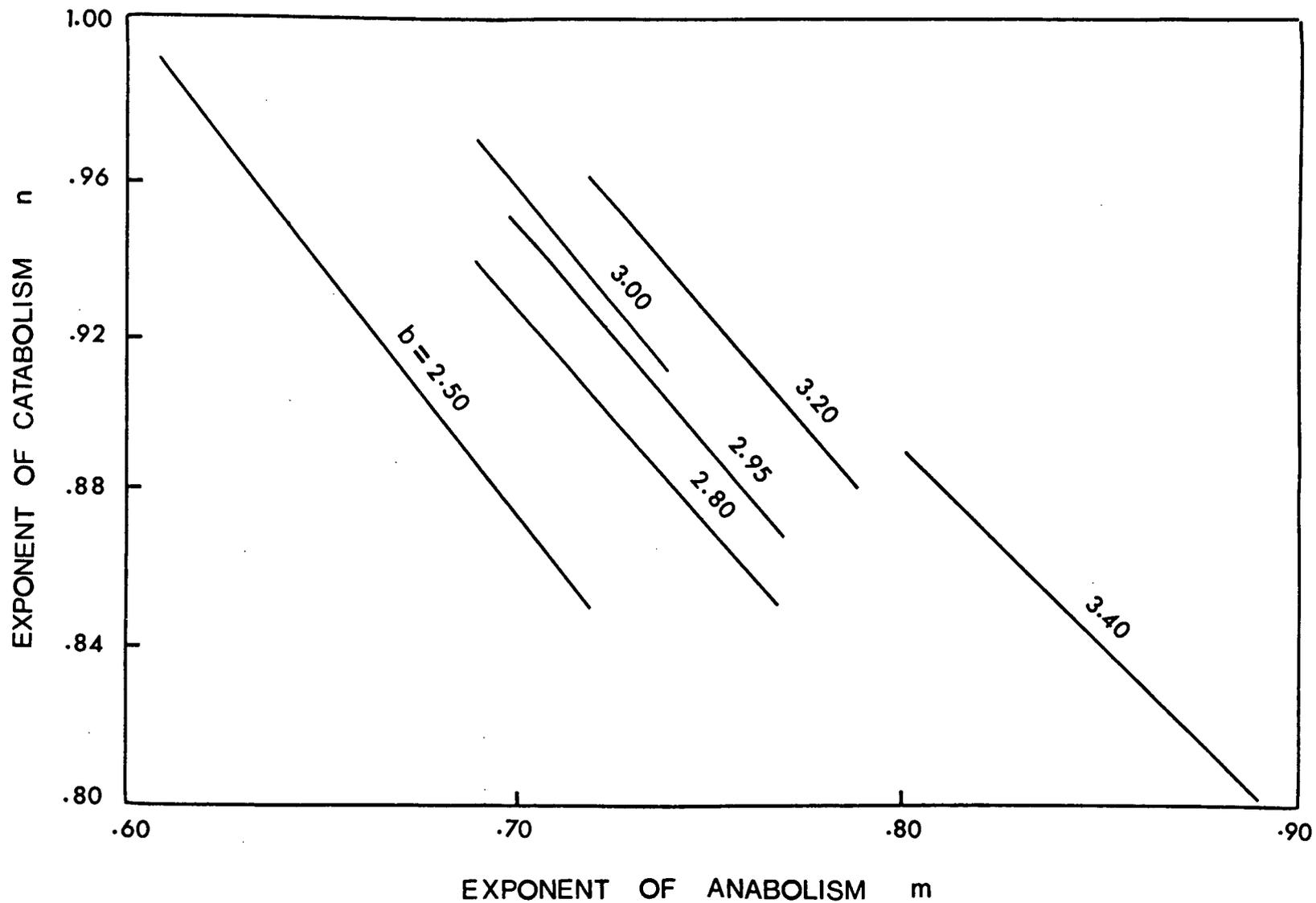
Figure 2 - The effects of exponents of anabolism and catabolism on the weight
length relationship of fish.

Variability of Weight Length Exponent b for *Tilapia nilotica*

Analysis of data collected by Lowe (1958) shows that the weight length exponent for *Tilapia nilotica* in various localities in East Africa is variable. Table 2 gives the parameters a and b for the relation:

$$W = aL^b$$

Since the age of a fish at the inflexion point is a function of the reciprocal of K and b, it follows that if natural mortalities are the same, the age of maximum biomass in the different localities is different. The variability of b shown in Table 2 for *Tilapia nilotica* is most probably true for other species of *Tilapia* in various waters in East Africa. There is need to determine the weight length exponent for other species of *Tilapia* . Piennar and Thomson (1969) have pointed out the importance of allometric weight length relationship and the statistical problems of such relationships.

Under the assumptions of isometric growth, the von Bertalanffy growth equation has proved extremely attractive to yield model building, for example the Beverton and Holt (1957) yield model. The importance of variability of the weight length exponent has been given little consideration. Because the parameters K and b control the inflexion point and because b is related to the processes of anabolism and catabolism, the first step in studying the dynamics of a fish population might be the estimation of K and b.

TABLE 2 - Parameters a and b of the model $W = aL^b$ for
*Tilapia nilotica* in various localities in
East Africa

| LOCALITY | a | b | pH | CONDUCTIVITY |
|---|---|---|---|---|
| LAKE ALBERT OPEN WATER | 0.017 | 3.34 | 9.0 | 710 |
| LAKE ALBERT BUHUKU LAGOON | 0.028 | 3.33 | 9.2 | 7200 |
| LAKE EDWARD | 0.479 | 2.99 | 9.1 | 900 |
| LAKE GEORGE | 0.010 | 3.29 | 9.1 | 900 |
| MALAGARASI SWAMPS | 0.39 | 2.96 | 7.6 | 300 |
| LAKE RUDOLF | 0.927 | 3.19 | 9.7 | 2800 |

SPAWNING, SEXUAL MATURATION

AND FECUNDITY

## Spawning

The species of the genus *Tilapia* do not seem to have a clear
spawning season. In favourable and uniform environmental conditions
*Tilapia* may spawn at frequent intervals (Lowe 1955). In waters with
marked seasonal changes *Tilapia* may have one or more well defined breeding
seasons. The frequency of spawning and the mechanism under which it
works is not understood.

Lowe-McConnell (1955) reports some of the approaches that have
been used to determine the frequency of spawning. A *Tilapia esculenta*
marked on the 13th April 1953 in Lake Victoria, had fry in the mouth
and when captured 9 1/2 weeks later on the 20th June 1953, was found
to have eggs in her mouth. Another *Tilapia esculenta* (in Lake Victoria),
having fry in her mouth, was marked on the 4th March 1953 and when captured
7 weeks later, the ovary was found to be in a ripening stage. Examination
of the ovary of *Tilapia* species reveals dark yellowish or brown specks
which are signs of recent spawning. Many times, an ovary in a ripening
stage will have small ova starting to develop and these ova form the
next batch of eggs to develop (Lowe 1955). On the evidence of ovary
observations several species of *Tilapia* may have three or more batches
of young in succession. If we can determine the time taken by each

23

batch to develop, this would give some measure of the length of the
breeding season.  The absence of a well marked breeding season creates
several problems in the management of *Tilapia* populations.

With no definite breeding season it is difficult to determine
annual recruitment and to relate recruits to the many batches of young
that occur in a year.  Repeated spawning within a year creates what may
be termed "sub-year classes" in a year class.  Because of differences
in growth rates the length frequency distributions show considerable
overlap and it becomes extremely hard to dissect them into age groups.


Sexual Maturation

Sexual maturation may be governed by attainment of a certain
size rather than age.  There are differences in growth rates and these
differences mean that a year class or a batch of young hatching at
the same time will reach maturity at different ages.  This point is
emphasized by Nikolskii (1969).  There are very few species of fish
in which maturity for a year class occurs at the same age, an exception
being the viviparous Poeciliidae. Even in this family variations in food
supply cause variation in age of maturation.   Size of maturation is a
vital parameter in management of fish populations.  Russell (1931) and
Graham (1935) stress the importance of "allowing fish to grow" before
catching them.

Beverton (1963) has established a relationship between length
at maturation (lm) and the maximum length (L∞).  The bigger the size

to which a fish grows, the bigger it is on first reaching maturity. This means that the ratio lm/L∞ is relatively constant for a family of fish. Though this is generally true, exceptions do occur. Table 3 shows variation in the ratio lm/L∞ in the genus *Tilapia* in East Africa.

Holt (1962) found correlations between the ratio lm/L∞ and K. Fish with high K have low lm/L∞ and mature at a smaller size while fish with a low K mature at a bigger size. From the ratio lm/L∞, the ratio Wm/W∞ can be established if we know the weight length exponent b. The ratio of weight at maturity to maximum weight (Wm/W∞) is about 0.3 for many fish species (Holt 1962). It is also known that the weight of a fish at the inflexion point is 0.3 of maximum weight for fish species with b = 3.0 (see equation 1.12). For all the fish species which mature before attaining the size of maximum dw/dt, catching the fish at the size corresponding to the point of inflexion would be the best way of getting maximum yield.

The ratios lm/L∞ and Wm/W∞ in Table 3 below are based on data in Lowe (1958), Garrod (1959, 1963) and Iles (MS.).

26

TABLE 3 - The ratios Lm/L∞ and Wm/W∞ for some *Tilapia*
species in East Africa. The numbers enclosed
in brackets refer to maximum length based on
the largest fish in samples taken.

| LOCALITY | Fish Species | lm | L∞ | lm/L∞ | Wm/W∞ |
|---|---|---|---|---|---|
| LAKE ALBERT OPEN WATER | *Tilapia nilotica* | 36 | 49 | .73 | 0.35 |
| LAKE ALBERT BUHUKU LAGOON | *Tilapia nilotica* | 10 | 17 | .58 | 0.16 |
| LAKE EDWARD | *Tilapia nilotica* | 25 | (36) | .69 | 0.33 |
| LAKE GEORGE | *Tilapia nilotica* | 28 | (40) | .70 | 0.31 |
| LAKE RUDOLF | *Tilapia nilotica* | 39 | (63) | .61 | 0.21 |
| MAGALASI SWAMPS | *Tilapia nilotica* | 22 | (30) | 0.73 | 0.39 |
| LAKE VICTORIA | *Tilapia esculenta* | 22.8 | 34 | 0.67 | 0.30 |
| LAKE VICTORIA JINJA REGION | *Tilapia variabilis* | 22 | (30) | 0.73 | |

From the results of Table 3 above it is evident that mesh size
of gillnets or codend mesh size will be different in the various localities.
The size of maturation and the weight at maturation must be considered
seriously when setting the mesh size of the fishing gear.

<u>Fecundity</u>

One of the factors controlling the size of a year class is the number of eggs laid. The number of eggs laid is governed by the fecundity of a species and the number of mature females. There is no simple relationship existing between number of eggs and the number of offspring that survive to sexual maturity; the main reason being variable mortality in the several stages of development between egg laying and sexual mortality. Svärdson (1949) gave several generalizations about fecundity and egg production all of which are noted in various ways within *Tilapia* populations of East Africa. The generalizations are:

(1) There is a negative correlation between number of eggs and individual size of the eggs.

(2) The number of eggs produced is positively correlated with female size.

(3) The growth of a fish is greatly dependent upon the amount of food available. Since growth and consequently size is modified by environment, egg number might be strongly influenced by environment.

(4) Fish species with some parental care produce relatively fewer eggs than fish with no parental care.

(5) Closely related species may have egg number showing geographical clines.

(6) Egg numbers may show intraspecific variation and this might correspond to geographical clines.

(7) The largest larvae hatch from the largest eggs.

*Tilapia* species are subdivided according to mode of reproduction into guarders and mouth brooders. *Tilapia zilli* is a guarder and the eggs are guarded by both male and female parents. Characteristics of

the guarders is a large number of eggs (see Figure 3). *Tilapia nilotica,*
*Tilapia esculenta* and *Tilapia variabilis* belong to the mouth brooders.
For these species, development of fry takes place in the mouth. In the
case of *Tilapia leucosticta,* also a mouth brooder, fry are first re-
leased when about 8 mm. or within 11 to 15 days of egg fertilization
(Welcomme 1966).

The fecundity of *Tilapia* species increases with length following
an exponential curve. The model describing the relationship of fecundity
and length is:-

$$F = aL^B \qquad\qquad (2.1)$$

where F is the fecundity at the length L and B is the exponent relating
fecundity to length. A logarithmic transformation of the above model
leads to

$$Log\ F = log\ a + B\ log\ L \qquad\qquad (2.2)$$

In cases where the parameter B is equal to the weight length
exponent b, fecundity is said to vary directly with weight.
Note that,

$$F = aL^b$$

and

$$W = qL^B$$

Therefore

$$\frac{W}{F} = \frac{qL^B}{aL^b}$$

If b = B, then

$$\frac{W}{F} = \frac{q}{a}$$

or
$$F = \frac{a}{q} W$$

Setting
$$C = \frac{a}{q}$$

$$F = CW \tag{2.3}$$

where W is the weight of a fish and C is the coefficient of regression of F on weight.

The estimated parameters of equations (2.1) and (2.2) for *Tilapia leucosticta* and *Tilapia nilotica* are given below:

*Tilapia leucosticta*
$$F = 0.131L^{2.30}$$

or
$$\log_e F = -0.118 + 2.30 \log L$$

*Tilapia nilotica*
$$F = 2.65L^{2.96}$$

or
$$\log_e F = 0.423 + 2.96 \log L$$

Therefore the fecundity of *Tilapia leucosticta* increases with about the square of length while the fecundity of *Tilapia nilotica* increases with about the cube of length. This means that the fecundity of *Tilapia nilotica* increases linearly with weight as shown in equation (2.3).

Several factors including seasonal changes in weight of a fish and improper sampling seriously affect the values of the parameters in

equation (2.1). If some length groups are not sampled, there will be bias in the estimated parameters.

In fisheries management, it is important to know how fecundity varies with age so as to assess the effect of fishing on total egg production and its consequences on recruitment. Though it is not easy to determine age of tropical fish and fecundity with age directly, we can determine indirectly the age of a fish of a given fecundity.

The age of a fish of a given fecundity is determined using the von Bertalanffy growth equation

$$l_t = L\infty (1 - e^{-K(t - t_0)})$$

and the fecundity length model

$$F = aL^B$$

Let $F_t$ be the fecundity of a fish of length L and age t. Then the fecundity at age t is given by the relationship

$$F_t = a(L\infty (1 - e^{-K(t - t_0)}))^B \qquad (2.4)$$

It must be noted that this equation is only true for ages that produce eggs. Equation (2.4) gives fecundity of a fish as a function of time. Thus fecundity increases with age to an asymptotic value. This is to be expected since length of a fish reaches an asymptote with time.

