Chapitre 17

POPULATION STRUCTURE AND DYNAMICS

STRUCTURE ET DYNAMIQUE DES POPULATIONS

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1 - INTRODUCTION

Recent trends in the study of fish population dynamics have been toward a detailed analysis of variables affecting yield and the construction of theoretical mathematical models for the prediction of equilibrium yields. However, attempts to manage fishery resources in tropical Africa reveal that classical fishery models requiring explicit knowledge of age are not easily applicable. The concept of steady state or equilibrium yield is being viewed more and more as a simplification of the effect of fishing on exploited populations. It is still difficult to account for rapid changes in species composition in multispecies fisheries. Besides, the incorporation of socio-economic variables in the analysis of fishing trends introduces complexities that require more and more basic data. In the circumstances of rapid development of African fisheries, it may be difficult to meet the data required for realistic population assessment models.
It is therefore desirable to consider some alternative approaches.

In this paper, consideration is given to the following aspects of population dynamics :

- historic trends in the study of population dynamics,
- ecological attributes of tropical African fish comnunities related to 'r' and 'K' selection,
- ecological succession, diversity, stability and productivity concepts, and
- simplification in the study of fish population dynamics.

Emphasis is put on certain ecological concepts which are developing rapidly and which have been stressed differently by Margalef (1968), Odum (1969), Regier and Henderson (1972), Regier (1973), Lowe-McConnell (1975, 1977) and Pauly (1979, 1980).

2 - HISTORICAL TRENDS IN THE STUDY OF POPULATION DYNAMICS

Conventional generalized models to describe the dynamics of populations were mainly based on population parameters, the degree of structuring and the length of food-chains. The mathematical model given by Baranov (1918) had appropriate size structuring of the population but it was deficient in predator : prey interaction, presuming that food supply was in proportion to an animal's feeding requirements. Hence, this model could not estimate the absolute biomass of a population. Later, Lotka & Volterra (1928) introduced the concept of limited food supply, thereby proposing for the first time the notion of an asymptotic maximum biomass, but these models were still deficient in structural details as perceived by Baranov (1918).

Von Bertalanffy (1934, 1938) regarded an organism as a reacting chemical system by asserting that the processes of anabolism and catabolism control the weight of an organism. Thus, for an individual fish von Bertalanffy expressed the length (l_t) at age t as function of asymptotic length (L_x) and (K) the rate at which an individual approaches its asymptotic length.

Since the early 1930s, it has been realized that the biomass of a fish stock is affected by natural mortality, fishing mortality, recruitment and growth. It was consideration of these factors that led Russell (1931) to formulate a simple yield equation, *viz.*

$$S = R + G - M - F$$

where S = population biomass, R = recruitment, G = growth, M = losses due to natural mortality and F = losses due to fishing mortality.

On the basis of Russell's model, the maximum sustainable yield should be obtained if exploitation (fishing) reduces a fish stock to a level where [R + G - M] is largest, i.e., where the natural rate of increase is maximum.

Mathematical modelling of the dynamics of fish populations advanced significantly during the 1940s. Ricker (1940, 1944) developed models with more structural details and population biomass changes by considering in more detail the concepts of production, growth and recruitment.

A much used surplus production model was developed by Schaefer (1954), and a few years later the dynamic pool model was formulated by Beverton & Holt (1957). Schaefer's model has the following major shortcoming : the natural rate of increase of a population is not a mere function of stock size at any time; it is also affected by factors controlling the state of equilibrium. In these circumstances, it is often very difficult to fit statistically the relationship between catch per unit effort (cpue) and effort. On the other hand, the Beverton & Holt (1957) yield per recruit model is more realistic, considering the biological principles evoked, although attempts to determine stock size and recruitment rates are difficult and in general still statistically unsatisfactory. Besides, there is a growing awareness that isometric growth for all fish species has no biological basis (e.g., Paulik & Gales, 1964). Nevertheless, the simplified Beverton & Holt (1957) model is quite applicable in the study of fish population dynamics in tropical Africa because of simple methods given by several authors (e.g., Gulland, 1955, 1969; Jones, 1957; Ricker, 1958; Garrod, 1963; Wilmovsky & Wicklund, 1963; Beverton & Holt, 1964, 1966).

