

Population Dynamics and Management

Kai Lorenzen

T.H. Huxley School of Environment, Earth Science and Engineering

Imperial College of Science Technology and Medicine,

8 Princes Gardens,

London SW7 1NA,

United Kingdom.

In:

Tilapias: Biology and Exploitation.

Edited by M.C.M Beveridge and B.J. McAndrew. 2000.

Kluwer Academic Publishers, Dordrecht. pp. 163-225.

CONTENTS

6.1 INTRODUCTION	3
6.2 POPULATION PROCESSES	4
6.2.1 Growth.....	4
(a) Describing growth: the VBGF.....	5
(b) Comparative analysis of growth patterns.....	6
(c) Plasticity in growth	7
(d) Sexual growth dimorphism	9
(e) Individual variability and genetics.....	9
6.2.2 Mortality.....	10
(a) Describing mortality.....	10
(b) Comparative information on mortality rates	11
(c) Size dependence	11
(d) Factors determining mortality rates	12
6.2.3 Reproduction.....	12
(a) Describing size and age at maturity	13
(b) Variation in reproductive traits.....	13
(c) Mechanisms underlying variation in reproductive traits.....	14
(d) Individual variability and genetics.....	16
6.3 DYNAMICS AND MANAGEMENT OF POPULATIONS	17
6.3.1 The diversity of tilapia populations.....	17
6.3.2 Population regulation and responses to exploitation	18
6.3.3 Fishery yields and ecosystem properties.....	19
6.3.4 Quantitative assessment of exploitation	20
(a) Empirical yield models	20
(b) Production models.....	21
(c) Dynamic pool models.....	21
(d) Accounting for environmental variation and life history plasticity	22
6.3.5 Culture fisheries.....	23
6.3.6 Dynamics and management of isolated cohorts.....	24
6.3.7 Controlling reproduction and “stunting” in culture	25
6.3.8 Tilapia as invaders.....	27
(a) Arrival and establishment	27
(b) Spread	28
(c) Equilibrium and effects.....	28
6.4 LIFE HISTORY VARIATION AND “STUNTING”.....	30
6.4.1 Tilapia life history variation	30
6.4.2 “Stunting”	31
(a) Life history variation within species.....	31
(b) Phenotypic response or genetic selection?.....	32
(c) Environmental characteristics associated with “stunting”	33
(d) Conclusion	34
6.4.3 Towards a mechanistic understanding of life history plasticity.....	34
6.5 CONCLUDING REMARKS.....	35
ACKNOWLEDGEMENTS.....	36
REFERENCES.....	37

Chapter six

Population Dynamics and Management

K. Lorenzen

6.1 INTRODUCTION

The tilapias are of major economic and ecological importance, being exploited in capture fisheries and aquaculture systems at all levels of intensity, and having invaded tropical fresh and brackish water ecosystems on all continents as a result of intentional or accidental introductions. Perhaps the most striking ecological feature of the tilapias is their ability to reproduce readily in almost any environment, from lakes to aquaculture tanks or aquaria. This ability, together with a remarkable plasticity in life history traits, is seen as a reason for their successful colonisation of such a wide range of habitats. It is also, however, a source of management problems in culture where early maturation and prolific breeding may lead to “stunting”, dense populations of small individuals below marketable size. Population dynamics, the study of the abundance and biomass dynamics of populations, their underlying mechanisms and their management consequences, is therefore relevant to all forms of tilapia exploitation. At the same time, the wide range of manipulations to which tilapia populations are being subjected provides a unique opportunity to investigate fundamental problems in fish population biology.

The phenomenon of “stunting” or “dwarfing” in tilapias has attracted much attention in the literature, not least because of the practical problem it presents in aquaculture. It has often been suggested that “stunting” is a response, possibly unique to the tilapias, to conditions of stress and high mortality (e.g. Iles 1973). However, a review of “stunting” in wild and farmed tilapias (section 6.4) indicates that this view is misleading: “stunting” is a collective term applied to different life histories linked in but one trait (low maximum size), it may occur under conditions of low as well as high mortality, and it is by no means unique to tilapias. Because the term “stunting” is so poorly defined, it will not be used in this chapter except in until section 6.4 where the phenomenon is reviewed in depth.