Knowing the parameters K and L∞ and knowing the fecundity weight relationship, the age of a fish can algebraically be expressed.

$$\frac{F_t}{a} = (L\infty (1 - e^{-K(t - t_0)}))^B$$
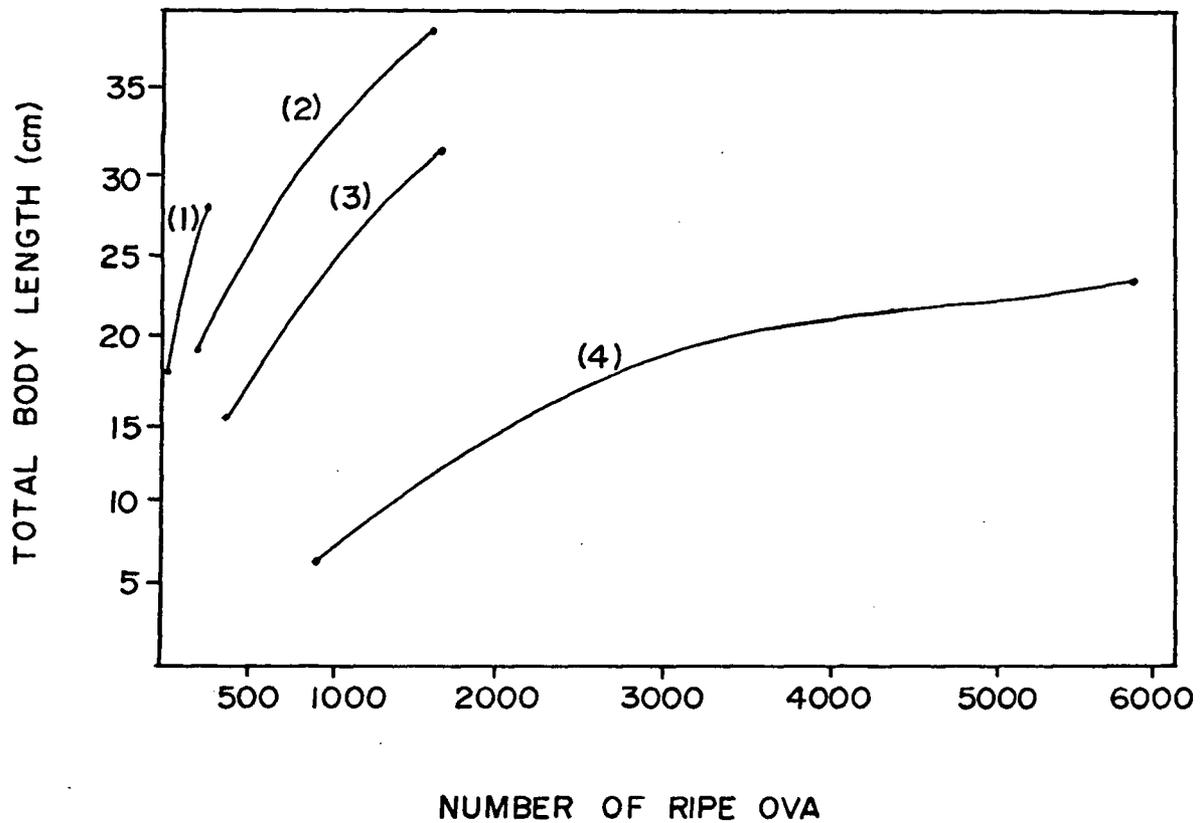
Figure 3 - Number of eggs produced by *Tilapia* at different sizes.
(1) *Tilapia karome*, (2) *Tilapia esculenta*, *Tilapia nilotica*,
and *Tilapia variabilis*, (3) *Tilapia galilaea*, (4) *Tilapia
zilli*. After Lowe McConnell (1955).

$$\left(\frac{F_t}{a}\right)^{\frac{1}{B}} = L\infty\,(1 - e^{-K(t - t_0)})$$

$$\left(\frac{F_t}{a}\right)^{\frac{1}{B}} - L\infty = L\infty\,e^{-K(t - t_0)}$$

so that

$$e^{-K(t - t_0)} = \frac{\left(\frac{F_t}{a}\right)^{\frac{1}{B}} - L\infty}{L\infty}$$

$$-K\,(t - t_0) = \ln\left(\frac{\left(\frac{F_t}{a}\right)^{\frac{1}{B}} - L\infty}{L\infty}\right)$$

$$t - t_0 = -\ln\left(\frac{\left(\frac{F_t}{a}\right)^{\frac{1}{B}} - L\infty}{L\infty}\right) \cdot \frac{1}{K}$$

$$t = -\ln\left(\frac{\left(\frac{F_t}{a}\right)^{\frac{1}{B}} - L\infty}{L\infty}\right) \cdot \frac{1}{K} + t_0 \qquad (2.5)$$

The accuracy of the estimated age t in (2.5) depends on whether our estimates of K, L∞, B and $t_0$ are reliable. All the above parameters can be determined with reasonable accuracy provided sampling is conducted in such a way that many length groups are covered. For many species of *Tilapia* the parameter $t_0$ is about zero so that equation (2.5) reduces to

$$t = -\ln\left(\frac{\left(\frac{F_t}{a}\right)^{\frac{1}{B}} - L\infty}{L\infty}\right) \cdot \frac{1}{K} \qquad (2.6)$$

Again it must be underlined that this expression is only valid for estimating age of fish which are in mature age groups. Deterministic expressions for age such as that in (2.5) and (2.6) could enable biologists working in the tropics to make approximations of relative indices of yield from fecundity, growth rate and the weight length exponent.

# ESTIMATION OF MORTALITY RATES FOR

## TROPICAL FISH

The theoretical foundation for solving the problem of natural mortality was given by Baranov (1918) when he said that the age limit determines the coefficient of natural mortality. Beverton and Holt (1954, 1959), Taylor (1960), Beverton (1963) and several other fishery biologists have pointed out that life span is dimensionally the same as the coefficient of total mortality.

The equations formulated here for estimating mortality rates from the mean age of fish in the catch, are based on the usual assumptions of negative exponential models of mortality.

Below are the symbols used in the equations:

$E$ = expected value

$K$ = the growth rate (von Bertalanffy growth parameter)

$l$ = length

$\bar{l}$ = mean length

$l_c$ = length of recruitment

$L_\infty$ = maximum length (a von Bertalanffy growth equation parameter)

$M$ = instantaneous rate of natural mortality

$n$ = sample size

$t$ = time or age

$\bar{t}$ = mean age

$t_c$ = age of first capture

$t_L$ = age of oldest fish in the catch

$t_\lambda$ = age of exit from a fishery

$t_o$ = time at which the size of a fish is theoretically zero

$Z$ = the instantaneous rate of total mortality

In developing the following models, it is assumed that recruitment is constant and the instantaneous rate of total mortality Z is constant. The recruitment can either be of a discrete or continuous form. The model based on continuous recruitment should be applicable to the *Tilapia* species which breed several times in a year. The model based on discrete recruitment is very useful in temperate latitudes where fish spawn once a year.

## Continuous Recruitment Model

In an unexploited fish population the number of fish at any age t is given by

$$N_t = N_0 \, e^{-M(t - t_0)} \qquad (3.1)$$

where $N_t$ is the number of fish at the age or time t and $N_0$ is the initial number at time $t_0$.

We can express $N_t$ as a proportion of $N_0$

$$\frac{N_t}{N_0} = e^{-M(t - t_0)} \qquad (3.2)$$

In the case of exploited fish populations, the number of fish at any of the expoited ages is given by

$$N_t = Re^{-Z(t - t_c)} \qquad (3.3)$$

where R is the number of fish recruited at age $t_c$.
The number of fish $N_t$ can be expressed as a proportion of R

$$\frac{N_t}{R} = e^{-Z(t - t_c)} \qquad (3.4)$$

In an unexploited fish population the total area under the negative exponential curve is unity.  Similarly for exploited fish populations, the total area under the negative exponential between age $t_c$ and infinity is unity.  This property can be used to find the probability of a fish attaining age t.

The probability density function is defined as

$$F(x) = \int_a^x f(x)\, dx = 1$$

This means that the sum of the probabilities of all ages in a population will be equal to one.

For the derivation of a probability density function for the negative exponential, see Appendix 1.

In an unexploited fish population, the probability of a fish attaining age t is

$$P(t) = P(T = t) = Me^{-M(t - t_0)}$$

$$P(t) = Me^{-M(t - t_0)} \text{ for } t > t_0 \qquad (3.5)$$

In the case of an exploited fish population the relative probability of catching a fish of age t is

$$P(t) = Ze^{-Z(t - t_c)} \text{ for } t > t_c \qquad (3.6)$$

An observation t has an expected value $\frac{1}{Z} + t_c$ and the variance is $1/Z^2$. The expected mean age is given as

$$E(\bar{t}) = \frac{1}{Z} + t_c \qquad (3.7)$$

The variance of the mean age $\bar{t}$ of the catch is

$$\text{Var } (\bar{t}) = \frac{1}{nZ^2} \qquad (3.8)$$

The total instantaneous mortality is a parameter but in practice it is estimated as a statistic. Let us suppose that the mean age $\bar{t}$ is

$$\bar{t} = E(\bar{t}) + e \qquad (3.9)$$

where e is a random error and the expected error is zero

$$E(e) = 0$$

Then the variance of the error is

$$\text{Var } (e) = \frac{1}{nZ^2} \qquad (3.10)$$

From equations (3.7) and (3.9) the relationship is established:-

$$\bar{t} - t_c = \frac{1}{Z} + e \qquad (3.11)$$

Notice that the error term e can either be negative or positive. From equation (3.11) we can derive an expression for estimating total mortality from a catch sample drawn from a population.

$$Z' = \frac{1}{\bar{t} - t_c - (e)} \tag{3.12}$$

where e is positive or negative. When the error is large and negative the total mortality is under estimated. But when the error is large and positive Z' is over estimated. Let $\bar{t} - t_c = U$. If we assume $\bar{t}$ is a constant, a formal expression for the distribution of Z is obtained by a binomial expansion of the equation:

$$Z = \frac{1}{U + e} \tag{3.13}$$

$$Z' = U^{-1} - eU^{-2} + e^2 U^{-3} - e^3 U^{-4} + \ldots \tag{3.14}$$

The expected Z' is

$$E(Z') - U^{-1} + E(e^2)\, U^{-3}$$

Therefore
$$E(Z') = Z + \frac{Z^3}{n\bar{Z}^2} \tag{3.15}$$

$$E(Z') = Z + \frac{Z}{n} \tag{3.16}$$

Square Z' in equation (3.14)

$$Z'^2 = U^{-2} - e^2 U^{-4} + \ldots \tag{3.17}$$

If we treat total mortality Z' as a random variable and if we denote the expected total mortality as d, it is possible to measure the dispersion of the expected value of total mortality

$$(Z' - d)^2$$

The dispersion of the expected value is known as the variance of Z, denoted as Var (Z).

The variance of a random variable for example total mortality Z, is

$$Var (Z) = E(Z' - d)^2 \qquad (3.18)$$

As Hodges and Lehmann (1965) put it, this variance is the expectation of the squares of the difference between Z and its expectation. From equation (3.18) the variance of Z can be expressed as

$$Var (Z) = Z^2 - 2Zd + d^2 \qquad (3.19)$$

From the law of expectation, the variance becomes

$$Var (Z) = E(Z^2) - 2dE(Z) + d^2 \qquad (3.20)$$

But expected Z equals d. Therefore

$$E(Z) = d$$

$$Var (Z) = E(Z^2) - d^2 \qquad (3.21)$$

But from equation (3.16)

$$E(Z^2) = (Z + \underline{z})^2 \over n \qquad (3.22)$$

and $\qquad d = Z + \dfrac{Z}{n} + \ldots$ .

Therefore $\qquad d^2 = (Z + \dfrac{Z}{n} + \ldots)^2 \qquad\qquad$ (3.23)

Therefore the variance of total mortality estimated by equation (3.12) is

$$\text{Var } (Z) = (Z + \frac{Z}{n})^2 - (Z + \frac{Z}{n} + \ldots)^2$$

$$\text{Var } (Z) = \frac{Z^2}{n} \qquad\qquad (3.24)$$

From the above considerations

$$E \left( \frac{1}{t - t_c} \right) = \left( \frac{n + 1}{n} \right) \cdot Z \qquad\qquad (3.25)$$

Therefore the total estimated mortality based on a taken sample is

$$\hat{Z} = \frac{1}{\overline{t} - t_c} \cdot \frac{n}{n + 1} \qquad\qquad (3.26)$$

This is an unbiased estimator of total mortality Z. The variance of Z is

$$\sigma^2 (Z) = \left( \frac{n}{n + 1} \right)^2 \cdot \frac{Z^2}{n} \qquad\qquad (3.27)$$

The variance of Z can be estimated from the sample as

$$\sigma^2 (\hat{Z}) = \left( \frac{n}{n + 1} \right)^2 \cdot \frac{1}{n(\overline{t} - t_c)^2} \qquad\qquad (3.28)$$

Total mortality estimates for *Tilapia esculenta* are made using equation
(3.26) and given in Table 4. Note that Table 4 does not give total
mortality at each age. But if one sampled the catch and found the mean
age $\bar{t}$ where $\bar{t} \geq t_c$, to be 3 years, the total mortality of *Tilapia esculenta*
which is recruited at 2.5 years, would be 1.99 and the variance of this
estimate would be 0.0079. It is expected that the mean age in the catches
from various localities will vary and each region will be characterized
by its own total mortality.

In the case of maximum likelihood, the total mortality is estimated
as

$$\hat{Z} = \frac{1}{\bar{t} - t_c} \qquad (3.29)$$

Equation (3.29) gives a biased estimate of Z whose variance is

$$\sigma^2(\hat{Z}) = \frac{1}{n \, (\bar{t} - t_c)^2} \qquad (3.30)$$

The variance of Z in the case of maximum likelihood is bigger than the
variance determined from the expected value of Z. While estimates of
total mortality can be determined with equation (3.29), it is better to
estimate total mortality with equation (3.26) so as to avoid bias in the
estimate.

TABLE 4 – Estimates of total mortality for *Tilapia esculenta* in Lake Victoria. It is assumed that recruitment is continuous. $t_c$ = 2.5 years and n is the sample size.

| $\bar{t}$ | n = 500 | | n = 1000 | | n = 1500 | | n = 2000 | |
|---|---|---|---|---|---|---|---|---|
| | Z | $\sigma^2(Z)$ | Z | $\sigma^2(Z)$ | Z | $\sigma^2(Z)$ | Z | $\sigma^2(Z)$ |
| 3.0 | 1.99 | .00796 | 1.99 | .00399 | 1.99 | .00266 | 1.99 | .00199 |
| 3.5 | .99 | .00199 | .99 | .00099 | .99 | .00066 | .99 | .00049 |
| 4.0 | .66 | .00088 | .66 | .00044 | .66 | .00029 | .66 | .00022 |
| 4.5 | .49 | .00049 | .49 | .00024 | .49 | .00016 | .49 | .00012 |
| 5.0 | .39 | .00031 | .39 | .00015 | .39 | .00010 | .39 | .00007 |
| 5.5 | .33 | .00022 | .33 | .00011 | .33 | .00007 | .33 | .00005 |
| 6.0 | .28 | .00016 | .28 | .00008 | .28 | .00005 | .28 | .00004 |
| 6.5 | .24 | .00012 | .24 | .00006 | .24 | .00004 | .24 | .00003 |
| 7.0 | .22 | .00009 | .22 | .00004 | .22 | .00003 | .22 | .00002 |

## Estimation of Total Mortality Rates for Fish with Discrete Age Groups

If a quantity X takes on the possible discrete values $x_1$, $x_2$, ..., $x_k$ and if $x_1 < x_2 < x_k$, then the probability that X takes a value $x_i$ (for finite series) is defined by

$$px_i = P(X = x_i) = f(x_i) \quad (i = 1, 2, \ldots, k)$$

and the sum of $f(x_i)$ is unity (Burington and May 1958)

$$\sum_{i=1}^{k} f(x_i) = 1$$

Similarly for an infinite series, the probability that X takes the values $x_i$ is

$$px_i = P(X = x_i) = f(x_i) \quad (i = 0, 1, 2 \ldots, \infty)$$

$$P(X = x_i) = \sum_{0}^{\infty} f(x_i) = 1$$

From the properties of a discrete probability distribution, we can derive expressions for estimating total mortality for fish with discrete age groups. But two assumptions have to be made: (1) constant recruitment and (2) constant total mortality for all ages.

If we draw a sample of size n from an exponential distribution, the probability of getting age t is

$$P(t) = P(T = t) = (1 - e^{-Z}) e^{-Zt} \quad \text{for } t > t_c$$

$$P(t) = (1 - e^{-Z}) e^{-Zt} \quad \text{for } t > t_c \tag{4.1}$$

The mean age $\overline{t}$ for a population with discrete age groups is

$$\overline{t} = e^{-Z} (1 - e^{-Z}) \qquad (4.2)$$

The derivation of equations (4.1) and (4.2) is given in Appendix 2. The survival rate is given by

$$S = e^{-Z}$$

Therefore the mean age is given by

$$\overline{t} = \frac{S}{1 - S} \qquad (4.3)$$

From equation (4.2) and (4.3) it is obvious that if total mortality Z is zero the mean age of a fish in a sample will be infinity. Re-arranging equation (4.3), we have

$$\overline{t} = \frac{1}{1 - S} - 1 \qquad (4.4)$$

so that

$$\overline{t} + 1 = \frac{1}{1 - S} \qquad (4.5)$$

Taking the inverse of equation (4.5), we have

$$\frac{1}{t - 1} = 1 - S \qquad (4.6)$$

Therefore the survival rate S is given by

$$S = 1 - \frac{1}{\overline{t} - 1} \qquad (4.7)$$

which is rearranged to give

$$S = \frac{\bar{t}}{1 + \bar{t}} \tag{4.8}$$

But $\qquad S = e^{-Z}$

Therefore $\qquad e^{-Z} = \frac{\bar{t}}{1 + \bar{t}} \tag{4.9}$

$$- Z = \ln \left( \frac{\bar{t}}{1 + \bar{t}} \right)$$

$$Z = \ln \left( \frac{1 + \bar{t}}{\bar{t}} \right) \tag{4.10}$$

Equation (4.10) estimates total mortality Z if the age $t_c$ is zero. The age of first capture $t_c$ is not zero and therefore it must be sub-tracted from the denominator and numerator of equation (4.9), ie.,

$$e^{-Z} = \frac{\bar{t} - t_c}{1 + \bar{t} - t_c} \tag{4.11}$$

The total mortality in the case of discrete recruitment is

$$Z = \ln \left( \frac{\bar{t} + 1 - t_c}{\bar{t} - t_c} \right) \tag{4.12}$$

The above estimator of Z has statistical bias if the mean age is deter-mined from a small sample. A more reliable estimate of Z is given by

$$Z = \ln \left( \frac{t + 1 - t_c}{\bar{t} - t_c} \right) \cdot \frac{n}{n + 1} \tag{4.13}$$

The variance of the total mortality Z is

$$\sigma^2 = \left(\frac{n}{n+1}\right)^2 \cdot \frac{1}{n} \cdot Z^2 \qquad (4.14)$$

Total mortality estimates for *Tilapia esculenta* are made using equation (4.13) and given in Table 5. The estimates given in Table 5 are very close to those in Table 4. Under discrete recruitment a mean $\bar{t}$ of 5 years in the catch would mean that the total mortality is about 0.33. But under continuous recruitment a mean age of 5 years gives a total mortality estimate of 0.39. Note that the age of first capture is 2.5 years. The variances of the estimates in Table 5 show that using large samples makes the estimated Z more reliable.