3 - ECOLOCICAL ATTRIBUTES RELATING TO 'r' and 'K' SELECTION

The tropical African fisheries are characterized by multiple species populations of which most component species are small and mostly occur in relatively shallow waters. A second important feature is that stocks often comprise assemblages of species with common evolutionaly histories and dependences so that removal of certain species by fishing interfers with the original food web of the system (Odum, 1969). Lastly, a third important feature of tropical fish communities (at least in lacustrine and riverine systems) is the predominance of specialist taxa adapted to certain environmental conditions. These important aspects of tropical fisheries have been discussed differently by Pianka (1970), Garrod (1973), Ricklefs (1973), Lowe-McConnel (1975, 1977) and Welcomme (1979).

MacArthur & Wilson (1967) and Pianka (1970) recognized two types of natural selection : (a) 'r'- selection, and (b) 'K'- selection. The former refers to selection for maximal intrinsic rate of natural increase whereas the latter denotes qualitative selection of organisms for increased efficiency in the utilization of food resources. But especially with in aquatic ecosystem no organism is completely 'K'- selected or 'r'- selected. Therefore, all organisms are differently moulded by both types of selection. Among the more pressing questions we still need to assess are those about mechanisms or trigger effects regulating allocation of energy to somatic activities and reproduction.

The ecological attributes of 'r' and 'K' selected fish communities in Africa are given in Table 1. It is shown that feeding adaptations and the reproduction mode influence greatly the dynamics of populations in the different habitats. Upwelling areas, estuaries, continental shelf areas off large river deltas (e.g., the Nigerian sector between Benin River and Cross River estuaries), marshes, flood plains and swamps are characterized by high, catastrophic, indiscriminate density-independent natural mortality. But populations in the stable littoral and benthic areas of the East African Great Lakes (e.g., Malawi, Tanganyika, and Victoria) are subject to a lower natural mortality which is fairly density-dependent and mostly due to predation.

Table 1 : Distinctive featuree of 'r'- and 'K'- selected fish communities of tropical Africa (based on concepts given by Lowe-McConnell, 1977).

Ecological attributes	Type of selection	
	'r'- selection	'K'- selection
Habitat	Upwelling areas, estuaries, continental shelves off large deltas, flood plains, marshes, swamps, etc.	Coral reefs, rock reefs, littoral and benthic areas of the great lakes of East Africa
Species group	Mostly pelagic marine fishes (sardines, anchovy, Carangidae, etc.), but also *Engrauli-cypris, Stolothrissa, Limnothrissa*, etc.	Mostly demersal fishes (eels, Sciaenidae, cat-fishes, Cichlidae, Serranidae, *Synodontis,* etc.
Diversity index	Less diverse with dominant species. Example : *Oreochromis alcalicus grahami* in Lake Magadi	Very diverse and species with more or less equitable distribution
Environmental stability	Fluctuates seasonally, with variable influx of nutrients	Negligible fluctuations in environment
Survivorship curve of fish species	Sharply falling and concave	Distinctly rectangular
von Bertalanffy growth coefficient	Relatively high	Relatively low
Predation effects	Predation results in homogeneity which may restrict speciation, e.g., Lake Baringo	Predation results in heterogeneity which may promote speciation, e.g., Lakes Tanganyika and Malawi
Protection cover	Schooling behaviour	Formation and defence of territories
Movements by species	Schooling prey species with diurnal migrations	Schooling by day, dispersing and feeding by night
Energy flow per unit biomass	high : (a) with few trophic levels, energy flow per unit biomass is high; (b) in fluctuating and less efficiently organized systems, the cost of maintenance is high	low : (a) with many trophic levels, energy flow per unit biomass is low; (b) in stable efficiently organized systems, the cost of maintenance is low
Natural mortality	Usually high, sometimes catatrosphic, indiscri-minate and more or less density-independant with occasional mass mortalities	Relatively low and mostly due to predation also fairly density-dependant
Longevity	Prey fish with short life-span	Longer life-span

Table 1 : continued

Ecological attributes	Type of selection	
	'r'- selection	'K'- selection
Reproduction mode	Numerous pelagic eggs, some prolific substrate-spawners (e.g., the 'tilapias'), no parental care, protandry (change of sex from male to female) in Polynemidae	Spawning displays, pairing and highly developed parental care, protogyny (change from female to male), e.g., in Serranidae, Labridae and 'swamp-eels'
Competitive ability of individual	Competitive ability low; competition low and variable, absence of territorial behaviour	Competitive ability high, competition high and variable; presence of territorial behaviour
Status of trophic levels	Few trophic levels	More trophic levels
Feeding adaptation	Specialists at low trophic levels	Adaptative feeding types but with some specialists which may be stenophagous
Other favoured factors	• Rapid turnover, • High rate of natural increase 'r'- max, • Early reproduction, and • Small body size	• Slow turnover, • Low resource threshold, • Delayed reproduction, and • Large body size