The aims of this chapter are threefold: to provide an introduction to tilapia population dynamics, to show how population dynamics approaches can aid the management of wild as well as farmed stocks, and to explore the significance of life history variation to both areas. Significant advances in our understanding of tilapia population biology will require constructive interaction between experimentally orientated aquaculture, field studies of wild populations, and the development of a common theoretical framework. The chapter aims to foster this development by integrating across

wild and farmed populations, and emphasising the applicability of common concepts and approaches in aquaculture and fisheries ecology.

Because the aim of this chapter is to synthesise current understanding of tilapia population biology and its application to practical management, it relies heavily on the detailed information available for a few well-studied species, mainly of the genus *Oreochromis*. Although these species are not necessarily representative of the tilapias as a whole, they represent the most important exploited species and there is no reason to believe that their population biology is fundamentally atypical.

The chapter is organised as follows. The first section reviews information relating to the processes of individual growth, mortality and reproduction. This is followed by a discussion of the dynamics and management of tilapia populations, both in the wild and in culture, and the dynamics of tilapia invasions. The final section explores life history variation in the tilapias, with particular reference to the “stunting” problem and its underlying mechanisms.

6.2 POPULATION PROCESSES

The present section deals individually with the processes of body growth, mortality and reproduction. To analyse each trait in isolation helps to identify the key proximate factors governing them. Ultimately, however, the traits are related through fitness trade-offs, which lead to the evolution of certain relationships between them (Beverton and Holt, 1959; Beverton, 1992; Roff, 1992; Charnov, 1993; Mangel, 1996; Jensen, 1996). Such relationships in the tilapias are explored further in section 6.4.

6.2.1 Growth

Individual growth is of key importance to the management of wild and cultured stocks, and has been studied extensively in tilapias. To allow a quantitative comparison of growth, the relevant patterns must be described mathematically. Mathematical models of different degrees of complexity have been developed to describe growth in fish. Simple models such as the von Bertalanffy growth function describe growth by parameters that relate directly to key patterns (e.g. asymptotic size), and can be estimated relatively easily. Complex physiological and bio-energetic growth models have the potential to provide insights into the factors and mechanisms determining growth patterns, but require a larger number of parameters that describe physiological processes and are not in any obvious way related to particular growth patterns. Such models are outside the scope of this chapter, but interested readers are referred to Liu and Chang (1992); Van Dam and Pauly (1995); and Yi (1998).

In ecological studies the choice of growth model is usually determined by practical considerations, and how well alternative models fit the available data. In optimality models of life history theory, however, the choice growth model may have far-reaching implications and must be considered carefully (Day and Taylor 1997).

(a) Describing growth: the VBGF

Throughout this chapter, growth is described by the conventional von Bertalanffy growth function (VBGF) or closely related models. Von Bertalanffy (1957) developed the VBGF on the basis of physiological considerations. The commonly used forms of the equation,

$$L_t = L_\infty (1 - e^{-k(t-t_0)}) \quad (\text{Eq. 6.1a})$$

for growth in length and

$$W_t = W_\infty (1 - e^{-k(t-t_0)})^3 \quad (\text{Eq 6.1b})$$

for growth in weight were derived by Beverton and Holt (1957). In these equations, L_t and W_t are the length and weight at time t , and L_∞ and W_∞ are the asymptotic length and weight towards which the fish grow at rate K . The parameter t_0 defines the position of the growth curve along the time axis. Equation (6.1b) assumes an isometric length-weight relationship (i.e. weight proportional to the cube of length). An empirically determined allometric exponent may be substituted for the third power in Equation 6.1b to derive a more general weight growth equation (see also Pauly 1981).