TABLE 5 - Estimates of total mortality for *Tilapia esculenta* in Lake Victoria. It is assumed that recruitment is discrete. $t_c$ = 2.5 and n is the sample size.

| $\bar{t}$ | n = 500 | | n = 1000 | | n = 1500 | | n = 2000 | |
|---|---|---|---|---|---|---|---|---|
| | Z | $\sigma^2(Z)$ | Z | $\sigma^2(Z)$ | Z | $\sigma^2(Z)$ | Z | $\sigma^2(Z)$ |
| 3.0 | 1.09 | .00239 | 1.09 | .00120 | 1.09 | .00080 | 1.09 | .00060 |
| 3.5 | .69 | .00095 | 0.69 | .00047 | .69 | .00031 | .69 | .00023 |
| 4.0 | .50 | .00051 | .50 | .00025 | .51 | .00017 | .51 | .00013 |
| 4.5 | .40 | .00032 | .40 | .00016 | .40 | .00010 | .40 | .00008 |
| 5.0 | .33 | .00022 | .33 | .00011 | .33 | .00007 | .33 | .00005 |
| 5.5 | .28 | .00016 | .28 | .00008 | .28 | .00005 | .28 | .00004 |
| 6.0 | .25 | .00012 | .25 | .00006 | .25 | .00004 | .25 | .00003 |
| 6.5 | .22 | .00009 | .22 | .00004 | .22 | .00003 | .22 | .00002 |
| 7.0 | .19 | .00007 | .19 | .00004 | .20 | .00002 | .20 | .00002 |

Estimation of Total Mortality Rates and the Ratio Z/K from Length Data

Since it is difficult to age tropical fish species, the use of age in estimating total mortality may not easily apply to tropical species. Instead of age, one can use length to estimate the total mortality (Z) if the parameter K is known. Where K is unknown, the ratio Z/K is estimated from the negative exponential curve. The ratio Z/K is important in determining yields, for fish with allometric growth, by means of the incomplete Beta function.

In an exploited fish population, we can express the number of fish at any age t as

$$N_t = e^{-Z(t - t_c)} \tag{5.1}$$

It is assumed that the number of fish at age $t_c$ is constant and equal to unity.

The von Bertalanffy growth equation for length is

$$l_t = L\infty (1 - e^{-K(t - t_0)})$$

In the above equation, time t can be expressed as a function of length. Then t and $t_c$ in (5.1) are given as

$$t = \frac{1}{K} \left( - \ln \left( 1 - \frac{l_t}{L\infty} \right) \right) + t_0 \tag{5.2}$$

$$t_c = \frac{1}{K} \left( - \ln \left( 1 - \frac{l_c}{L\infty} \right) \right) + t_0 \tag{5.3}$$

Let $\quad X_1 = -\ln\left(1 - \dfrac{1_t}{L_\infty}\right)$

and $\quad X_c = -\ln\left(1 - \dfrac{1_c}{L_\infty}\right)$

Then $\quad t = \dfrac{1}{K} X_1 + t_0$ (5.4)

$t_c = \dfrac{1}{K} X_c + t_0$ (5.5)

Subtracting $t_c$ from t

$$t - t_c = \frac{1}{K} X_1 + t_0 - \left(\frac{1}{K} X_c + t_0\right)$$

$$= \frac{1}{K} (X_1 - X_c)$$

Replacing $t - t_c$ in equation (5.1)

$$N = e^{-Z/K(X_1 - X_c)}$$ (5.6)

The probability of $X_1$ is given by the probability density function below

$$P(X_1) = \frac{Z}{K} e^{-Z/K(X_1 - X_c)} \text{ for } X_1 > X_c$$ (5.7)

Note that equation (5.7) is similar to equation (3.6).

Therefore if we know the length distribution in the catch and the length of first capture, the ratio Z/K can be estimated.

$$\frac{Z}{K} = \frac{n}{n+1} \cdot \frac{1}{\overline{X}_1 - \overline{X}_c}$$ (5.8)

where $\bar{X}_1$ is the mean of $X_1$ from various samples. The variance of $Z/K$ is

$$\sigma^2 \frac{Z}{K} = \left(\frac{n}{n+1}\right)^2 \cdot \frac{Z^2/K^2}{n} \tag{5.9}$$

which can be estimated by

$$\sigma^2 \frac{Z}{K} = \left(\frac{n}{n+1}\right)^2 \cdot \frac{1}{n(\bar{X}_1 - X_c)^2} \tag{5.10}$$

Note that to determine $\bar{X}_1$ we have to take several samples each of size n. For each sample we determine $X_1$ according to:

$$X_1 = - \ln\left(1 - \frac{1_t}{L_\infty}\right)$$

Then $\bar{X}_1$ is given by

$$\bar{X}_1 = \frac{\sum\limits_1^m X_i}{m} \tag{5.11}$$

where m is the number of $x_1$ each determined from equation (5.8).

Table 6 shows estimates of total mortality based on the above method for *Tilapia esculenta* in Lake Victoria in the North Buvuma area. The length of first capture $1_c$ is 22 cm. and corresponds to age $t_c = 2.5$ years. In Table 6, the mean length in the catch is given instead of $X_1$.

The total mortality rates estimated with length are very close to the estimates determined from age data. For example, if the mean age in the catch is 3 years a population of *Tilapia esculenta* would

have a total mortality rate of 1.99. A 3 year old *Tilapia esculenta*

is about 24 cm. long. If the mean length in the catch is 24 cm., the

ratio Z/K and the total mortality (Z) would be 5.37 and 1.71 respectively.

Also note that a mean age of 5 years and a mean length of 29 cm give

total mortality estimates of 0.39 and 0.35 respectively (see Table 4

and Table 6).

TABLE 6 - Estimates of total mortality rates for *Tilapia esculenta*
in Lake Victoria. Length of first capture $L_c$ = 22 cm.,
K = 0.32, L∞ = 33.8 and n is the sample size.

| | n = 500 | | n = 1000 | | n = 1500 | | n = 2000 | |
|---|---|---|---|---|---|---|---|---|
| | Z | $\sigma^2(Z)$ | Z | $\sigma^2(Z)$ | Z | $\sigma^2(Z)$ | Z | $\sigma^2(Z)$ |
| 23 | 3.60 | .02590 | 3.60 | .01300 | 3.61 | .00868 | 3.61 | .00651 |
| 24 | 1.71 | .00589 | 1.72 | .00295 | 1.72 | .00197 | 1.72 | .00148 |
| 25 | 1.08 | .00236 | 1.08 | .00118 | 1.09 | .00079 | 1.09 | .00058 |
| 26 | 0.77 | .00118 | 0.77 | .00059 | 0.77 | .00039 | 0.77 | .00029 |
| 27 | 0.57 | .00066 | 0.57 | .00033 | 0.58 | .00022 | 0.58 | .00016 |
| 28 | 0.44 | .00040 | 0.45 | .00020 | 0.45 | .00013 | 0.45 | .00010 |
| 29 | 0.35 | .00025 | 0.35 | .00012 | 0.35 | .00008 | 0.35 | .00006 |
| 30 | 0.28 | .00015 | 0.28 | .00007 | 0.28 | .00005 | 0.28 | .00003 |
| 31 | 0.22 | .00009 | 0.22 | .00004 | 0.22 | .00003 | 0.22 | .00002 |
| 32 | 0.16 | .00005 | 0.17 | .00002 | 0.17 | .00001 | 0.17 | .00001 |

TABLE 7 - Estimates of total mortality rates for *Tilapia nilotica* (normal population) of Lake Albert Uganda. Length of first capture 28 cm., K = .50, L∞ = 49.0 and n is the sample size.

| $\bar{T}_t$ cm | n = 500 | | n - 1000 | | n = 1500 | | n = 2000 | |
|---|---|---|---|---|---|---|---|---|
| | Z | $\sigma^2(Z)$ | Z | $\sigma^2(Z)$ | Z | $\sigma^2(Z)$ | Z | $\sigma^2(Z)$ |
| 29 | 10.22 | .20837 | 10.23 | .10460 | 10.24 | .06982 | 10.24 | .05240 |
| 30 | 4.98 | .04951 | 4.99 | .02485 | 4.99 | .01659 | 4.99 | .01245 |
| 31 | 3.23 | .02087 | 3.24 | .01047 | 3.24 | .00699 | 3.24 | .00524 |
| 32 | 2.36 | .01110 | 2.36 | .00557 | 2.36 | .00372 | 2.36 | .00279 |
| 33 | 1.83 | .00670 | 1.83 | .00336 | 1.83 | .00224 | 1.83 | .00168 |
| 34 | 1.48 | .00438 | 1.48 | .00219 | 1.48 | .00146 | 1.48 | .00110 |
| 35 | 1.23 | .00301 | 1.23 | .00151 | 1.23 | .00101 | 1.23 | .00075 |
| 36 | 1.04 | .00215 | 1.04 | .00108 | 1.04 | .00072 | 1.04 | .00054 |
| 37 | .89 | .00158 | .89 | .00079 | .89 | .00053 | .89 | .00039 |
| 38 | .77 | .00118 | .77 | .00059 | .77 | .00039 | .77 | .00029 |
| 39 | .67 | .00090 | .67 | .00045 | .67 | .00030 | .67 | .00022 |
| 40 | .58 | .00069 | .58 | .00034 | .58 | .00023 | .58 | .00017 |
| 41 | .51 | .00053 | .51 | .00026 | .51 | .00017 | .51 | .00013 |
| 42 | .45 | .00041 | .45 | .00020 | .45 | .00013 | .45 | .00010 |
| 43 | .39 | .00031 | .39 | .00015 | .39 | .00010 | .39 | .00007 |
| 44 | .34 | .00024 | .34 | .00012 | .34 | .00008 | .34 | .00006 |
| 45 | .30 | .00018 | .30 | .00009 | .30 | .00006 | .30 | .00004 |
| 46 | .25 | .00013 | .25 | .00006 | .25 | .00004 | .25 | .00003 |
| 47 | .21 | .00008 | .21 | .00004 | .21 | .00003 | .21 | .00002 |
| 48 | .16 | .00005 | .16 | .00002 | .16 | .00001 | .16 | .00001 |

## Estimation of Total Mortality Rates and the Ratio Z/K
### Using Extreme Values

The oldest age in a fish population has statistical properties of extreme values. The age of a fish at death is a statistical variate and the negative exponential curve gives the probability of dying after a certain age. Fish populations with high total mortality have relatively fewer age groups than populations with low total mortality. By reducing the fishing intensity one expects more fish reach an older age. Several workers have investigated the application of statistics of extreme values in estimating the total mortality of fish (Gumbell 1954, Kendall 1955, Beverton 1963 and Holt 1965).

Suppose we have n independent observations $x_1$, $x_2$,..., $x_n$ with a common distribution

$$F(t) \equiv Prob \left\{ X \leq t \right\}$$

Then if $y_1$, $y_2$....$y_n$ are the same n observed numbers rearranged in descending order of magnitude, the largest value $y_1$ and the smallest value $y_n$ and the range $(y_1 - y_n)$ are new random variables the joint distribution of which depends on the distribution function F(t). The negative exponential distribution expressing mortality with age is

$$F(X) = 1 - e^{-X} \text{ for } X \geq 0$$

F(X) is the probability that a given observation has a value equal to or less than x. If $y$ is the largest value of x (age) in the sample of size n, then

$$y = v + \ln(n) \tag{6.1}$$

As n tends to infinity, v = 0.5772 (Euler's constant).

By taking several samples of size n, the mean largest y becomes

$$\overline{y} = .5772 + \ln(n) \tag{6.2}$$

Holt (1965) derived an equation for estimating the mean age of the oldest fish in a series of samples of size n

$$\overline{t}_L = \frac{0.5772 + \ln(n)}{Z} + t_c \tag{6.3}$$

where $\overline{t}_L$ is the mean age of the oldest fish in a series of samples of size n. Equation (6.3) can be written as

$$\overline{t}_L - t_c = \frac{0.5772 + \ln(n)}{Z} \tag{6.4}$$

The standard deviation of y in (6.1) is

$$\sigma y = \frac{\pi}{\sqrt{6}}$$

and the variance of y is $\sigma^2 y = \frac{\pi}{6}^2$

The variance of $\overline{t}_L - t_c$ in equation (6.4) is

$$\sigma^2 (\overline{t}_L - t_c) = \frac{1}{Z^2} \cdot \frac{\pi^2}{6}$$

From equation (6.4) an expression for estimating total mortality is derived:-

$$\hat{Z} = \frac{0.5772 + \ln(n)}{\overline{t_L} - t_c} \tag{6.5}$$

But the expected total mortality $E(\hat{Z})$ is

$$E(Z) = Z \left( 1 + \frac{\pi^2}{6\ (.5772 + \ln(n))^2} \right) \tag{6.6}$$

The variance of $E(\hat{Z})$ is

$$\text{Var}\ (\hat{Z}) = \frac{\pi^2\ Z^2}{6\ (.5772 + \ln(n))^2} \tag{6.7}$$

It is important to note the differences between the negative exponential distribution and the extreme value distribution as estimators of total mortality.

(1) The mean age of a population estimated from a negative exponential is smaller than the mean age estimated from the extreme values.

(2) The variance of the mean age (of a negative exponential) is bigger than the variance of the mean age determined from extreme values.

(3) The coefficient of variation for the mean age estimated from a negative exponential is unity because mean age is equal to the standard deviation. But the coefficient of variation of the mean age from the extreme value function is less than one.

(4) As estimators of total mortality Z, the negative exponential is more reliable than the extreme value function. The variance of Z estimated from a negative exponential is smaller than the variance of Z as estimated from the extreme value function.

A comparison of variances from both estimators is given in Table 8. It is assumed that the total mortality Z = 0.5, and the variances of Z from samples of various sizes, are calculated.

TABLE 8 - Comparison of variance of exponential and extreme value functions for Z = 0.5

| Sample Size (n) | Variance | |
|---|---|---|
| | Exponential $\text{Var}(Z) = Z^2/n$ | Extreme Value $\text{Var}(Z) = \dfrac{\pi^2 Z^2}{6\,(.5772 + \ln(n))^2}$ |
| 10 | 0.025 | 0.049 |
| 100 | 0.0025 | 0.015 |
| 1000 | 0.00025 | 0.0073 |
| 10000 | 0.000025 | 0.0043 |

The extreme value function can be used to determine the ratio Z/K from length data. If we replace ages $t_c$ and $\bar{t}_L$ in equation (6.5), the longest fish in the catch can be used for estimating total mortality

$$X_1 = - \ln (1 - l_t/L\infty)$$

where $l_t$ is the longest fish in the catch of sample size n

$$X_c = - \ln (1 - l_c/L\infty)$$

and

$$\bar{t}_L - t_c = \frac{1}{K} X_1 + t_0 - \frac{1}{K} X_c + t_0$$

Therefore
$$\overline{t}_L - t_c = \frac{1}{K} (\overline{X}_1 - X_c)$$

Then the ratio Z/K is given by

$$\frac{\hat{Z}}{K} = \frac{.5772 + \ln(n)}{\overline{X}_1 - X_c} \qquad (6.8)$$

If the ratio Z/K is constant for a given fish population, then as we increase the size of the sample, we would expect the parameter $\overline{X}_1$ to increase. If $\overline{X}_1$ does not increase with n then the ratio Z/K estimated with large samples, will be over estimated. Instead of taking one very large sample from a population, one could take small samples of size n from the several strata and reduce the variance of $\overline{X}_1$. For each stratum the ratio Z/K would be estimated and the mean of the various ratios would be the parameter for the population. Extensive sampling is required to show that the extreme age and length in a population have properties of the extreme value function, which in this case is a double exponential.

# CATCHES AND FACTORS AFFECTING CAPTURE
## IN AFRICA

## Variables Affecting Catches

The most serious problem connected with determining yields from tropical lakes is the estimation of annual recruitment. Many fish species,especially those of the genus *Tilapia*,have no definite breeding season and it is extremely difficult to relate the notions of recruitment to several batches of young that appear in a year. For *Tilapia*, which spawns in the inshore waters, fluctuation of water level is an important environmental factor influencing the success of spawning.