In the case of 'r'- selected fish communities, reproduction has the following distinctive features : (a) numerous pelagic eggs, (b) some prolific substrate-spawners, c) lack of parental care, and (d) protandry; whereas the 'K'- selected fish communities have the converse distinctive features. It is useful to point out that no species is completely 'r' selected or 'K' selected, but in natural conditions all species reach some compromise between the two extremes. Pianka (1970) refers to an 'r-K' continuum and a position of an organism along it. On one extreme is the 'r' endpoint extreme for which the optimal strategy is abundance through high reproductive rates, whereas the 'K' endpoint represents the qualitative extreme for which the optimal strategy is efficient utilization of the resources and individual persistance.

In the case of 'K' selected fish communities in the littoral and benthic areas of the Great Lakes of Africa, density-dependent effects are dominant. These environments have a diversified assemblage of organisms. e.g., Lake Victoria, with more than 170 cichlid species and more than 38 non-cichlid species; and Lake Malawi with more than 200 cichlid species and more than 42 non-cichlid species (Lowe McConnell, 1975). It is presumed that fish species in Lakes Tanganyika, Malawi and Victoria were initially dominated by 'r' selection, but during the course of evolution each vacuum was filled through selective speciation and species invasions, resulting in a shift from 'r'- to 'K'- selection in the species assemblages.

Finally, Adams (1980) stresses that the genetic and ecological properties of a species are closely linked since natural selection moulds the morphological and reproductive characteristics, as well as the population size and genetic frequencies of species in various environments. The criterion for a species' success in an ecosystem is the number of surviving offspring that a parent produces (Crow & Kimura, 1970). Hence, there must be a compromise between production of larger numbers of offspring ('r'- selection) and production of offspring with the highest fitness or persistence ('K'- selection).

4 - ECOLOGICAL SUCCESSION, DIVERSITY, STABILITY AND PRODUCTIVITY

Many ecologists have presumed that succession is a simple straightforward concept, whereas succession actually involves a complex of interacting processes. Hence, succession is one of the key concepts in the study of the dynamics of tropical fish populations.

Odum (1969) gives the following three useful characteristics of ecological succession : (a) it is an orderly process of community development, fairly directional and predictable; (b) it is community-controlled, although the physical environment determines the pattern, rate of change and limits of its influence; and (c) the «strategy of succession as a short-term process» is basically the same as the strategy of long-term development.

When viewed in this way succession is explanatory and predictive. But any ecosystem is a complex evolutionarily moulded structure. Consequently, the transition from one state to another state is not easy to determine precisely. The concept of ecological succession facilitates the study of changes in the dynamics of tropical multispecies fish populations. The trends expected during ecological succession are shown in Table 2.

In the course of ecological succession, an ecosystem passes through different maturity stages. The final stage of succession is referred to as the 'climax' (= condition of maximal maturity). But it should be noted that succession is not necessarily uni-directional, for the process can be reversed at any stage by forces external to the system. Hence, there are discontinuous steps in succession. This partially explains why some old ecosystems (e.g., some tropical lakes) exhibit characteristics of less mature stages.

4.1 - Confusion about Succession

The term 'succession' means different processes to different people. First of all, succession relates to a gradual filling up of a lake, producing a marsh and eventually dry land ('geological succession'). Hence, nutrient loading, or eutrophication, is a typical natural aspect of 'geological succession'. Secondly, for lakes with fixed morphometry (e.g., Lakes Malawi, Tanganyika, etc.), one observes what Regier (1973) termed 'nutrient oligotrophication' (i.e., decline in nutrient

supply) which relates to ecological succession. Therefore, oligotrophication is a process that eliminates or heals natural or cultural eutrophication. Thirdly, 'succession' relates to a sequence of responses by the fish community to an intensifying natural or cultural stress. It is for this reason that Regier (1973) defined ecological succession as community response to a relaxation of stress. The cultural stress experienced by tropical fish populations is usually in the form of fishing pressure and pollution.