In order to facilitate the comparison of overall growth performance between populations that differ in both asymptotic size and growth rate, it is desirable to define an index that conveys growth performance information in a single number. An obvious candidate for such an index is the maximum weight growth rate, which is attained at the inflexion point of Equation (6.1b):

$$(dW/dt)_{\max} = (4/9) KW_\infty \quad (\text{Eq.6.2})$$

Pauly (1981) defined the growth performance index P , which is proportional to the logarithm of the maximum weight growth rate:

$$P = \log_{10}(KW_\infty) \quad (\text{Eq. 6.3})$$

Although other indices of growth performance have been proposed (Moreau *et al.*, 1986), P is the most readily interpretable in terms of the maximum growth rate. Jensen (1997) has added a further interpretation to the index, which is discussed below.

The physiological basis of the VBGF may be summarised as follows: growth is the net result of the opposing processes of anabolism and catabolism (metabolism). Anabolism is limited by the rate at which resources can be acquired by the organism, which is assumed to be approximately proportional to body length to the power of two. Different reasons have been advanced for this proportionality. The limiting effects of body surfaces on resource uptake in general, or of the gill surface area on oxygen uptake in particular, have been advanced by von Bertalanffy (1957) and Pauly (1981), while Walters and Post (1993) propose that the search rate and swimming speed of fishes scale with the second power of length. Catabolism is approximately proportional to body weight, i.e. the third power of length. Several authors have interpreted and extended the VBGF (Beverton and Holt, 1957; Pauly, 1981; Walters and Post, 1993; Roff, 1983; Lorenzen, 1996a; Jensen, 1997), and this has led to some generalisations with regards to the growth patterns that

can be expected under particular circumstances: (1) Differences purely in the rate at which resources are acquired by the organism (relative to the requirement, proportional to length to the power of two) will lead to differences in asymptotic size (L_4 and W_4), but not in the growth rate (K). (2) Differences in the allocation of resources to somatic growth and other body functions such as reproduction or predator avoidance will affect the growth rate (K) as well as the asymptotic size. The growth rate K may also be affected if the relative rate at which resources are acquired changes with the size of fish, for example because population biomass and therefore the degree of resource competition changes as the fish grow (e.g. single cohort aquaculture, Lorenzen, 1996a), or because competition between size groups is asymmetric (Walters and Post, 1993). Jensen (1997) shows that, for organisms that acquire resources at the same rate but allocate them differently, K and W_∞ can be expected to be inversely proportional. This also implies that the maximum weight growth rates and growth performance index P of these organisms will be the same (cf. Eq. 6.2, 6.3), but will be achieved at different sizes and ages (see also Fig. 6.1).

Beverton and Holt (1957), Walters and Post (1993) and Lorenzen (1996a) have extended von Bertalanffy's theory of growth to account for density-dependence resulting from competition for food. The model by Lorenzen (1996a), which will be applied to tilapia growth later on, assumes a linear relationship between asymptotic length and population biomass and the equivalent relationship for asymptotic weight:

$$L_{\infty B} = (L_{\infty L} - g B) \quad (\text{Eq. 6.4a})$$

$$W_{\infty B} = (W_{\infty L}^{1/3} - c B)^3 \quad (\text{Eq. 6.4b})$$

where $L_{\infty L}$ and $W_{\infty L}$ are the (extrapolated) asymptotic length and weight in the absence of competition ($B \rightarrow 0$), and g and c are the competition coefficients for length and for weight. The model of Walters and Post (1993) was developed specifically to address competitive asymmetries in age/size structured populations, and allows for more complex relationships between the abundance of age/size groups and asymptotic size. A result of general interest is that competitive asymmetries are expected to result in apparent changes in the growth rate K with density. This suggests that simple models will describe density-dependent growth well in omnivorous species that do not show major ontogenic shifts in diet or competitive asymmetries (inequitable partitioning of resources between fish of different ages/sizes). This has indeed been shown for carp (Lorenzen, 1996a).

(b) Comparative analysis of growth patterns

Extensive, comparative studies of tilapia growth performance in wild stocks and in aquaculture have been reported by Moreau *et al.* (1986) and Pauly *et al.* (1988). Tilapia growth patterns vary widely between and within species. In natural populations the highest asymptotic sizes of 500 mm in length or 7000 g in weight have been recorded for *O. niloticus*, while populations of *O. aureus* and *Tilapia zillii* rarely reach more than 250 mm in length or 600 g in weight. In aquaculture, asymptotic sizes of less than 200 mm in length or 500 g in weight are common regardless of the species used. Typical values for the growth rate K range from 0.2 to 0.8 y^{-1} in natural populations, but can be an order of magnitude higher in culture.