Welcomme (1966) reports that Lake Victoria levels show seasonal oscillation with a maximum in May-June and a minimum in October to November. Long-term fluctuations of water level also occur. Prior to 1927, Lake Victoria had a 10 or 11 year cycle of water level maxima. From 1927 to about 1961 the pattern of fluctuations changed markedly and the water level rose considerably. In 1964, the water level was 1.4 meters above previous records. The rise in water level was accompanied by changes in catch per unit effort for *Tilapia esculenta* (see Figure 4). Mean catches of three species of *Tilapia* from 4 and 4.5 inch gill nets are given in Table 9. These mean catches are based on catch effort data from several fish landings in Tanzania and Uganda.

TABLE 9 - Mean catch per effort (catch per net per set)
for *Tilapia* species from 1959 to 1965.

| Fish species | MEAN CATCH PER NET PER SET | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1959 | 1960 | 1961 | 1962 | 1963 | 1964 | 1965 |
| *Tilapia esculenta* | 1.09 | 0.84 | 0.92 | 1.11 | 1.59 | 5.85 | 3.80 |
| *Tilapia variabilis* | 0.72 | 0.81 | 0.99 | 1.16 | 1.03 | 0.93 | 0.26 |
| *Tilapia zilli* | 0.03 | 0.06 | 0.08 | 0.17 | 0.15 | 0.19 | 0.11 |

The spawning grounds of *Tilapia esculenta* are swampy sheltered

margins and these areas were increased considerably by flooding in 1961

to 1962 (Welcomme 1964). Lowe (1956) reports that breeding activity

of *Tilapia esculenta* increase with heavy rainfall. The heavy rainfall

of 1961 and 1962 seem to have induced a high response in breeding activity

of *Tilapia esculenta*. The year classes of 1961 and 1962 resulted in high

catches in 1964 and 1965. Note that *Tilapia esculenta* takes two to three

years to attain maturity (22 cm. to 24 cm.) and it is at this size that

a fish is caught in 4 and 4.5 inch gill nets. *Tilapia zilli* and *Tilapia*

*variabilis* spawn on harder bottomed exposed beaches (Fryer 1961 and

Welcomme 1964). The rainfall of 1961 and 1962 did not significantly

affect the catches of *Tilapia zilli* and *Tilapia variabilis* (see Table

9 and Figure 4).
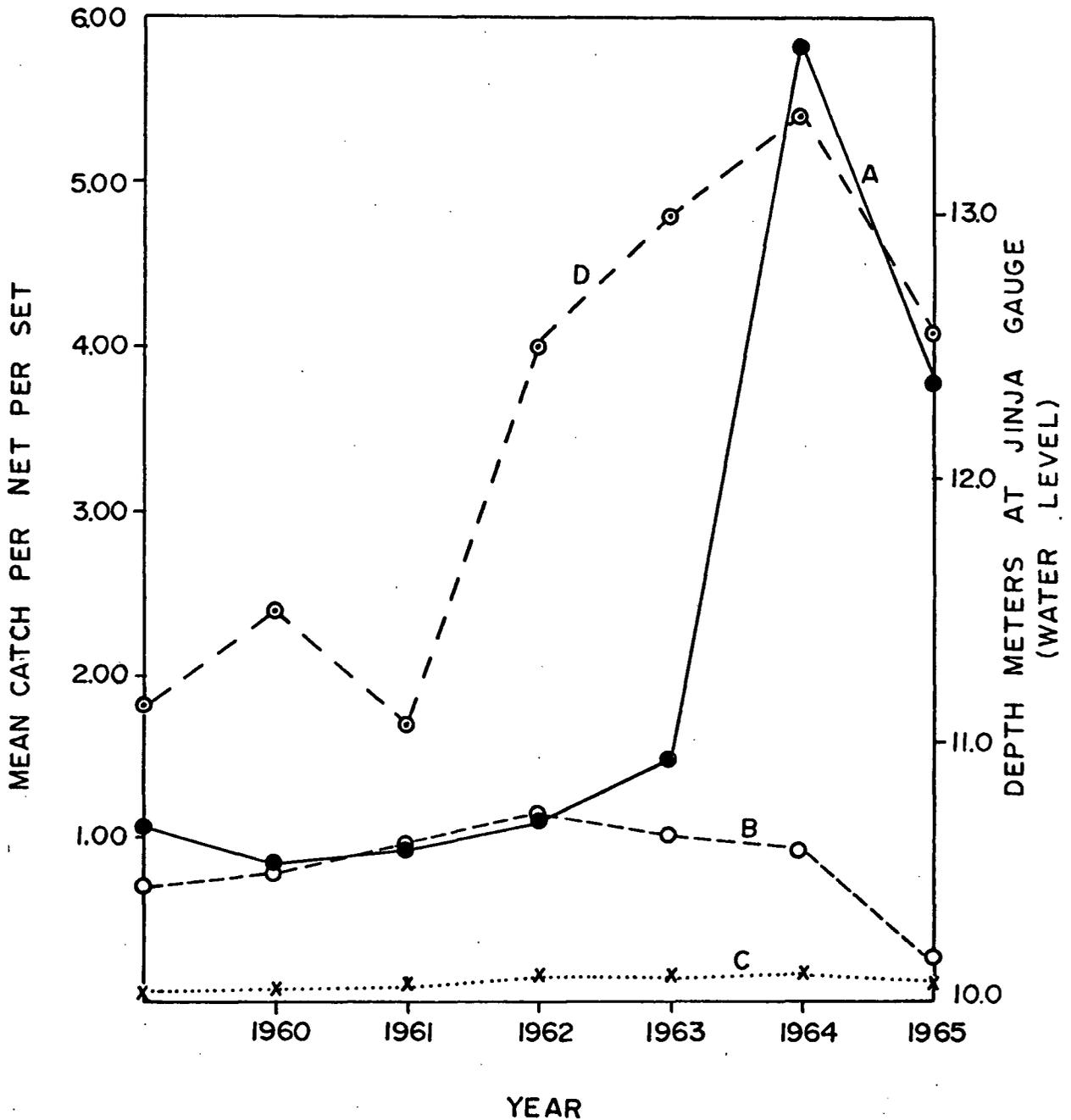
Figure 4 - Changes in mean catch per net (expressed as number of fish per 25 yd. set) of (A) *Tilapia esculenta*, (B) *Tilapia variabilis* and (C) *Tilapia zilli* for sampled fish landings in Tanzania and Uganda. (D) is Lake water level in meters at Jinja.

Information on other variables affecting catches is furnished by F.A.O. exploratory bottom trawling in Lake Victoria. These variables include depth of bottom, time of day of fishing and mesh size of codend. For some fish species, e.g., *Tilapia esculenta* and other *Tilapia* species, the catches decline with increasing depth of the lake. But catches of *Haplochromis* increase with increasing depth and the maximum catch occurs at about 44.5 metres. Beyond a depth of 44.5 metres, the catches decline. One of the important cat-fishes (*Bagrus docmac*) gives low catches at a mean depth of 6.5 metres. The catches increase with depth to about 24.5 metres beyond which the catches deline. A comparison of the effect of depth on catches of some fish species is given in Table 10 and Figure 5.

TABLE 10 - Mean catches in Kilograms of fish caught per hour
at various depths during exploratory bottom trawling
in Lake Victoria.

| | MEAN DEPTH IN METERS | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 6.5 | 14.5 | 24.5 | 34.5 | 44.5 | 54.5 | 64.5 | 74.5 |
| | Kg. | Kg. | Kg. | Kg. | Kg. | Kg. | Kg. | Kg. |
| *Haplochromis* | 320.4 | 524.8 | 462.8 | 524.0 | 465.9 | 496.7 | 185.2 | 28.8 |
| *Tilapia esculenta* | 52.6 | 31.7 | 3.5 | 0.3 | 0.1 | 0.0 | 0.0 | 0.0 |
| Other *Tilapia* | 15.0 | 0.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Bagrus docmac* | 24.6 | 42.3 | 45.1 | 35.5 | 31.3 | 38.6 | 21.9 | 0.3 |

The time of day when fishing is conducted is another variable influencing catches. Regier (1970) assumes that the diel vertical movement of some fish species affects trawl catches following a sine curve with nodes at dawn 07:00 hours and at dusk 19:00 hours. The nodes are the periods of minimum catches and the antinodes are periods of maximum catches. The antinodes occur at 13:00 hours and at 01:00 hours. There is therefore a period of 12 hours between nodes as shown in Figure 6. The catch is expressed as a function of time of day of fishing as

$$y = b_3 \sin \left[ \pi \frac{(T - 7.00)}{12} \right] \qquad (7.1)$$

where T is the time of day of fishing and ranges from 1 to 24 hours, $b_3$ is the amplitude of the sine wave and $y = b_3$ at the antinodes. A series of preliminary analyses support the assumption of catches following a sine curve. The multiple regression analyses were done using the sine curve in the form of (7.1). However through personal interviews with local fishermen in the northern end of Lake Victoria, I learnt that a number of fishermen utilize the 01:00 hour antinode. Most fishermen set their gillnets between 17:00 and 19:00 hours and pick up their gill nets between 02:00 and 05:00 hours. This implies that some fishermen are aware that after 02:00 hours, the catch declines. Local fishermen in Lake Victoria do not conduct day time fishing and information on the catches at 13:00 hour antinode is from trawl catches. Since there are two antinodes (one at 01:00 hour and another at 13:00 hours it might be desirable to take the absolute values of (7.1)

$$y = \left| b_3 \sin \left[ \pi \frac{(T - 7.00)}{12} \right] \right|$$
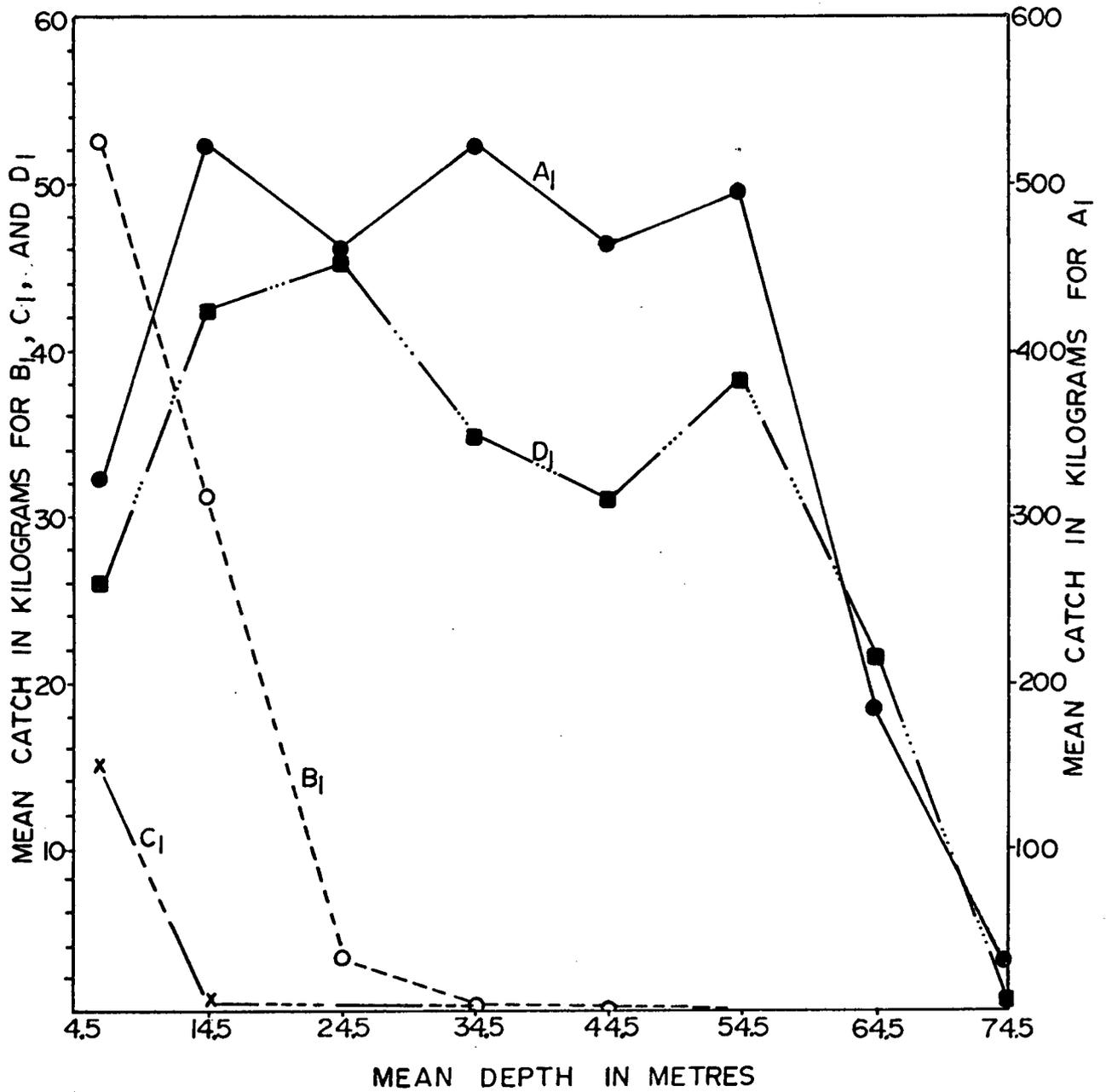
Figure 5 - Mean catch per hour (in kilograms) at various depths of bottom
trawling in Lake Victoria, East Africa. $A_1$ *Haplochromis*,
$B_1$ *Tilapia esculenta*, $C_1$ *Tilapia* (other species) and $D_1$ *Bagrus docmac*.
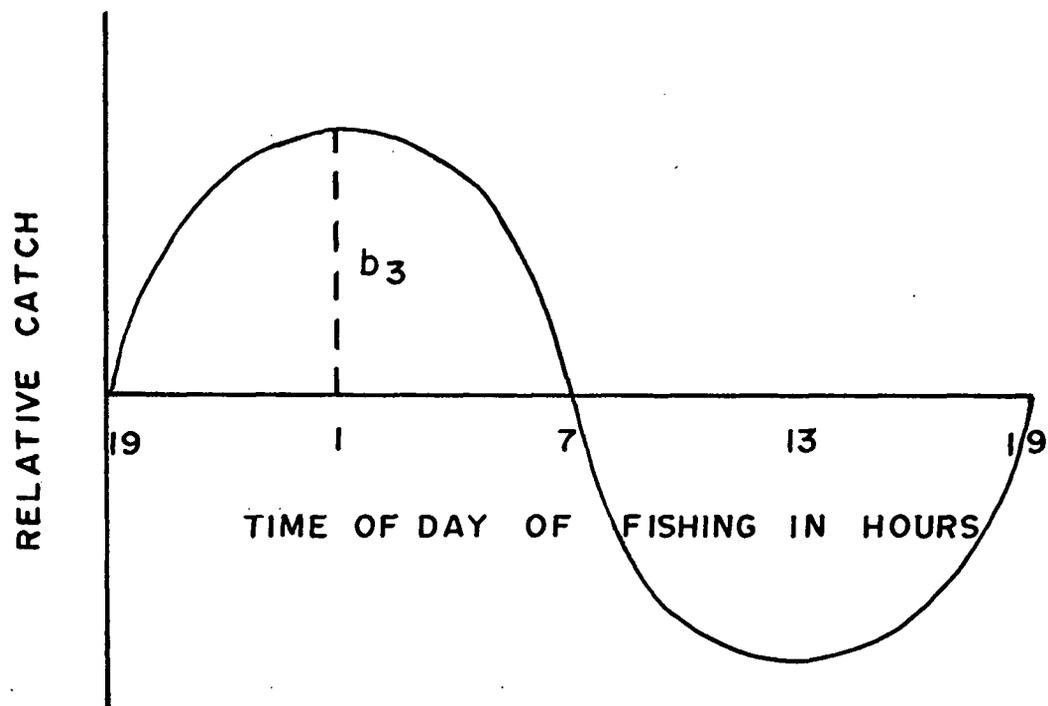
Figure 6 - A hypothetical curve of catches against time of day with nodes at 7 and 19 hours. $b_3$ is the amplitude of the sine wave (see equation 7.1).

It is necessary to estimate the effect of a number of variables on the catch of different species. Regier (1970) suggested a step-wise multiple regression analysis on the catches from bottom trawling. This analysis gives useful information on the distribution and standing crop of certain fish species. An outline of a step-wise multiple regression analysis is given below.

The relationship between yield and variables like depth of a lake and mesh size of codend of a trawl may not be simply linear. Therefore a simple linear relationship is commonly modified by use of a polynomial regression, viz.

$$y = b_0 + b_1 X + b_2 X^2 + \dots + b_n X^n \tag{7.2}$$

The effect of type of bottom, time of fishing, depth of lake and mesh size, on yield is investigated for the genus *Haplochromis* and for *Tilapia esculenta* and *Tilapia nilotica*. The area studied is that between Bugoma-Salisbury channel and Rosebery channel for depth less than 50 metres.

Below is a symbolic notation of the independent variables.