The ecological characteristics of fish communities in stressed and relatively unstressed ecosystems are shown in Table 2. Generally, equilibrium catches of fish are higher in eutrophic lakes (e.g., Lake George with 156 kg ha^{-1}) than in oligotrophic lakes (e.g., Lake Malawi with 9 kg ha^{-1}). There are differences in biotic and abiotic variables, between 'less mature' and 'more mature' ecosystems. Hence, different fish populations are under varying stress and often very different. Stress may be caused by one factor or a group of factors and this stress often results in a change of the ecosystem characteristics. In fresh water ecosystems, natural stress may be caused by temperature differences, high or low salinity, high variability or constancy in other abiotic factors. In addition to the above, fish populations might be stressed by exploitation, excessive nutrient supply and pollution. It is a combination of these factors which accounts for the ecological characteristics shown in Table 2.

4.2 - Diversity, Stability and Productivity

There are two useful types of diversity index : (a) one type designates the presence or absence of given species (species richness), and (b) the other type refers to equitability or shape of the frequency distribution of species. Some useful information concerning diversity and statistical expressions for measuring diversity are given by Margalef (1968) and Odum (1969).

Diversity deals mostly with the expression of the dynamic properties of a system. It illustrates how groups of organisms fall into sub-systems comprising a community. Hence, it is an important measure of the occurring interactions. The addition of a species through invasion, colonization and stocking, or extermination of some species either by excessive fishing or environmental pollution, alters diversity. It is important to differentiate measures of diversity from those of stability. Diversity describes species richness and equitability whereas stability refers to the successive states a system passes through. For example in Lake Malawi a population of individuals of *Haplochromis heterotaenia* is a unit, this species forms a team in the competition game, and the whole *Haplochromis* complex of more than 120 species is part of the interacting cichlid community; then it can be perceived that diversity and stability have demographic and taxonomic meaning. It appears that conditions which stimulate high diversity in the Great Lakes of East Africa and in tropical coral and rock reef areas also permit high stability or constancy in taxonomic-assemblages.

There is a hierarchial structure of these ecosystems in space. Some species may comprise several different races and sub-species. Then a small group of species comprise larger fish communities which in turn form larger and larger species complexes. Therefore, the diversity index is a useful tool in examining changes in composition of fish communities, in making comparative fish population studies of different ecosystems and in assessing changes in population structure of exploited fish species. One apparent effect of exploitation is that most of the biomass of exploited fish communities tend to comprise small short-lived species. Regier & Loftus (1972) indicate that fish communities dominated by short-lived species fluctuate considerably in abundance. This would suggest that in the past, unfished fish communities occurring in relatively constant environments tended to be more stable, for the constituent fish species most likely did not fluctuate greatly in abundance in comparison to exploited communities. These fish communities were dominated by large old individuals. When fishing was initiated, fish of old age and greater length were captured and hence gradually displaced by small short-lived individuals.

Adams (1980) considers the response of 'r' and 'K' selected species to exploitation. Fisheries operating in areas where 'r' selection is predominant (i.e., fisheries based on 'r' selected species) will be generally more productive. The 'r' selected species mostly occur in upwelling areas, estuaries, flood plaing, shallow eutrophic lakes, marshes and swamps (Tables 1 and 2). These species can be fished at young ages, small sizes and at high levels of fishing mortality. Species

Table 2 : Ecological succession : characteristics of less mature ecosystems (based on concepts given by Odum, 1969)

Ecosystem Variables	Ecological Characteristics	
	'Less mature' stages	'More mature' stages
Fish production	Generally high : e.g., Lake Kioga (= Kyoga) 389 kg ha^{-1} : Lake George, 156 kg ha^{-1}; Lake Mweru-wu-Ntipa, 100 kg ha^{-1}	Generally low : e.g., Lake Tanganyika, 22 kg ha^{-1}; Lake Victoria, 15 kg ha^{-1}; Lake Malawi, 9 kg ha^{-1}
Foof chains/trophic levels	Few and simple : e.g., in Lake Baringo (Kenya) with six fish species	Many and complexe : e.g., in Lake Malawi with about 242 species and Lake Tanganyika with about 190 species
Morpho-edaphic index	Relatively high : e.g., Lake Upemba MEI = 667; Kitangiri, MEI = 157; Lake George, MEI = 72	Relatively low : e.g., Lake Kivu, MEI = 5.1; Lake Victoria, MEI = 2.4; Lake Tanganyika, MEI = 0.8; Lake Malawi, MEI = 0.5
'r' and 'K'-selection	'r'-selection for rapid growth of fish species, e.g., in Kafue Flats and other flood plains	'K'-selection for a lower growth rate in the deeper East African great lakes
Reproductive strategy	Greater quantity of fry to ensure that some can survive density-independent mortality by chance	High quality of fry to ensure competition ability when resources are limited
Exchange of nutrients between species and environments	High : e.g., in the flood plains of Africa where the 'tilapias' and other fishes feed and grow quickly soon after a flood	Low : e.g., in Lakes Tanganyika, Malawi, etc.
Stability of systems	Seasonally fluctuating, e.g., Niger inland delta, Lakes Kitangiri, Chisi, etc.	Relatively stable : e.g., Lakes Tanganyika, Kivu, Malawi and Victoria