An overview of observed growth parameters in natural and cultured populations of *O. niloticus* is given in Figure 6.1(a). There are two clearly separated clusters, one of wild populations with high W_∞ and low K, and one of cultured populations with low W_4 and high K. The line of slope -1 indicated in Figure 6.1(a) connects points of equal growth performance P (Eq. 6.3; Pauly, 1981). The average growth performance P and therefore maximum growth rates in natural and farmed populations of *O. niloticus* overlap widely, although on average P is higher in culture (see also Fig. 6.2). The different growth patterns implied by different points on the same isoline of P are illustrated on Figure 6.1(b).

[Figure 6.1 about here]

The question remains why values of K in aquaculture tend to be much higher than in natural stocks. The above discussion of VBGF patterns and their physiological interpretations suggests several, not mutually exclusive possibilities. Under culture conditions, fish may increase allocation of resources to maintenance metabolism (Pauly, 1981) and reproduction, and/or resource acquisition may decline relative to requirements as the population approaches the system's carrying capacity (Lorenzen, 1996a). The analysis of density-dependent growth in pond culture of *O. spilurus niger* (see below) suggests a combination of both mechanisms: density-dependence accounts for some apparent variation in K, but even the value of K estimated for the density-dependent VBGF is high relative to the values found in natural populations.

Pauly *et al.* (1998) compared overall growth performance of different tilapia species in the wild and in culture. Growth performance P measured in wild stocks overlapped widely among the species (Fig. 6.2). Median growth performance in culture was higher in culture than in natural stocks for most species, with the differences in growth performance P evident in *O. aureus* and *T. zillii* (22 and 33% respectively). These conclusions are moderately sensitive to the choice of growth performance index: Pauly *et al.* (1988) based their final assessment on a different growth performance index (ϕ'), which indicated a far greater magnitude of differences between cultured and wild stocks, but similar relative patterns.

[Figure 6.2 about here]

The maximum or asymptotic size in tilapia populations tends to be positively related to the size of the water body in which they live. This has been noticed by Lowe (McConnell) (1958) for *O. niloticus*, and is also borne out in the *O. mossambicus* data assembled in table 6.1. (Fig. 6.3). This suggests that the absolute allocation of resources to growth is higher in individuals living in larger water bodies, either because of higher acquisition or because of a higher relative allocation to growth (or a combination of the two).

[Figure 6.3 about here]

(c) Plasticity in growth

The growth of tilapias is highly plastic, responding immediately to changes in resource availability and other factors. Van Someren and Whitehead (1959) transferred mature males of *O. spilurus niger* from a densely populated pond where they were approaching their asymptotic weight to a less densely populated pond, where they resumed rapid growth towards a higher asymptotic

weight. This demonstrates clearly that, rather than being determined early on in life, the growth of tilapias responds quickly to changing conditions throughout life.

An aspect of plasticity of particular interest to the management of populations and the “stunting” problem is density-dependence. Perhaps the best experimental data on density-dependent growth in tilapias can be found in van Someren and Whitehead (1961), who stocked and harvested, in a staggered fashion, four cohorts of *O. spilurus niger* in a pond and monitored their growth. The resulting growth patterns are illustrated in Figure 6.4(a), together with a fitted density-dependent VBGF model. Total biomass in the experimental pond increased rapidly over six months and declined thereafter, and this pattern is mirrored by changes in asymptotic weight (Fig. 6.4(b)). Density-dependence has generated a wide variety of growth patterns. The most striking differences are apparent between the first stocked cohort, growing to a low asymptotic weight at a high apparent growth rate as biomass increases, and the last stocked cohort growing almost linearly towards a large size as biomass is gradually reduced. Using a conventional (non density-dependent) VGBF (Eq. 6.1b), growth in the first cohort is described by $W_{\infty}=132\text{g}$ and $K=4.1/\text{year}$, while growth in the last stocked cohort is described by $W_{\infty}=349\text{g}$ and $K=1.3/\text{year}$. The full range of patterns is well described by a simple density-dependent model with constant K and asymptotic size as function of total biomass (Equation 6.8, parameter values: $W_{\infty L} = 394\text{g}$, $K=2.1/\text{year}$, and $c= 0.019\text{g}^{1/3}\text{ha/kg}$). The estimated value of $K = 2.1/\text{year}$ is somewhat higher than the values estimated for conventional VGBF models applied to wild populations (Pauly *et al.*, 1988; see also Fig. 6.1(a)). This suggests that the high values of K estimated in single cohort aquaculture (Pauly *et al.*, 1988) result from a combination of increasing resource competition as the culture cycle progresses, and a higher allocation to functions other than growth.