$X_1$ = type of bottom

$X_s$ = soft mud bottom

$X_m$ = mud bottom

$X_h$ = hard bottom

$X_2$ = depth of bottom

$X_3$ = time of day of fishing

$X_4$ = mesh size of codend

The relationship between the yield $y$ and the independent variables is given by a multiple regression model below.

$$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + U \qquad (7.3)$$

The parameters $\beta_0$, $\beta_1$, $\beta_2$, $\beta_3$ and $\beta_4$ are unknown population coefficients. $U$ is an unknown random variable measuring the departure of observed $y$ from the predicted $y$. The above parameters are estimated from samples taken from a population:

$$y = b_0 + b_1 X_1 + b_2 X_2 + b_3 X_3 + b_4 X_4 + e \qquad (7.4)$$

where $e$ is a random error term and the coefficients $b_1$, $b_2$, $b_3$ and $b_4$ are coefficients giving the slope of $y$ on the variables $X_1$, $X_2$, $X_3$ and $X_4$ respectively.

Because the regression of yield on each of the variables, except $X_3$, is of a polynomial form, the catches have been subjected to a logarithmic transformation. This transformation helps to reduce the polynomial terms, stabilizes the variance of the mean and make the regression model more efficient.

If we write a function for each of the independent variables, the model (7.4) becomes:

$$y = \log (Z) = U + f_1(X_1) + f_2(X_2) + f_3(X_3) + f_4(X_4) \qquad (7.5)$$

where $Z$ is a discriminant function and a linear function of the independent variables. Each of the independent variables contributes an effect independent of the other variables to the logarithm of the catch.

In the case of a multiple regression where a dependent variable (e.g. catch) is affected by several variables, it is necessary to discriminate

among the independent variables, and leave only those variables which contribute to the regression sum of squares. In an exploratory manner various combinations of the variables $X_1$, $X_2$, $X_3$ and $X_4$ are chosen in such a way as to minimize the unexplained residual variation. Any variable which does not significantly contribute to the regression sum of squares is dropped. We use the correlation coefficients between yield and the other variables as a criterion for entering variables in equation (7.4).

Correlation coefficients for the genus *Haplochromis* and for *Tilapia esculenta* and *Tilapia nilotica* are given in Table 11.

TABLE 11 - Correlation coefficients between catches and variables affecting catches in Bugoma-Salisbury Channel to Rosebery Channel in Lake Victoria Uganda .

| Independent Variables | FISH SPECIES | | |
|---|---|---|---|
| | *Haplochromis* log y | *Tilapia esculenta* log y | *Tilapia nilotica* log y |
| $X_s$ | 0.0160 | - 0.1179 | - 0.1247 |
| $X_m$ | 0.1796 | - 0.5325 | - 0.0760 |
| $X_h$ | - 0.1866 | 0.5784 | 0.1279 |
| $X_2$ | 0.4424 | - 0.7505 | - 0.3413 |
| $X_3$ | 0.4634 | - 0.3136 | - 0.2184 |
| $X_4$ | - 0.7371 | 0.2196 | 0.1243 |
| $X_2^2$ | 0.4459 | - 0.6581 | - 0.2867 |
| $X_3^2$ | - 0.0200 | 0.0833 | 0.1231 |
| $X_4^2$ | - 0.7852 | 0.2057 | 0.1351 |
| $X_2^3$ | 0.4369 | - 0.5606 | - 0.2358 |
| $X_3^3$ | 0.3913 | - 0.2546 | - 0.1990 |
| $X_4^3$ | - 0.8169 | 0.1886 | 0.1367 |

$X_s$ = soft mud bottom  $X_2$ = depth of bottom

$X_m$ = mud bottom  $X_3$ = time of day

$X_h$ = hard bottom  $X_4$ = mesh size of codend

## Multiple Regression Equations

By using the simple correlation coefficients in Table 11 as a criterion for entering variables in a multiple regression model, the equations below were established. Because the regression model is of a polynomial form, the multiple regression equation contain some variables raised to certain powers.

The equation to describe catches for *Haplochromis* species is

$$\log y = 1.9869 - 0.104\ X_4^3 + 0.0608\ X_4^2 + 0.2267\ X_3 +$$

$$0.0003\ X_2^3 \qquad\qquad (7.6)$$

Equation (6.7) shows that the catch of *Haplochromis* depends on mesh size, time of day of fishing and bottom depth. It is also evident that the smaller the mesh size $X_4$, the bigger the catch. The time of day of fishing $X_3$ will contribute to the catches depending on the time function (7.1). From above it is evident that high catches of *Haplochromis* will occur at a greater depth $X_2$.

For *Tilapia esculenta*, the multiple regression equation is:

$$\log y = 2.0407 - 0.0996\ X_2 + 0.00118\ X_2^2 + 0.2936\ X_1 \qquad (7.7)$$

Equation (7.7) shows that catches for *Tilapia esculenta* are more influenced by depth and type of lake bottom than any of the other variables. Also note that the correlation coefficient between log y and depth is - 0.7505 meaning that catches decline with depth. From the correlation coefficients

in Table 11, it appears high catches of *Tilapia esculenta* occur in hard bottom localities.

The equation for *Tilapia nilotica* is

$$\log y = 0.3213 - 0.02 \ X_2 + 0.00028 \ X_2^2 \tag{7.8}$$

Equation (7.8) shows that the catch of *Tilapia nilotica* is very much influenced by the depth of lake.

If all the important parameters are included, the multiple regression equations and the correlation coefficients provide a short-cut method of assessing the state of exploited fish stocks. Under steady state conditions, the catches of each year should be close to what is predicted. If there is overfishing and the stocks are declining, the catches will be less than what the multiple regression equations predict.

Analyses of catch data of two or more periods will give reliable indications of the relative degree of exploitation. The multiple regression equations could also be used in improving fishing success, since they provide information on the distribution of fish, mesh size of codend of trawl and time of day of fishing, likely to give high catch.

# YIELD EQUATIONS

## Beverton and Holt Yield Model

In exploited fish populations, fish are recruited to the fishery at age $t_r$ (the age of recruitment), but are not caught until the age of first capture ($t_c$). The only exception to this is the case of knife edge recruitment where $t_c = t_r$. The change in numbers with time in exploited fish populations is given by

$$\frac{dN_t}{dt} = - (F + M)\ N_t \qquad (8.1)$$

Integrating the above derivative with the lower limit of the integral equal to $t_r$ and the upper limit $t\lambda$, the "age of exit" from a fishery, gives

$$N_t = R\ e^{-Z(t - t_r)} \qquad (8.2)$$

where R is the number of recruits at the age $t_r$ and Z is the total mortality. Equation (8.2) describes change in number of recruits with age, in a fishery with knife edge recruitment.

Normally between age $t_r$ and age $t_c$, natural mortality reduces the recruits R. Therefore the recruits reaching age $t_c$ are

$$R' = R\ e^{-M(t_c - t_r)} \qquad (8.3)$$

The number of fish at each age for the exploited age groups is given by

$$N_t = R' e^{-Z(t - t_c)} \qquad (8.4)$$

Fishing mortality is responsible for a proportion of the numbers dying and the catch C is given by the integral

$$C = \int_{t_c}^{t_\lambda} F R' e^{-Z(t - t_c)} \cdot dt$$

which leads to an equation describing catch

$$C = R' \frac{F}{Z} \cdot (1 - e^{-Z(t_\lambda - t_c)}) \qquad (8.5)$$

For fish species with a large $t_\lambda$, the expression in brackets approaches one and the catch is approximated by

$$C = \frac{FR'}{Z} \qquad (8.6)$$

In terms of weight, the yield at any time is given by

$$\frac{dY_t}{dt} = FN_t W_t$$

The total yield in weight from a year class is given by the integral

$$Y = \int_{t_c}^{t_\lambda} F N_t W_t \cdot dt \qquad (8.7)$$

A major problem facing fishery biologists is one of finding an unbiased expression for weight in equation (8.7). The von Bertalanffy growth equation for length is

$$l_t = L_\infty (1 - e^{-K(t - t_0)})$$

Beverton and Holt (1957) assumed isometric growth and expressed weight in terms of a cubic expression of length

$$W_t = W_\infty (1 - e^{-K(t - t_0)})^3$$

Replacing weight in (8.7) by a cubic expression is a convenient method for evaluating the integral in (8.7). Though it is well accepted now that growth of many fish species is not isometric, the easiest approach to evaluating the yield integral (8.7) is the assumption of isometric growth. However, numerical evaluation of (8.7) for fish with allometric growth can be done using an incomplete Beta function. The above cubic equation when expanded and rearranged can be written as a summation.

$$W_t = \sum_{n=0}^{3} U_n e^{-nK(t - t_0)} \tag{8.8}$$

where $U = 1.0, -3.0, 3.0, -1.0$, for $n = 0, 1, 2, 3$ respectively.

If we replace $W_t$ in (8.7) by the expression in (8.8) and replace $N_t$ by the expression for $R'$ in (8.3), the integral (8.7) leads to the Beverton and Holt yield equation.

$$Y = FW_\infty \ e^{-M(t_c - t_r)} \sum_{0}^{3} \frac{U_n \ e^{-nK(t_c - t_0)}}{F + M + nK} \cdot (1 - e^{-(Z + nK)(t_\lambda - t_c)}) \tag{8.9}$$

where Y is the yield per recruit. For fish species with large $t\lambda$ , the last expression in brackets in (8.9) could be eliminated without affecting significantly the value of yield. But most tropical fish species have a short life span and therefore a small $t\lambda$. Without the expression within the brackets, equation (8.9) would give biased estimates of yield for fish species in the tropics.

Using equation (8.9) yields have been calculated and yield isopleths constructed for *Tilapia esculenta* in Lake Victoria and *Tilapia nilotica* in Lake Albert Uganda.

The ages for *Tilapia nilotica* have been estimated from length by the equation

$$t = \frac{1}{K} (- \ln (1 - l_t/L\infty)) + t_0$$

expressed in the same conventional form of the von Bertalanffy equation:

$$l_t = f(t) = L\infty (1 - e^{-K(t - t_0)})$$

where for *Tilapia nilotica* $L\infty$ = 49.0 cm., K = 0.5 and $t_0$ = 0.

*Tilapia esculenta* in Lake Victoria lives for 12 "ring" years, equivalent to six calendar years (Garrod 1963). *Tilapia esculenta* in the Jinja region of Lake Victoria have the following population parameters: $L\infty$ = 33.8 cm., K = 0.32, $t_0$ = - 0.8. The natural mortality estimated by Garrod (1963) is 0.17 which is close to the natural mortality rate of 0.16 estimated on the assumption that the mean natural mortality is a reciprocal of life span. With this natural mortality, there is a probability of 0.07 that a fish will reach a maximum age of 6 years.

In the calculation of yield, W∞ was taken as 730 gm. It is possible that *Tilapia esculenta* now being caught in bottom trawling may exceed that weight. Whether the actual maximum weight is less or greater than 730 gm., does not affect the shape of the yield isopleths. The age of recruitment $t_r$ is taken as zero but this does not mean that the young and adult *Tilapia esculenta* live in the same habitat. Actually, *Tilapia esculenta* is recruited at a length of about 20 cm. corresponding to about 2 years of age. Setting $t_r$ as zero in model (8.9) is a matter of computational convenience. But this is based on prior information that $t_r$ does not influence the shape of yield isopleths but only reduces the value of yield.

Observations on yields of *Tilapia esculenta* as revealed by the yield isopleths in Figure 7, are given below.

The greatest yield can be obtained by catching *Tilapia esculenta* at a size of 28 cm. but this would require a fishing mortality of 2.55. The relative yield obtained under such conditions is 186.66 gm. per recruit. If we catch *Tilapia esculenta* at the same size 28 cm. but with a fishing mortality of 0.9, the yield is ≈ 182.51 gm/recruit. This means that if we increase the fishing mortality by 183 per cent, the yield increases only by 2.1 percent. If these fish are caught at 26 cm., a fishing mortality of 0.5 would be necessary to obtain maximum yield. From the total mortality estimates of Garrod (1963) for the years 1958 to 1960, the mean total mortality for that period was 0.3. Since natural mortality for *Tilapia esculenta* is about 0.17, the fishing mortality for that period was about 0.13. Doubling or trebling the fishing mortality
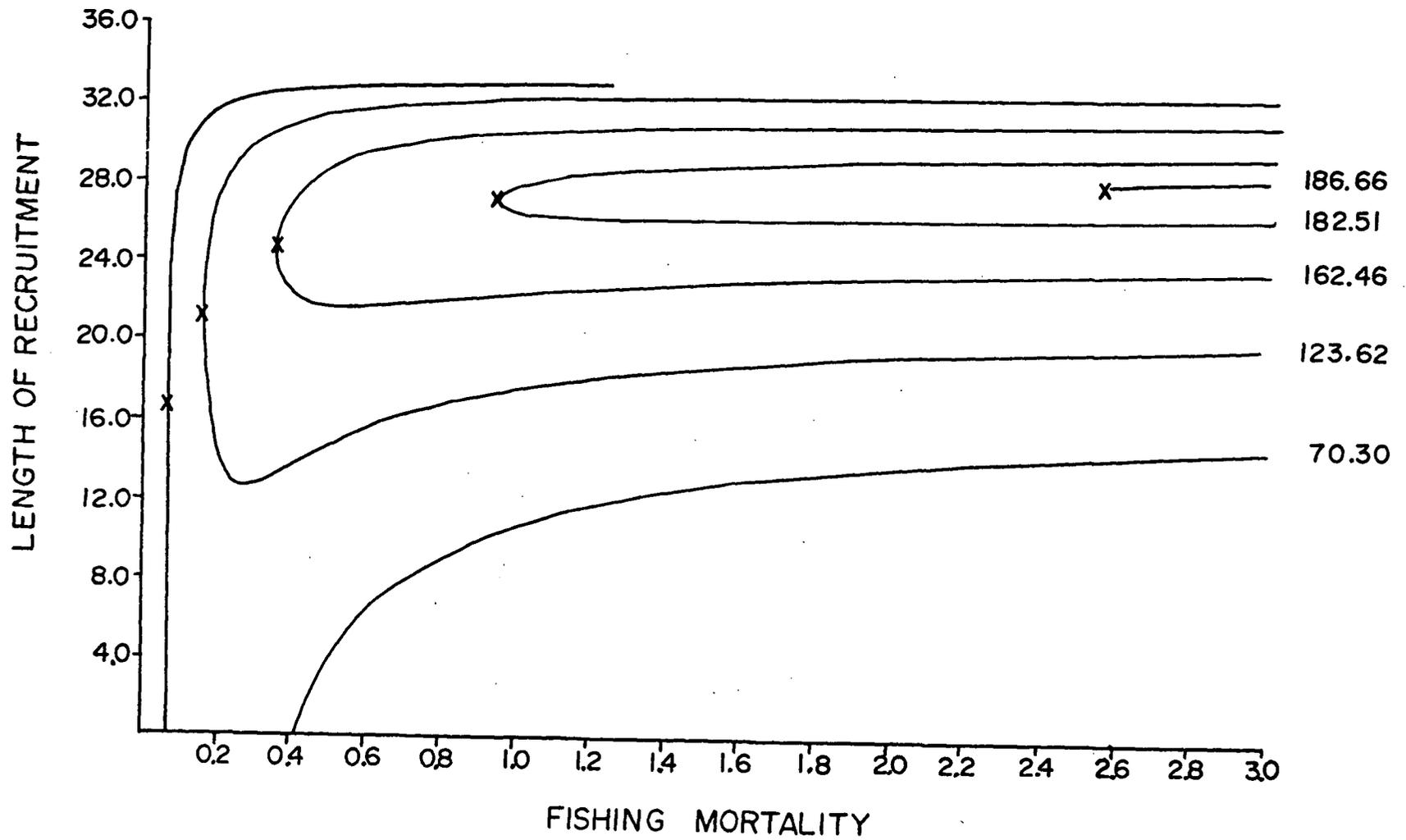
Figure 7 - Yield isopleth diagram for *Tilapia esculenta* (Lake Victoria)
[M = 0.17, W∞ = 730.0, tλ = 6.0, K = 0.32, $t_r$ = 0, $t_o$ = 0]

would have no adverse effects on the fishery if the length of capture of 26 cm. and mesh size 4.5 inches were maintained and provided there was no fishing in the inshore waters where the fish spawn. Catching *Tilapia esculenta* at any length less than 17 cm. would mean catching a lot of immature fish, and this will have adverse effects on spawning and recruitment.

*Tilapia nilotica* in Lake Albert forms two subpopulations, a stunted population in the Buhuku lagoon and a normal population in the open lake. The normal population has the following estimated parameters: $L∞ = 49$ cm., $K = 0.50$, length of maturity $Lm = 36$ cm. and natural mortality $M = 0.30$. The probability density function for the negative exponential is

$$P(t) = M e^{-M(t - t_0)}$$

*Tilapia nilotica* could live up to 8 years and with a natural mortality of 0.3 about 3 fish out of 100 would attain an age of eight if there was no fishing.