which are more 'r' selected are quite resilient to exploitation but their resilience is affected by the physical forces in the harsh environments where they occur. Fish production in areas with more 'r' selected spacies is of a bloom and recession nature, e.g., in African flood plains, Lake Kitangiri (Tanzania), etc. Exploited fish populations with more 'K' selected species produce a high maximum yield per recruit. Rational exploitation of these species requires a later age at first capture (t) and large size at first capture (1). But the 'K' selected species are more susceptible to overfishing due to their lower relative productivity and numbers and these species have rather stable interspecific relationships. It is also more difficult to understand their population dynamics because of the relationship between competition and harvesting as considered by Larkin (1963). Additionally, there is the consideration of stability and the intrinsic growth rates of prey and predator populations as explained by Tanner (1975).

5 - SIMPLIFICATION IN THE STUDY OF POPULATION DYNAMICS

It is shown that the tropical multiple species fisheries are very complex. Nevertheless, some simplifications can be made in the study of the dynamics of tropical fish populations if we consider the functional relationships among population variables that influence yield. This paper also focuses on the most relevant population parameters as well as simple analytical and theoretical models that can be used to make quick and reliable assessment of the dynamics of tropical fish populations. In the view of ecologists, population dynamics refers to changes in populations of organisms under natural conditions. These changes consist of recruitment, growth, mortality as well as spatial and temporal migrations of organisms. One assumes that the biological processes involved occur only under specific conditions and in a certain sequences. There also must be limits to the rates of these processes. But biological processes change with respect to time and to spatial frame of reference. In these circumstances, the derivatives of rates of biological processes such as growth and mortality have particular significance.

5.1 - Growth Rate and Indices

In the circumstances of rapid development exhibited by some African freshwater and marine fisheries, it is rather difficult to meet data requirements of modern mathematical models for studying the dynamics of fish populations. It is therefore very desirable to examine instead the functional relationships of factors influencing biomass and yield.

The von Bertalanffy growth equations describe rates of change of Length or weight of individual organisms with time. *viz.* :

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

$$W_t = W_\infty(1-e^{-K(t-to)^b}) \quad (2)$$

where K = the growth coefficient, L_∞ = the asymptotic length, W_∞ = the asymptotic weight, l_t is the length at age t, t_0 is the age at which the length or weight of a fish is theoretically zero and b is the length-weight exponent.

Von Bertalanffy's growth equation is used here because it is mathematically simple and gives parameters (L, W, K and b) which can be used to compute yields. Note that Von Bertalanffy's growth parameter K is different from the selective speciation variable 'K' of ecosystems.

The processes of anabolism and catabolism control the weight of an organism. Hence, the rate of change of weight of an organism (dw/dt) can also be expressed in terms of exponents relating metabolism to weight, *viz.*

$$dw/dt = Hw^m - kw^n \quad (3)$$

where m is the exponent relating anabolism to weight, n is the exponent relating catabolism to weight, H is the coefficient of anabolism, k is the coefficient of catabolism and w is the weight.

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 should be either 0.66 for species obeying the surface rule of metabolism, or unity for cases where oxygen consumption is proportional to veight instead of surface area, and that for other fish species ranges between

0.66 to 1.0. Parker & Larkin (1959) and Ricker (1960) criticise 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 and effect of maturity. Von Bertalanffy argues that the rate of metabolism is proportional to the mth power of the weight where m is the exponent of metabolism. The rate of catabolism is proportional to weight itself, thus n = 1.

Ssentengo (1971) considered some simple algebraic relationships which could be used in the management of exploited stocks of tropical Africa. Rational exploitation of a fishery requires knowledge of the weight and age of a fish at the growth inflexion point where a fish has maximum change in weight dw/dt. In some fish species the maximum growth increment is attained before sexual maturity. Exploitation of such a fish population requires catching the fish only at a size or age beyond the inflexion point so that there will be sufficient individuals remaining to reproduce. The age at the inflexion (t_i) is given by

$$t_i = \frac{1}{K} \cdot \ln b + t_o \quad (4)$$

Equation (4) thus describes the necessary inter-relationship between the age at the point of inflexion, the growth rate (K) and the length-weight exponent (b).

The age t_o often has a theoretical negative-value and for many fishes so far studied to satisfies the inequality, $-1.0 \leqslant$ to $\leqslant 0$. However, age t_o should be slightly positive $(t_o > 0)$ to be realistically consistent and this implies that some fish species grow faster in later life stages than during early life stages of metamorphosis. A negative t_o implies underestimation of growth rates at early life stages or bad estimate of growth parameters in general.

For many fish species so far studied the length-weight exponent b lies within the limits 2.5-3.5. The length-weight exponent outside this range cannot apply over a wide range of length without causing profound changes in body form. When b > 3 the fish is increasing in weight at a greater rate than required to maintain constant body proportions, and *vice versa*. Many fish species with b > 3 would experience problems of bouyancy and hydrodynamic stability unless they possess a gas bladder or are capable of reducing their density by increased fat content (Webb, 1978). Although most fishes grow approximately isometrically during their final growth stanza, there are exceptions. For example Carlander (1969) reports three populations of *Coregonus artedi* with b ranging from 3.62 to 3.69 and five populations of the same species with b < 2.5. There may be a few other exceptional fish species with b outside the 2.5 - 3.0 range but we should ascertain that such values are not due to biased sampling.

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). In these circumstances, there should be a relationship between the exponent b of equation (2) and the exponent m of equation (3). When the exponent of catabolism n is less than 1 the length weight exponent b cannot be expressed explicitly in terms of m and n of equation (3). If we set the limit of b we can solve the transcendental expression relating b to m and n. Thus, if b satisfies the inequalities $2.5 \leqslant b \leqslant 3.5$, m ranges from 0.6 to 0.9 and n ranges from 0.8 to 1.0 (Ssentongo, 1971).

5.2 - Mortality Rates for Tropical Fishes

The theoretical foundation for the mathematical modelling of natural mortality was given by Baranov (1918) when he said that maximum age determines the coefficient of natural mortality. Beverton & Holt (1954, 1959), Taylor (1960), Beverton (1963) and several other fishery biologists have pointed out that life span is inversely related to the coefficient of natural mortality M. Hence, fishes with high M have a short life span and *vice versa*.

5.2.1 - Total mortality rate when recruitment is continuous. Sssentongo & Larkin (1973) give an estimator of total mortality coefficient Z, *vis.*

$$\hat{Z} = \frac{1}{t - t_c} \cdot \left(\frac{n}{n + 1} \right) \quad (5)$$

and the variance of Z is given by

$$\text{Var } (\hat{Z}) = \left(\frac{n}{n+1}\right)^2 \cdot \frac{1}{n(\bar{t} - t_c)^2} \quad (6)$$

where $\bar{t}$ is the mean age of the catch, t_c is the age of first capture and n is the size of the catch sample.

Expression (5) has been used by Ssentongo & Larkin (1973) to estimate total mortality of *Oreochromis esculentus* (= *Tilapia esculenta*) in Lake Victoria for various sample sizes. Any other method requiring explicit knowledge of age is applicable whenever the age structure of a fish population can be determined by using rings on skeletal structures and by analysis of length frequency distributions and tagging data.

5.2.2 - Total mortality rate for populations with discrete age groups. For a fished population with discrete age groups and with all fish above age first capture t_c, being equally likely to be caught, the probability density function is given by :

$$P(t) = (1 - e^{-Z})e^{-Zt} \text{ for } t > t_c \quad (7)$$

It can be shown that the unbiased estimator of the total mortality coefficient is :

$$\hat{Z} = \ln\left(\frac{\bar{t} + 1 - t_c}{\bar{t} - t_c} \cdot \frac{n}{n+1}\right) \quad (8)$$

when n is the sample size.
The unbiaised variance estimator is

$$\text{Var } (\hat{Z}) = \left(\frac{n}{n+1}\right)^2 \cdot \left(\frac{1}{n}\right) \cdot Z^2 \quad (9)$$

Expression (8) has been used by Ssentongo & Larkin (1973) to estimate total mortality (Z) of *Oreochromis esculentus* in Lake Victoria for various sample sizes. It should be noted that the unbiased variance estimated by equation (6) when recruitment is assumed continuous is less than the variance given by Expression (9) when recruitment is assumed discrete.