The maximum weight $W∞$ for the normal *Tilapia nilotica* in Lake Albert is unknown. For the purpose of calculating relative yields and constructing yield isopleths, $W∞$ is taken as 1000 gm. It is accepted that absolute yield values are not of primary importance to fisheries management. But what is of prime importance is yield response to fishing intensity and mesh size. At a low fishing intensity $F = 0.1$ the best size to catch *Tilapia nilotica* is 24 cm. However at 24 cm., the fish is still immature and the relative yield is small (76.37 gm/recruit). If the size of capture is increased to 34 cm., the fishing mortality

required to give a maximum yield would be 0.4 (see eumetric fishing
curve in Figure 8).        With a fishing mortality of 0.4 and length
of capture of 34 cm. the relative yield would be 159.12 gm/recruit.
If we raise the length of capture to 36 cm., the fishing mortality required
for maximum yield is 0.7.  The highest yield for *Tilapia nilotica* is
obtained at 39 cm., but this length of capture requires a fishing mortality
rate exceeding 2.1.  Note that if we catch these fish at 39 cm. and with
a fishing mortality rate of 0.5, we obtain yield of 159.2 gm/recruit.
Increasing the fishing mortality four times increases yield by a factor
of only 1.2.  It is possible to obtain sustained yields, if *Tilapia
nilotica* is caught at 35 cm. and above with a fishing mortality of 0.5
to 0.6.  It is also of interest to note that the highest yield is obtained
after the length of maturity 36 cm(see Figure 8).

Iles (MS.) reports a natural mortality rate of 3.37 for the
stunted population of *Tilapia nilotica*.  But this population has a high
growth rate (K = 2.77) and maximum length is 17 cm.  The life span is
for about one year and sexual maturity is attained at 10 - 12 cm. corres-
ponding to an age of 4 months.

With a natural mortality rate as high as 3.37 about one fish
out of a hundred would survive to an age of one year.  Is it possible
to manage rationally a fishery of this nature?  Because of a high natural
mortality, the maximum biomass occurs at a length before sexual maturity.

The highest yield would be obtained by catching the fish at
9 cm. but a high fishing mortality exceeding 1.8 would be needed (see
Figure 9).  If we follow the eumetric fishing curve we should catch the
stunted *Tilapia nilotica* at 8 cm. at about 2.5 months of age.  But catching
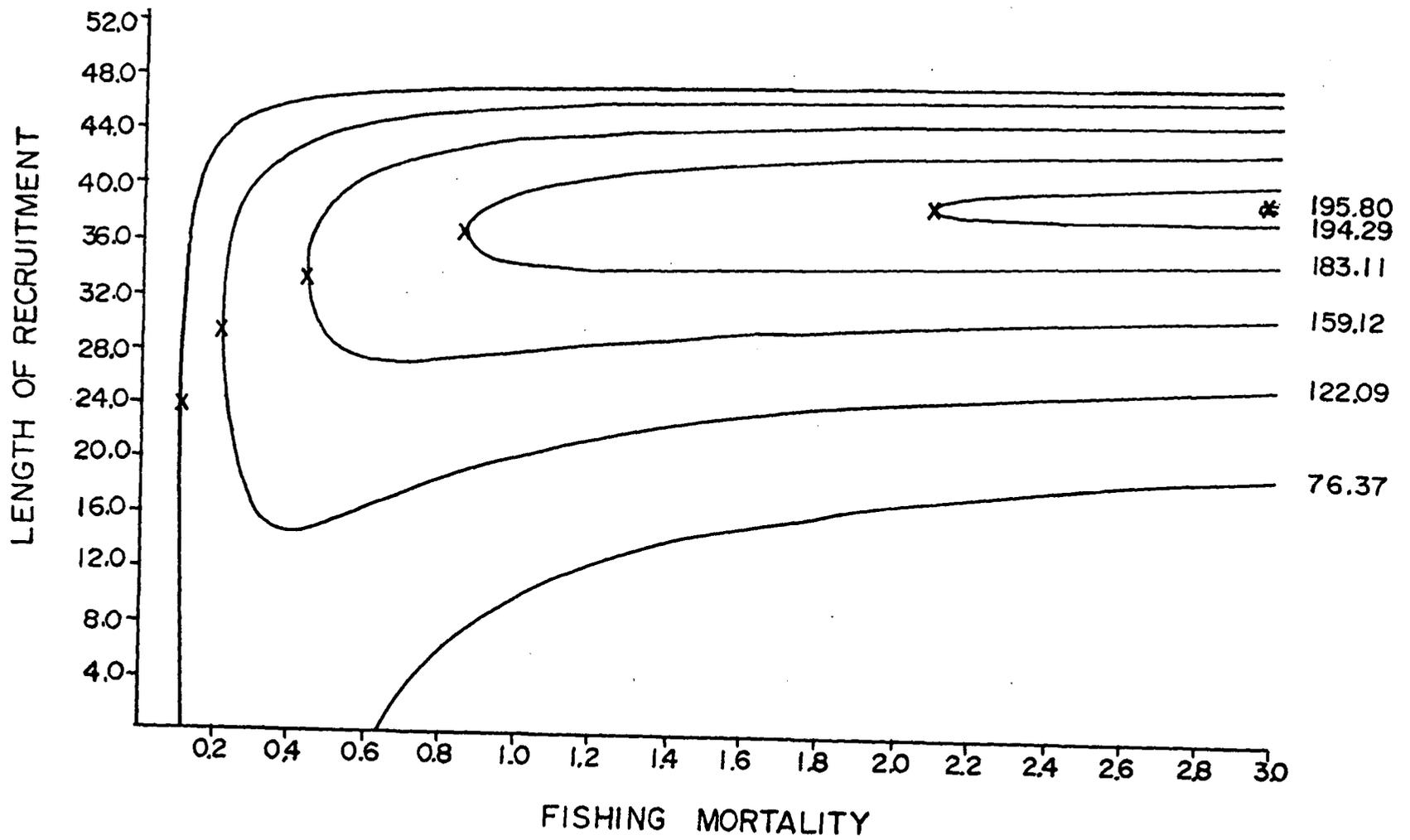
Figure 8 - Yield isopleth diagram for *Tilapia nilotica* (with normal growth) in open water, Lake Albert, Uganda.
[M = 0.30, W∞ = 1000.0, tλ = 8.00, K = 0.50, $t_r$ = 0, $t_o$ = 0]
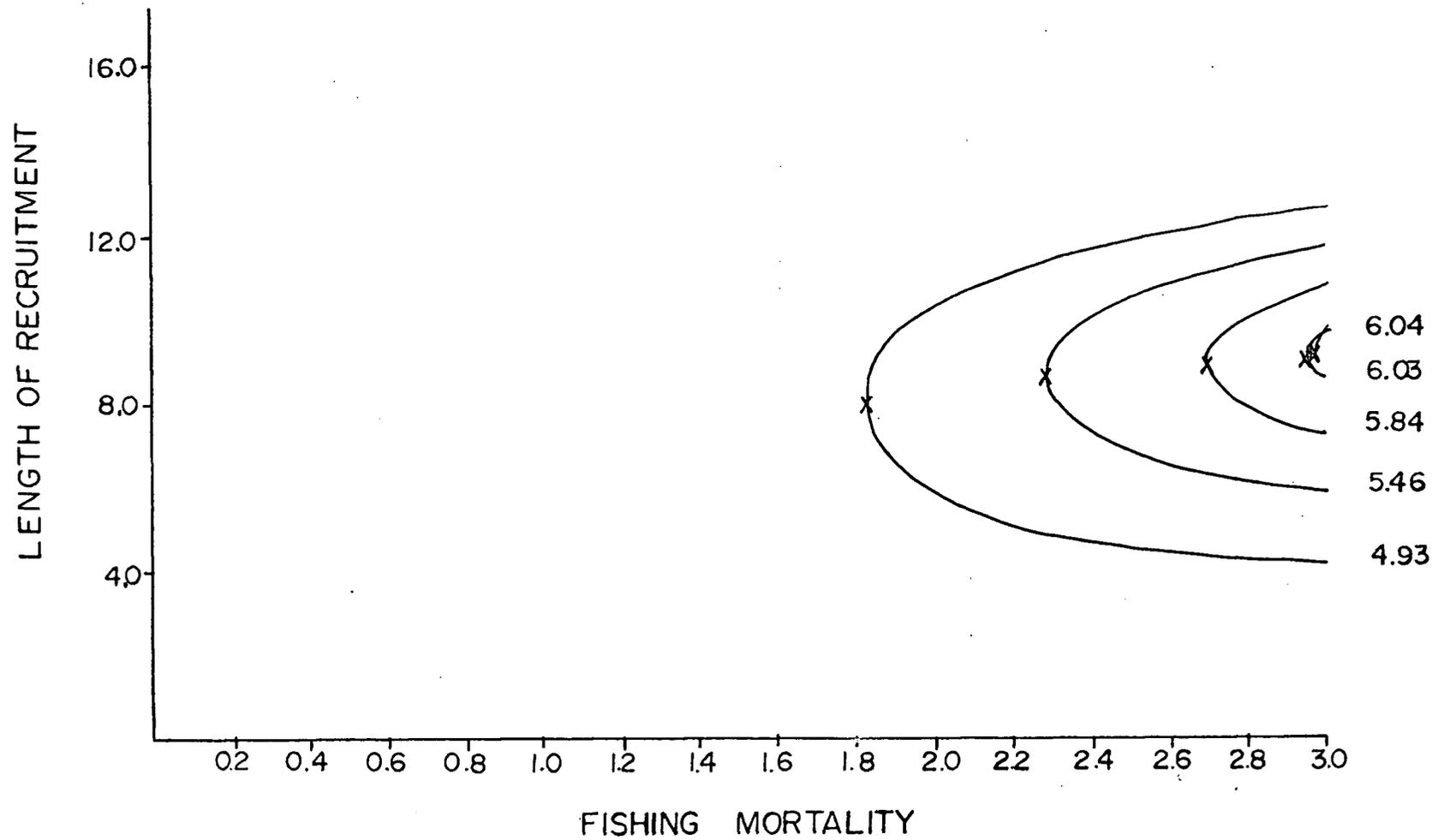
Figure 9 - Yield isopleth diagram for the stunted *Tilapia nilotica* in Lake
Albert, Uganda.
[M = 3.37, W∞ = 100.0, tλ = 1.10, K = 2.77, $t_r$ = 0, $t_o$ = 0]

these fish at 8 cm. would require a fishing mortality of 1.9 so as to obtain maximum yield. The total mortality (F + M) in such circumstances would be 5.27. With a total mortality of this magnitude, one fish out of 1000 reaching the age of 2.5 months, would survive to the age of maturity of 4 months. This deduction is made from the probability density function

$$P(t) = Z e^{-Z(t - t_1)}$$

where t = 4 months, $t_1$ = 2.5 months and Z = 5.27.

In these circumstances, it might be better to allow fish to attain maturity at 10 - 12 cm. and have at least one spawning. Then a high fishing mortality rate can be applied to the fish of a size greater than 12 cm. For fisheries of this nature, the eumetric fishing curve is not helpful. Populations such as the stunted *Tilapia nilotica*, have little commercial value.

## Other Yield Models

Because age of tropical fish species cannot easily be determined, there is a need for use of yield models that are based on the length of a fish. The yield model presented by Thompson and Bell (1934) uses age as well as length. Thompson and Bell assume that weight increase by some constant percentage in each year of life. Ricker (1944) expresses growth as a simple exponential function. Under the assumption of exponential growth and if we suppose life span to be of infinite duration, yield is given by

$$Y = \frac{F W}{F + M - g} \tag{8.10}$$

where Y is the yield, F the fishing mortality, M the natural mortality and g the instantaneous rate of growth and W is the total weight of each year's brood of recruits. If natural mortality M is greater than the growth rate g, then for all values of F, there is a positive yield which approaches an asymptotic value as F approaches infinity. When M = g, the yield is simply the initial weight of all the recruits. Finally, when M < g, the yield is infinitely large when $F \leq (g - M)$.

A number of fish species show allometric growth and the yield for these fish species can be determined by means of an incomplete Beta function. Jones (1957) and Paulik and Gales (1964) discuss the usefulness of the incomplete Beta function in determining yields. The function denoted by $B_X$ (p, q) is defined by the integral

$$B_X(p, q) = \int_0^X X^{p-1} (1 - X)^{q-1} \, dx \qquad (8.11)$$

where p > 0 and q > 0.

In the above integral, the parameters X, P and Q are defined as:

$$X = e^{-K(t_c - t_0)}$$

$$P = Z/K$$

$$Q = 1 + b$$

where b is the weight length exponent.

It is obvious from the parameters above that yields can be determined with just a few parameters. The integral above leads to the equation given by Wilimovsky and Wicklund (1963).

$$\frac{Y}{R} = \frac{F}{K} W\infty \, e^{-Z(t_c - t_0)} \left\{ \beta (X, P, Q) - \beta (X_1, P, Q) \right\} \qquad (8.12)$$

where $X_1 = e^{-K(t\lambda - t_0)}$

and $t\lambda$ is the age of exit from a fishery. The yield per gram recruit is then given by

$$\frac{Y}{R' \, W\infty} = \frac{F}{K} \, e^{Z(t_c - t_0)} \left\{ \beta \, (X, P, Q) - \beta \, (X_1, P, Q) \right\} \qquad (8.13)$$

The point of inflexion on the growth curve, is the point of maximum biomass. For many fish species the greatest yield is obtained by catching them at an age or size corresponding to the point of inflexion. At the point of inflexion the relationships below hold.

$$X = e^{-K(t - t_0)} = \frac{1}{b}$$

Therefore by knowing the weight length exponent b, the growth rate K and total mortality Z, one can predict the maximum yield expected for various fishing mortality rates. The yield when $t_c$ is the age of a fish at the inflexion point is

$$\frac{Y}{R \, W\infty} = \frac{F}{K} \, e^{Z(t_c - t_0)} \left\{ \beta \left( \frac{1}{b}, P, Q \right) - \beta \, (X_1, P, Q) \right\} \qquad (8.14)$$

For fish species with a large age of exit from a fishery, $t\lambda$, equation (8.14) reduces to

$$\frac{Y}{R \, W\infty} = \frac{F}{K} \, e^{Z(t_c - t_0)} \left\{ \beta \left( \frac{1}{b}, P, Q \right) \right\} \qquad (8.15)$$

If we replace age in (8.13) by a length expression an incomplete Beta function that can be used for tropical fish species is obtained.

From equation (5.3) the age of capture $t_c$ is

$$t_c = -\ln\left(1 - \frac{1_c}{L\infty}\right)\frac{1}{K} + t_0$$

where $1_c$ is length of capture corresponding to age $t_c$ and $L\infty$ = maximum length.

Let $\quad X_1 = -\ln\left(1 - \frac{1_c}{L\infty}\right)$

Therefore $\quad t_c = X_1\frac{1}{K} + t_0$

Similarly $\quad t\lambda = -\ln\left(1 - \frac{1\lambda}{L\infty}\right)\frac{1}{K} + t_0$

$$t\lambda = X\lambda \cdot \frac{1}{K} + t_0$$

where $1\lambda$ is the length of exit from a fishery corresponding to the age $t\lambda$ and where

$$X\lambda = -\ln(1 - 1\lambda/L\infty)$$

Then the parameters for the incomplete Beta function (B) are X, P, Q and $X_L$. Note that

$$\frac{1}{K}X_1 = t_c - t_0$$

and $\quad \frac{1}{K}X\lambda = t\lambda - t_0$

Therefore $\quad X = e^{-X_1}$

$$P = Z/K$$

$$Q = 1 + b$$

$$X_L = e^{-X\lambda}$$

If we use length, the yield per gram recruit is given by

$$\frac{Y}{R\ W\infty} = \frac{F}{K}\ e^{(Z/K)X}{}_1 \left\{ \beta\ (X,\ P,\ Q) - \beta\ (X_L,\ P,\ Q) \right\} \tag{8.16}$$

Tables of the incomplete Beta function for calculation of fish population yields are given by Wilimovsky and Wicklund (1963). According to equation (8.16), one can determine yields and construct yield curves with 4 parameters namely (1) maximum length (L∞), (2) the growth rate (K), (3) the weight length exponent (b) and (4) the total mortality (Z). The incomplete Beta function gives unbiased yield estimates for fish with allometric growth.

TABLE 12 - Comparison of yields estimated with equations (8.13) and (8.16) and which are based on age and length respectively. Both equations use the incomplete Beta function. The parameters used are K = 0.5, F = 0.2, M = 0.3, Z/K = 1, b = 3, $t\lambda$ = 6.39 years, L∞ = 49 cm., and $1\lambda$ = 47 cm.

| $L_c$ cm. | Age Yrs. | Equation(8.13) Yield in gm/recruit | Equation (8.16) Yield in gm/recruit |
|---|---|---|---|
| 28 | 1.69 | 0.171 | 0.172 |
| 32 | 2.11 | 0.189 | 0.191 |
| 36 | 2.65 | 0.207 | 0.210 |
| 40 | 3.38 | 0.214 | 0.220 |
| 44 | 4.56 | 0.187 | 0.203 |
| 46 | 5.58 | 0.104 | 0.142 |

There is little difference between yields estimated with equations (8.13) and (8.16). Table 12 shows yields calculated with both equations. If fish are caught at a length close to the maximum length ($L\infty$), the yields estimated with (8.16) differ significantly from yields estimated with equation (8.13). This is caused by logarithmic transformations made when replacing age by length in equation (8.13).