5.2.3 - Mean length and mortality rates. Since it is still difficult to age tropical fish species, the use of age in estimating total mortality may not easily apply to many tropical fish species. Instead of age, one can use length to estimate the total mortality (Z) if the parameter K is known. When K is unknown, the ratio Z/K can be estimated from length distribution data. It should be noted that the ratio Z/K is important in determining yields, for fish with allometric grouth, by means of the incomplete Beta function (Jones, 1957) Wilimovsky & Wicklund. 1963). Several expressions in wich age is not explicit variable have been formulated.

For a given gear, total mortality Z can be estimated from mean length $\bar{l}$ of fish beyond age t_c in a catch sample. Beverton & Holt (1956) and Gulland (1969) give the following formulation :

$$Z = \frac{K(L_\infty - \bar{l})}{\bar{l} - l_c} \quad (10)$$

where L_∞ and K are parameters of the von Bertalanffy growth equation (1). The mean length at first capture l_c is normally estimated from gear selection data.
When the growth rate K is not known, the ratio Z/K is given by

$$(\hat{Z}/K) = \frac{L_\infty - \bar{l}}{\bar{l} - l_c} \quad (11)$$

Equations (10) and (11) are easily applicable to exploited fish populations in tropical Africa for they do not require explicit knowledge of age. Equation (10) has been used by Le Guen (1971) to study the dynamics of *Pseudotolithus elongatus* off the Congo and by Durand (1978) to study the dynamics of *Alestes baremose* in Lake Chad.
Von Bertalanffy's growth equation (1) is fairly descriptive of growth in fish. This equation

can be rearranged to express time as a function of length, *viz.*

$$t = \frac{1}{K} \cdot \left[- \ln \left(1 - \frac{l_t}{L_\infty} \right) \right] + t_o \quad (12)$$

From equation (12) are derived quantities y and y_c defined, respectively as

$$y = -\ln (1 - l_t/L_\infty)$$
$$y_c = -\ln (1 - l_c/L_\infty)$$

where l_c is the length of first ch of first capture, l_t is the average length of an individual fish of age t in a sample catch (it is assumed l_t is fixed at age t).

It can be shown that the number N_t at age t and with length l_t is given by

$$N_t = R.e^{-Z/K}.(y - y_c)$$

from which an unbiased estimator of the ratio Z/K was derived by Ssentongo & Larkin (1973), *viz.*

$$(\hat{Z}/K) = \left(\frac{n}{n+1} \right) \cdot \left(\frac{1}{\bar{y} - y_c} \right) \quad (13)$$

where $\bar{y}$ is the mean of y values of what is in a catch sample of size n.

The unbiased estimator of the variance of Z/K is

$$\text{Var} (\hat{Z}/K) = \left(\frac{n}{n+1} \right)^2 \cdot \frac{1}{n(\bar{y} - y_c)^2} \quad (14)$$

If K is known we can estimate Z directly. In tropical Africa; Von Bertalanffy's K may be estimated from tagging data without explicit knowledge of age (Rinne, 1975).

$$\hat{Z} = K \cdot \left(\frac{n}{n+1} \right) \cdot \left(\frac{1}{\bar{y} - y_c} \right) \quad (15)$$

Expressions (14) and (15) have been used by Ssentongo (1971) and Ssentongo & Larkin (1973) to estimate total mortality of *Oreochromis n. niloticus* (= *Tilapia nilotica*) in the Uganda waters of Lake Albert and *O. esculentus* in Lake Victoria respectively.

Finally, Marten (1978) assumes linear growth until a maximum length L (as an approximation to von Bertalanffy curve) and gives useful estimates of total mortality Z and natural mortality M.

Total mortality Z is given by

$$\hat{Z} = \left(\frac{L_\infty}{\bar{L} - L_o} \right) \cdot \left[1 - e^{\left(\frac{L_\infty - L_o}{L_\infty} \right)} \right] \hat{Z} \quad (16)$$

where L_o is the minimum length used in a sample and $\bar{L}$ is the average length in a sample.

In Marten's model, it is assumed that a unit time (t = 1) is required by a fish to grow from hypothetical size 0 to maximum length (L_∞). Hence, the mortality rates F, M and Z are instantaneous rates with respect to this special time scale. Equation (16) does not have an explicit solution but it can be solved by iteration using L_∞ /($\bar{L}$ - L_o) as an initial guess of Z. Total mortality Z is within 1% of L_∞ /($\bar{L}$ — L_o) when Z (L_∞ — L_o)/L_∞ is > 5.

For estimating natural mortality rate M, we compare two or more populations at different times or locations with different fishing efforts and consequent average lengths and fit the regression

$$Z = M + qf \quad (17)$$

where q is the catchability coefficient and f is the fishing intensity.

The Z intercept gives an estimate of M. Equations (16) and (17) have been used by Marten (1978) to estimate Z and M, respectively, for *Bagrus docmac* in Lake Victoria. These expressions have been used to compare the fishing intensity of the heavily fished Nyanza Gulf (Kenyan waters) and the lightly fished Emin Pasha Gulf (Tanzanian waters) of Lake Victoria.

6 - SUMMARY

The tropical multispecies fish populations have strong interspecific relationships. In the circumstances of rapid development of some African fisheries, it may be difficult to meet the data requirements of realistic assessment models. Consideration is given to alternative approaches that account for the effects of ecological succession. diversity, stability and productivity. There is a compromise between production of a larger number of offspring ('r selection') and production of offspring with high competitive ability and persistance ('K' selection). Natural selection moulds population size and genetic frequencies of species in various habitats. Hence, derivatives of rates of growth and mortality are vital to the analysis of trends of fish populations.

RESUME

Le concept de production équilibrée est de plus en plus considéré comme une simplification abusive de l'effet de la pêche sur les populations exploitées. On est encore incapable d'expliquer les changements rapides de composition spécifique dans les pêcheries multispécifiques et en outre, l'incorporation des variables socio-économiques dans l'analyse des tendances des pêcheries introduit des complexités qui requièrent des données de base de plus en plus nombreuses. Etant donné le développement rapide de quelques pêcheries africaines, il peut être difficile de satisfaire aux exigences de modèles d'évaluation réalistes. Il faut donc considérer l'utilisation d'autres approches rendant compte des effets des successions écologiques, de la diversité, de la stabilité et de la productivité.

Une relation existant entre l'habitat, les stratégies écologiques et les paramètres des populations est appelée sélection 'r' ou 'K'. La sélection naturelle modèle les caractéristiques morphologiques et reproductrices d'une espèce de même que la taille de la population et les fréquences génétiques d'une espèce dans divers habitats.

La mesure du succès de la reproduction est le nombre de descendants survivants produits par un parent. Il existe un compromis entre la production d'un grand nombre de descendants (sélection 'r') et celle de descendants ayant une grande capacité de compétition et de résistance (sélection 'K'). L'examen des variables mesurant les caractéristiques globales de l'éco-système conduit à un certain nombre de règles générales approximatives sur la dynamique des populations de poisson.

Les espèces à sélection 'r' sont rencontrées surtout dans les habitats temporairement instables (plaines d'inondations, marécages, estuaires, zones d'upwelling, etc.) avec des alternances de développements rapides puis de récessions de la taille de la population. Ces espèces sont, en géneral, de petite taille, à vie courte, et sont caractérisées par un taux de croissance élevé, une mortalité naturelle et une fécondité élevées. Les espèces à sélection 'r' montrent une bonne résilience lors de l'exploitation et les pêcheries basées sur ces espèces sont généralement productives.

Inversement, les espèces à sélection 'K' occupent des environnements plus stables (par exemple les grands lacs africains) et la taille de leurs populations fluctue peu. Les poissons atteignent des tailles plus grandes et ont des durées de vie plus longues. Elles ont, en outre, de faibles taux de croissance, mortalité naturelle et fécondité. Les espèces à sélection 'K' sont moins résilientes vis-à-vis de l'exploitation bien qu'elles puissent produire un rendement par recrue maximum élevé.

Quelques simplifications sont possibles pour permettre l'étude des populations multispécifiques tropicales. Les changements qui se produisent dans une population d'organismes sont le recrutement, la croissance, la mortalité et les migrations saisonnières, spatiales et temporelles.

Les processus biologiques changent avcc le temps, dans un cadre spatial de référence. On a donc également considéré les paramètres dérivés des taux des processus biologiques tels que la croissance et la mortalité qui ont une importance particulière.

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