Note that $X_1$ in equation (8.16) is given by

$$X_1 = - \ln (1 - 1_c/L\infty)$$

As $1_c$ approaches $L\infty$, the expression $(1 - 1_c/L\infty)$ approaches zero and therefore $X_1$ tends to infinity.

In practice very few fish are caught at a length close to the maximum length ($L\infty$) and therefore the above observation does not affect yield predictions made from normally exploited length groups. If one plotted yield against length of capture, the extreme lengths would represent the descending limb of the yield curve as shown in Figure 11.

Equation (8.16) requires very few parameters and provides a quick way of determining yields for those fish which are difficult to age.

Another yield model based on length is given by Beverton and Holt (1964). The model was derived from the von Bertalanffy growth equation and has the inherent assumption of isometric growth. The parameters required are M, K, the ratio $L_c/L\infty$ and the fishing mortality (F). With these parameters, the yield and the eumetric fishing curve can be directly read from the tables of yield functions given by Beverton and Holt (1964, 1966).

From the von Bertalanffy growth equation we obtain the ratio c

$$c = \frac{L_c}{L_\infty} = 1 - e^{-K(t - t_0)}$$

The ratio c represents the total growth in length which is made up before fish enter the exploited phase.

$$1 - c = e^{-K(t - t_0)}$$

The exponential term within the summation in equation (8.9) can be written as

$$(1 - c)^n$$

where the above expression satisfies the equality

$$(1 - c)^n = e^{-nK(t - t_0)} \tag{8.17}$$

The rate of exploitation E is given by

$$E = \frac{F}{F + M} = \frac{F}{Z}$$

The fishing mortality F is expressed algebraically in terms of E and M

$$F = \frac{M\ E}{1 - E} \tag{8.18}$$

and the reciprocal of fishing mortality is

$$\frac{1}{F} = \frac{1 - E}{M\ E} \tag{8.19}$$

After transforming the age variables to the length expressions and if we replace F and 1/F by the appropriate expressions, the yield model (8.9)

becomes

$$\frac{Y}{R\,W\infty} = E\,(1-c)^{M/K} \sum_{n=0}^{3} \frac{U_n\,(1-c)^n}{1+\frac{nK}{M}(1-E)} \tag{8.20}$$

Using equation (8.20), yields have been calculated for the
normal and stunted population of *Tilapia nilotica* in Lake Albert Uganda.
For the normal *Tilapia nilotica* the highest yield is obtained by catching
the fish at a length of 36 cm. (see Figure 10). If we catch a fish at
a small size, we require a low fishing mortality rate to obtain maximum
yield (see Figure 11). For the stunted *Tilapia nilotica* with a natural
mortality of 3.37, yield increases at all rates of fishing mortality
up to 1.05 (see Figure 12). The stunted *Tilapia nilotica* mature at 10
to 12 cm. but maximum yield is obtained between 7 cm. and 10 cm. (see
Figure 13).

For tropical fish species whose age can be directly or in-
directly determined the yield can be estimated with equation (8.9).
But this yield model assumes isometric growth which is not true for all
fish species. Ricker (1958) gives a yield model which does not require
age and this could be used in the tropics to make yield predictions.
The incomplete Beta function (8.13) and (8.16) are unbiased estimators
of yield for fish species with allometric growth. Equation (8.16) requires
four parameters namely $L\infty$, K, Z and the weight length exponent b.
Though equation (8.20) has the assumption of isometric growth, it is
still very valuable in estimating yield for fish that are difficult to
age. If the parameters $L\infty$, K, M and F are known, the yield for the ratio
$L_c/L\infty$ is read from the tables of yield functions given by Beverton and
Holt (1964, 1966).
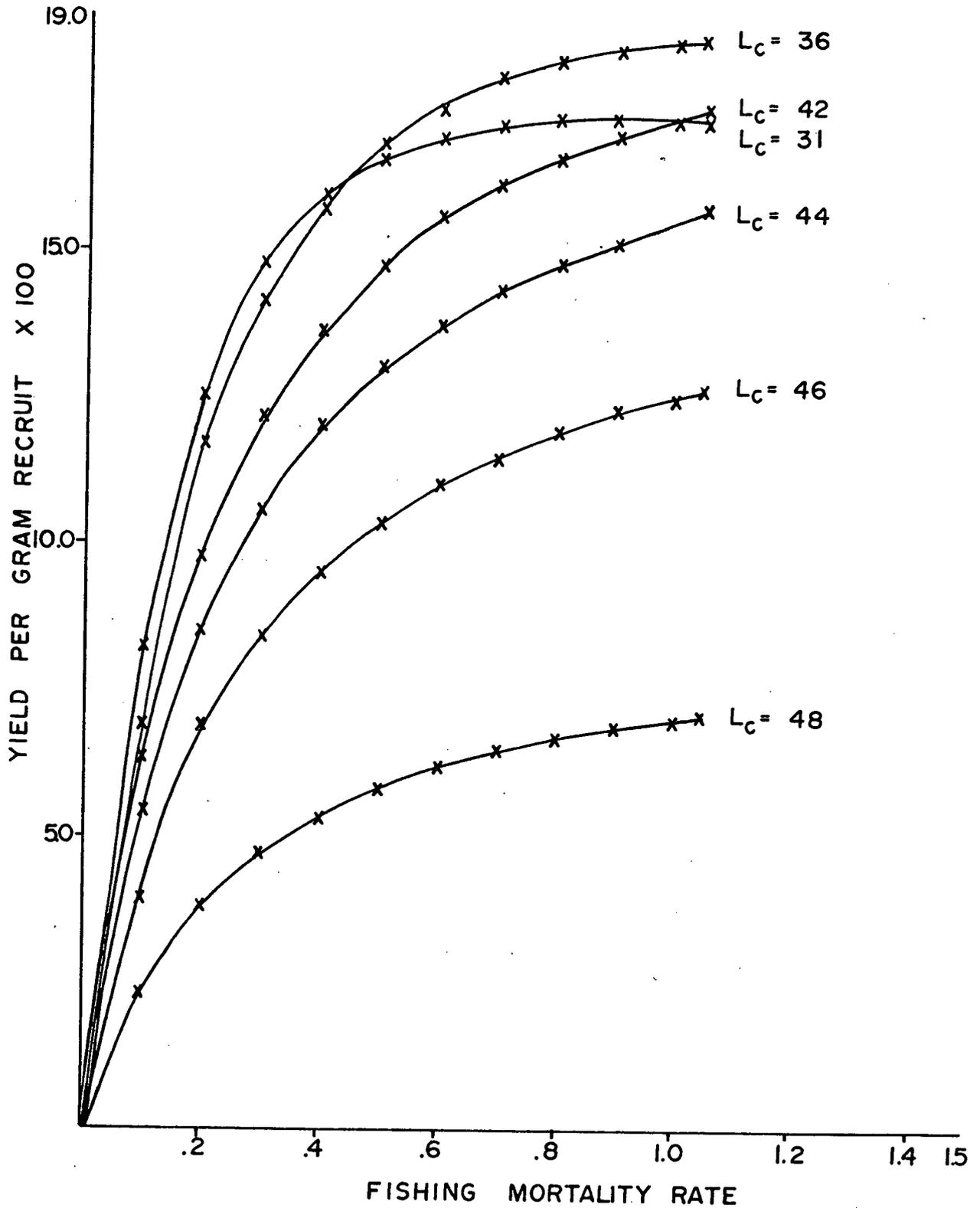
Figure 10 - Yield per 100 gm. recruit plotted against fishing mortality rate (for *Tilapia nilotica* in Lake Albert, Uganda). $L_c$ is length of capture in cm., M = 0.3, K = 0.5, and L∞ = 49.0 cm.
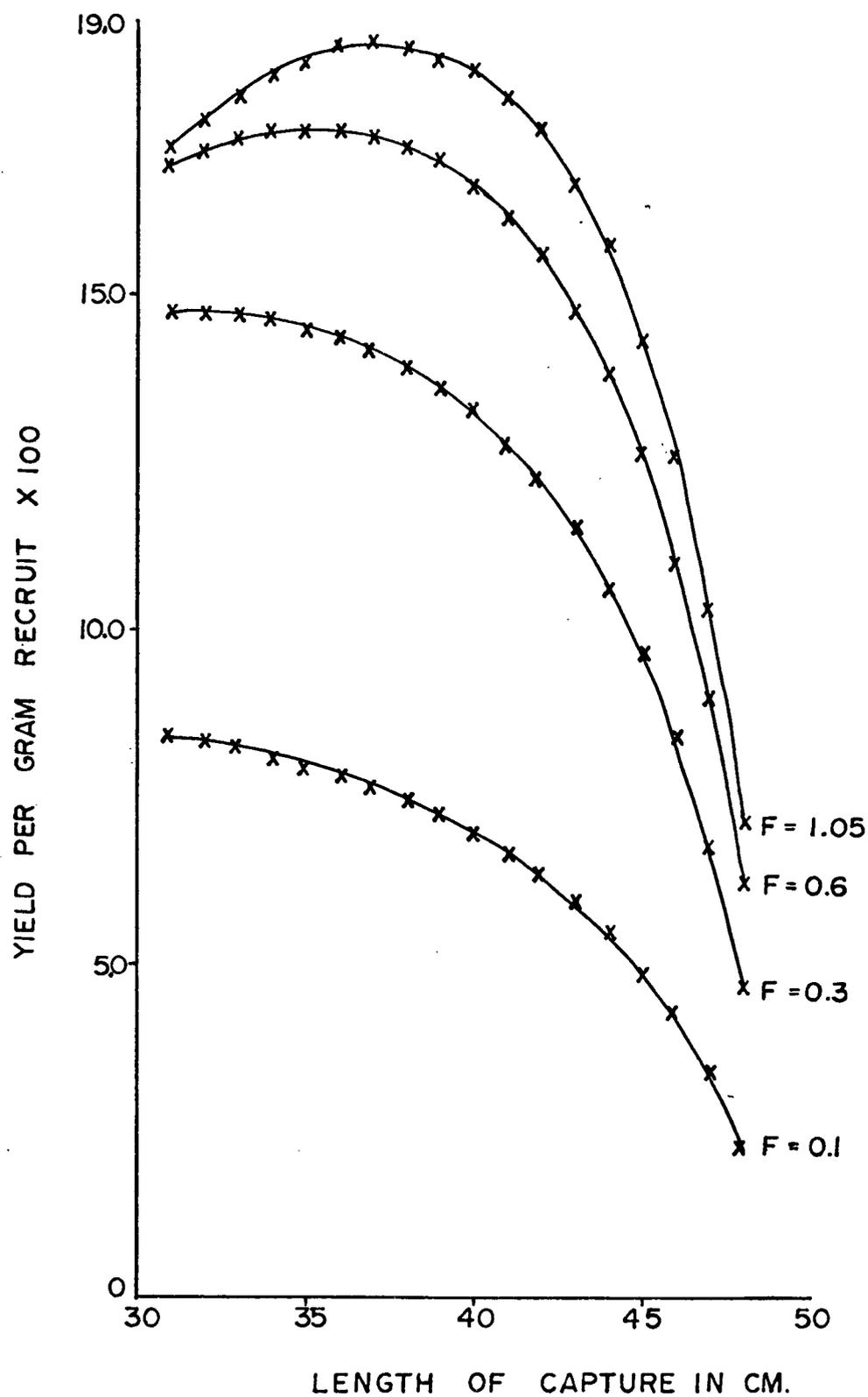
<u>Figure 11</u> - Yield per 100 gm. recruit plotted against length of capture at different fishing rates (F) (for *Tilapia nilotica* in Lake Albert, Uganda). M = 0.3, K = 0.5 and L∞ = 49.0 cm.
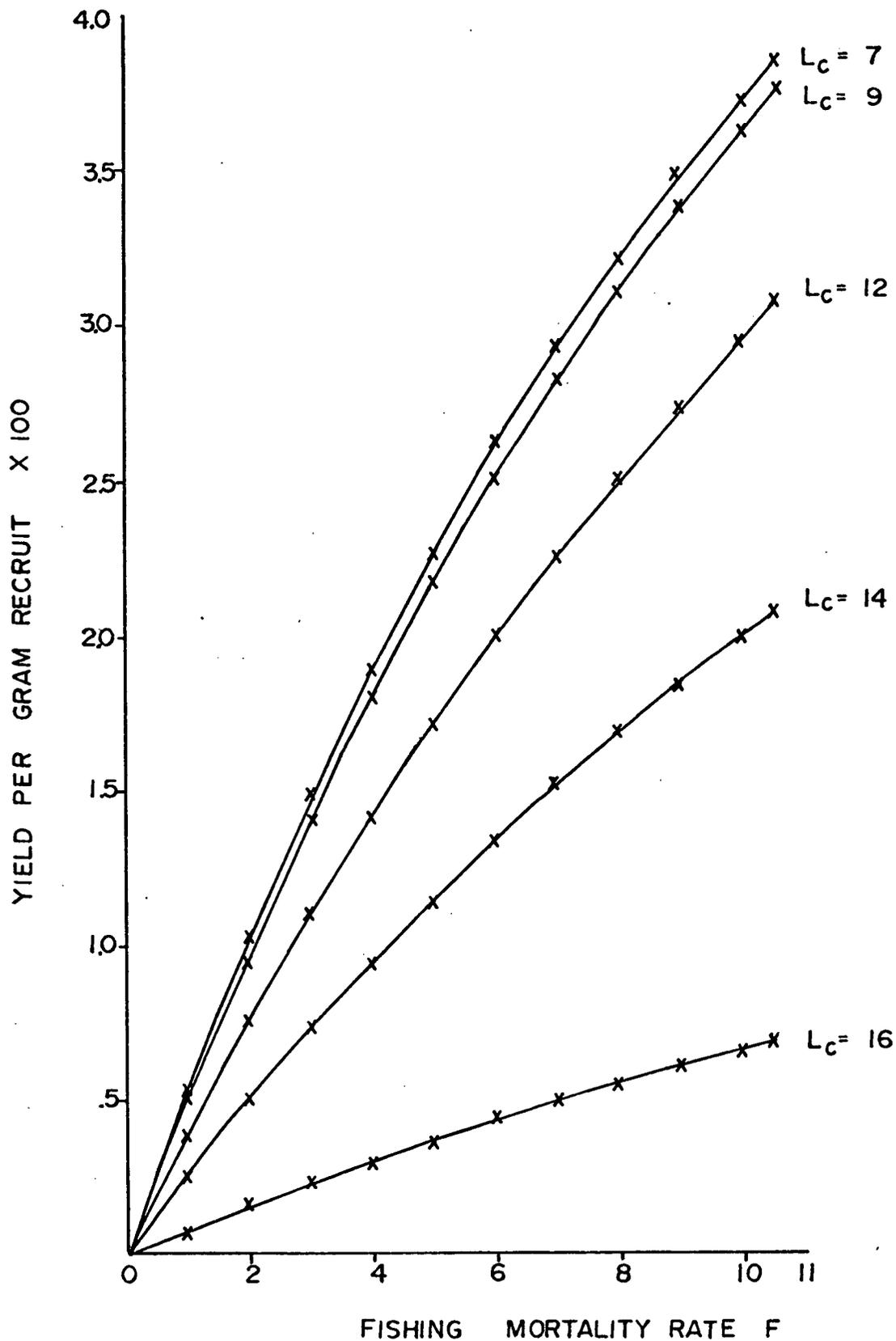
Figure 12 - Yield per 100 gm. recruit plotted against length of capture
at different fishing rates (F) (for stunted *Tilapia nilotica*
Lake Albert, Uganda). M = 3.37, K = 2.77, L∞ = 17.0 cm. and
$L_c$ is the length of capture.
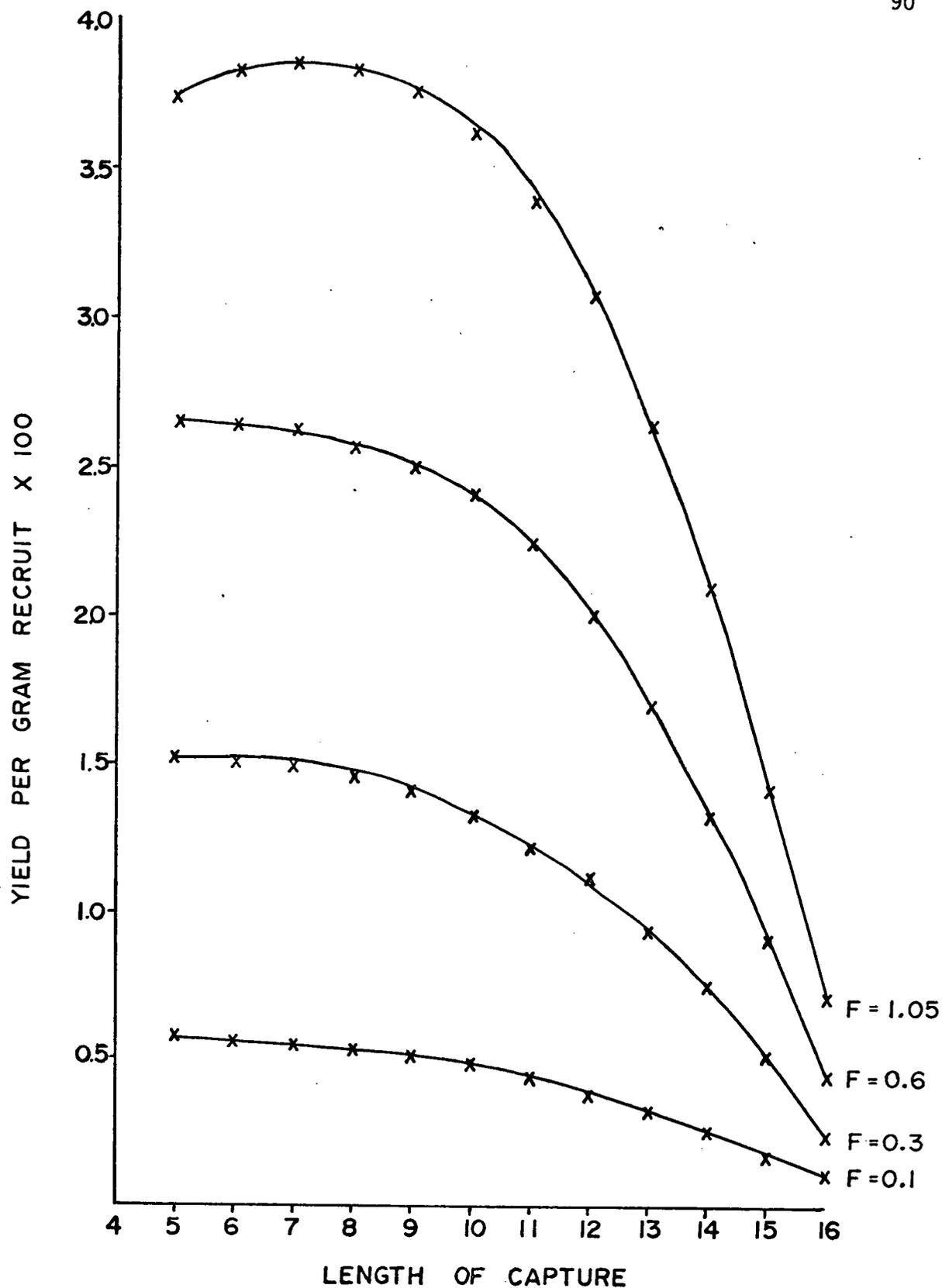
Figure 13 - Yield per 100 gm. recruit plotted against length of capture
at different fishing rates (F) (for *Tilapia nilotica* in Lake
Albert, Uganda). M = 3.37, K = 2.77 and L∞ = 17 cm.

## GENERAL DISCUSSION

The alegebraic relationships, analytical methods and the models
here developed should provide short-cut methods that require a minimum
of factual data to manage a fishery.

Some generalizations can be made about the growth processes.
The growth rate K and the weight length exponent b determine the age
and size of a fish at the inflexion point on the growth curve. The age
of a fish at inflexion is inversely related to K and directly related
to the natural logarithm of b. The significance of this to fisheries
management is evident when setting  the mesh size of gillnets and codend
of trawl. Since maximum biomass occurs at the inflexion point, the mesh
size should be chosen so as to catch fish at the inflexion.

For *Tilapia* species, it is shown that the age and size at the
inflexion correspond to the age and size of maturity. Since it is always
easier to determine the size at maturity, this could serve as a measure
of the size of maximum biomass. The ratios lm/L∞ and Wm/W∞ are useful
constraints in safeguarding against exploitation of immature fish.
With the parameters K and b and the ratios lm/L∞ and Wm/W∞ one will
have some rough appreciation of relative rate of exploitation of a fish
population.

A fish species inhabiting different localities may have different
weight length exponents as exemplified by *Tilapia nilotica* in East Africa.

The differences in b for a fish species are due to the differences in metabolic processes of the fish in the various localities. Assuming the exponent of catabolism is unity as proposed by von Bertalanffy (1957), fish with b = 3.0 have m = 0.67. Fish with b > 3.0, have m > 0.67 while fish species with b < 3.0, have m < 0.67. These relationships may partly explain why some fish species may not obey the von Bertalanffy growth equation.

In order to appreciate some of the causes of population fluctuations and the decline of catches and catch per effort, one should make estimates of natural and total mortality rates. The quickest and easiest way of describing mortality rates is with a negative exponential. One should determine the mean age or mean length in the exploited population by analysing catch samples. If the age or length of first capture is known, total mortality rates can be estimated with the equations given. These estimators are based on the assumption that the age distribution of exploited populations conforms to the expectations of the probability density function or the discrete probability function of the negative exponential. It is also possible to use the extreme age or length to estimate total mortality and this has previously been suggested by Holt (1965). But it has been noted that the extreme value estimator is less reliable than the negative exponential estimator. The total mortality rate estimated with the extreme value has a larger variance. Therefore extensive sampling is required to show that the extreme age and length in a population have the properties of the extreme value function.

Some of the difficulties met in estimating growth and mortality rates are due to population fluctuations and seasonal changes in distribution

of fish species. Analyses of catch statistics by multiple regression
methods provide useful information on abundance and distribution of
fish. A number of variables affect catches and one should know which
variables are of greatest importance. Such information may be given by
the step-wise multiple regression analysis of trawl catches. Some of this
information is useful in advising fishermen where and when to fish.
If this analysis is carried out at spaced periods, one can easily assess
the relative degree of exploitation. For example, the analysis of recent
catches of *Tilapia* in Lake Victoria shows that depth of the bottom,
mesh size of codend and time of day of fishing are the most important
variables determining catches.

Assessing the state of the fish stocks poses special complexities.
It is very unlikely that it will be possible in practice to quickly solve
the problems of taxonomy and to collect all the limnological, biological
and statistical data ideally desirable for a detailed evaluation of
tropical fish stocks and yields. Instead we must use simple mathematical
models that require a minimum of parameters for making predictions.
The parameters that are vital to yield prediction are: $K$, $b$, $L\infty$, $M$ and
$Z$. These parameters can be used to determine yield and construct yield
curves as has been shown for *Tilapia* species. Without age, the same
parameters can be used to determine yields for fish with allometric
growth by means of the incomplete Beta function. For fish species with
enough estimated parameters, the yield model of Beverton and Holt (1957)
may be used to determine yields as shown for *Tilapia nilotica* and *Tilapia*
*esculenta*. It is important to note that a model with a few very relevant

parameters, has almost the same predictive power as a model requiring
more parameters.

Realizing that the resources for sampling and analysis are often
limited, simple yield models should be used to speed up assessment.

# RECOMMENDATIONS FOR FUTURE

## MANAGEMENT

In order to assess quickly the fish stocks in tropical fresh water, research should follow the lines of attack given below:

(a)  Representative samples should be collected from the population to estimate the weight length exponent b.  In large lakes like Victoria, stratified sampling will give more reliable estimates of b than unrestricted random sampling.

(b)  Large random samples should be taken in order to determine the largest size to which certain fish species grow.  The mean maximum length in the different samples could serve as a rough measure of $L\infty$.

(c)  At present the easiest way of estimating K for tropical fish is to carry out tagging experiments and make Walford graphs.  The present methods of estimating K needs refinement to avoid the shortcomings introduced by age.  The possibility of estimating K by means of maximum likelihood should be investigated.

(d)  The length of first capture should be set using information on maturity and size of maximum biomass.

(e)  The catch samples at various fish landings should be sampled to give estimates of mean length in the catch.  By means of the equations given the ratio Z/K and total mortality Z, can easily be estimated.

(f)  It is realized that several variables affect the catch.  The abundance and distribution of fish species should be investigated by

multiple regression methods. If this analysis is repeated at certain intervals one can appreciate the relative degree of exploitation. Information on fish distribution is necessary for efficient fishing.

(g) After determining the parameters K, b, L∞, M and Z some yield predictions should be made and yield curves constructed. No calculations are needed where the length yield model of Beverton and Holt is used. The yield values can be read from the tables given by Beverton and Holt (1966).

If the incomplete Beta function is used very few simple calculations are needed and the yield values can be read from the tables of the incomplete Beta function given by Wilimovsky and Wicklund (1963).

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97

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# APPENDIX 1

## DERIVATION OF PROBABILITY DENSITY
## FUNCTION FOR A NEGATIVE EXPONENTIAL

For an unexploited fish population the number of fish at age
t is given by

$$N_t = N_0 e^{-M(t - t_0)} \tag{9.1}$$

The proportion of number of fish at age t to the initial numbers at age
$t_0$ is

$$\frac{N_t}{N_0} = e^{-M(t - t_0)} \tag{9.2}$$

Since the area under a negative exponential curve is unity, summing up
the proportions described by equation (9.2) should yield 1.

The probability density function is defined as

$$F(X = x) = \int_a^x f(x) \, dx = 1$$

Integrating the right hand side of (9.2) between t = o and t = ∞ gives

$$\int_0^\infty e^{-M(t - t_0)} \, dt = \frac{1}{M} \tag{9.3}$$

The right hand side of (9.2) is normalized to a probability density
function by dividing by its integral.

101

Therefore

$$\frac{e^{-M(t - t_0)}}{\int_0^\infty e^{-M(t - t_0)} \, dt} = M \, e^{-M(t - t_0)} \tag{9.4}$$

The probability of age t is given by

$$P(T = t) = M \, e^{-M(t - t_0)} \text{ for } t > t_0 \tag{9.5}$$

and

$$F(T) = \int_0^\infty M \, e^{-M(t - t_0)} \, dt = 1$$

where F(T) is the integral of the derivative below:

$$M \, e^{-M(t - t_0)}$$

For a fished population we can think of the proportions of fish beyond age $t_c$ as adding to unity. The numbers at each age t can be expressed as a proportion of the recruits, so that

$$\frac{N_t}{R} = e^{-Z(t - t_c)} \tag{9.6}$$

The right hand side of equation (9.6) is normalized to a probability density function by dividing by its integral,

$$\frac{e^{-Z(t - t_c)}}{\int_0^\infty e^{-Z(t - t_c)} \, dt} = Z \, e^{-Z(t - t_c)} \tag{9.7}$$

and the probability of obtaining age t in a sample catch is

$$P(t) = Z \, e^{-Z(t - t_c)} \text{ for } t \geq t_c \tag{9.8}$$

Equation (9.8) integrated gives 1 and hence it is a probability density function.

$$F(T) = \int_0^\infty Z\, e^{-Z(t - t_c)}\, dt = 1$$

## DERIVATION OF DISCRETE PROBABILITY FUNCTION

## FOR A NEGATIVE EXPONENTIAL

In an exploited fish population the number of fish at age t is given by

$$N_t = N_0 \, e^{-Z(t - t_c)} \tag{10.1}$$

and the number of fish age t + 1 is given by

$$N_t + 1 = N_0 \, e^{-Z(t + 1 - t_c)} \tag{10.2}$$

The proportion of $N_t + 1$ over $N_t$ is

$$\frac{N_t + 1}{N_t} = e^{-Z(t + 1 - t_c - (t - t_c))} \tag{10.3}$$

$$= e^{-Z}$$

With a discrete time model with an infinite number of time periods, the total exploited population is given by

$$N = N_0 + N_0 \, e^{-Z} + N_0 \, e^{-2Z} + \ldots + N_0 \, e^{-Z\infty} \tag{10.4}$$

where N is the total number of fish from all exploited age groups $N_0$, here refers to the number of fish recruited at age $t_c$. Because the area under the exponential curve between $t_c$ and $\infty$ is unity, we can refer to $t_c$ as zero time.

Then $\qquad N = N_0 (1 + e^{-Z} + e^{-2Z} + \ldots + e^{-Z\infty})$ $\qquad$ (10.5)

for $\qquad$ $(t = 0, 1, 2, \ldots, \infty)$

$\qquad$ Under the assumption of constant recruitment $N_0$ is taken as unity and equation (10.5) reduces to

$$N = 1 + e^{-Z} + e^{-2Z} + \ldots + e^{-Z\infty} \qquad (10.6)$$

Note that equation (10.6) is an infinite series. The sum of this series is given by

$$N = \frac{1 (1 - e^{-Z\infty})}{1 - e^{-Z}} \qquad (10.7)$$

when $t = \infty$, the numerator of the right hand expression of (10.7) becomes unity. Then N is estimated by

$$N = \frac{1}{1 - e^{-Z}} \qquad (10.8)$$

But for finite age groups N is given by

$$N = \frac{1 - e^{-Zt}}{1 - e^{-Z}} \qquad (10.9)$$

The expressions in (10.9) can be evaluated for a given t and Z. Note that equation (10.9) can be used to estimate the adult exploited population provided we know the recruits or if we can estimate the recruits. The exploited population is given by

$$N = R \frac{(1 - e^{-Zt})}{(1 - e^{-Z})} \qquad (10.10)$$

where R are the recruits and t the oldest age in a population.

From the derivation of the geometric series in (10.5) and (10.6), the probability of any age t is given by

$$e^{-Zt}$$

By the definition of a discrete probability distribution

$$\sum_0^\infty f(x_i) = 1$$

where $px_i = P(X = x_i) = f(x_i)$

Note that $f(x_i)$ above represents $e^{-Zt}$ but

$$\sum_0^\infty e^{-Zt} \neq 1$$

The term $e^{-Zt}$ can be normalized to a discrete probability function by dividing by

$$\sum_0^\infty e^{-Zt}$$

Therefore the probability of age t in the case of discrete recruitment is

$$P(T = t) = \frac{e^{-Zt}}{\sum_0^\infty e^{-Zt}} \tag{10.11}$$

The denominator of the right hand side of (10.11) is an infinite series and for $e^{-Z} < 1$, the expression is equal to

$$\sum_{0}^{\infty} e^{-Zt} = \frac{1}{1 - e^{-Z}}$$

Therefore for a discrete time model the probability of age t is

$$P(t) = (1 - e^{-Z}) e^{-Zt} \text{ for } t > t_c \tag{10.12}$$

The mean age U of the exploited age groups is given by the equation below (Burington 1958).

$$U = \sum_{0}^{\infty} t \cdot f(x_i)$$

Note that          $f(x_i) = e^{-Zt} (1 - e^{-Z})$

Therefore          $U = \sum_{0}^{\infty} t \cdot e^{-Zt} \cdot (1 - e^{-Z})$ $\tag{10.13}$

U can be estimated by mean age $\overline{t}$ of a sample.

$$\overline{t} = \sum_{0}^{\infty} t \cdot e^{-Zt} \cdot (1 - e^{-Z}) \tag{10.14}$$

Evaluate expression

$$\sum_{0}^{\infty} t \cdot e^{-Zt} (1 - e^{-Z})$$

factoring

$$1 - e^{-Z} \cdot \sum_{0}^{\infty} t \, e^{-Zt}$$

This summation above gives the infinite series:

$$S = \sum_{0}^{\infty} t \, e^{-Zt}$$

Let

$$S = 0 + e^{-Z} + 2 \, e^{-2Z} + 3 \, e^{-3Z} + \ldots + \infty \, e^{-Z\infty}$$

$$S \cdot e^{-Z} = + e^{-2Z} + 2 \, e^{-3Z} + \ldots + (\infty - 1) e^{-Z\infty}$$

Subtracting $S \, e^{-Z}$ from S

$$S - S \, e^{-Z} = 0 + e^{-Z} + e^{-2Z} + e^{-3Z} + \ldots + e^{-Z\infty}$$

The above is a geometric progression which can be written as

$$S (1 - e^{-Z}) = e^{-Z} \frac{(1 - e^{-Z\infty})}{1 - e^{-Z}}$$

$$S (1 - e^{-Z}) = e^{-Z} \cdot \frac{1}{1 - e^{-Z}}$$

Therefore the summation gives

$$S = \frac{e^{-Z}}{(1 - e^{-Z}) (1 - e^{-Z})}$$

$$S = \frac{e^{-Z}}{(1 - e^{-Z})^2}$$

The mean age $\bar{t}$ is therefore given by

$$\bar{t} = \frac{(1 - e^{-Z}) \, e^{-Z}}{(1 - e^{-Z})^2}$$

$$\bar{t} = \frac{e^{-Z}}{1 - e^{-Z}} \tag{10.15}$$