[Figure 6.4 about here]

The primary factor mediating density dependence in growth in natural and extensively farmed fish is competition for food (e.g. Lorenzen 1996a). Food availability in itself, of course, has a strong effect on tilapia growth (see Diana, 1997, for a review). Nutritional constraints in particular ontogenic stages have been linked to restricted growth in the *O. mossambicus* population of Lake Sibaya (Bowen 1979), and similarly “trophic bottlenecks” have been implicated in growth depression in non-tilapiines (Heath and Roff, 1996).

Apart from population density and food supply in general, a range of other environmental factors influence growth in tilapias. A frequently cited pond culture experiment by Chen and Prowse (1964) suggests that the size of the pond in which the population lives may affect the growth of tilapias even when density is held constant. However, this result rests on the markedly higher growth observed in a single, large pond and has not been replicated.

Changes in habitat availability have been shown to affect growth in resident tilapia populations. Dudley (1974) found a strong positive correlation between growth increments in three tilapia species and the extent of seasonal flooding in the Kafue floodplain, Zambia. The damming of the Zambezi to form Lake Kariba has led to a marked increase in the growth of the endemic *O. mortimeri* (Harding, 1965).

The relationship between oxygen availability and growth is of practical as well as theoretical interest. Pauly (1981) hypothesised that oxygen availability was the primary factor limiting the growth of fishes and developed a “generalised” version of the VBGF to account for the limitations to growth arising from geometric constraints on gill surface area. Although this hypothesis has not been tested explicitly, there is experimental evidence for an effect of oxygen availability on growth in tilapias (Tsadik and Kutty, 1987; Papotsoglou and Tziha, 1996). Van Dam and Pauly (1995) incorporated an oxygen limitation term based on Pauly’s theory into a dynamic simulation model for fish growth, and showed that the model can reproduce the effects of low oxygen saturation on final weights of *O. niloticus* observed by Tsadik and Kutty (1987). This does not, however, imply that oxygen availability is the principal factor limiting fish growth under natural or culture conditions. Many studies point to an overwhelming effect of food supply (e.g. Prein, 1993a; Lorenzen, 1996a; Diana 1997), but oxygen may become limiting under very high densities and rates of feed or fertiliser supply (Teichert-Coddington and Green, 1993; see also Ross, this volume).

(d) Sexual growth dimorphism

It has long been noted that in many tilapia species, males tend to grow at a higher rate and/or to a larger asymptotic size than females (e.g. Fryer and Iles, 1972). This pattern is unusual within the fishes, where females often grow larger than males. Among the reasons advanced for male growth “superiority” in tilapias are a sex-specific physiological growth capacity, cessation of feeding and growth during female mouth brooding, and behavioural interactions. Schreiber *et al.* (1998) demonstrate that in individually reared *O. niloticus*, males show a lower growth rate and feed conversion efficiency than females. This indicates that the physiological growth capacity is in fact higher in females than in males, and the opposite relationship commonly observed in group rearing must be due to either the effect of reproduction or behavioural factors. Empirical evidence with regards to the latter two possibilities is somewhat inconclusive. A number of studies indicate marked growth differences between monosex populations of the same species (*O. spilurus*: Van Someren and Whitehead, 1960; *O. niloticus*: Pauly *et al.*, 1988), implying that the differences persist even when no breeding takes place. Conversely, Bolivar *et al.* (1993) show that in some strains of *O. niloticus* at least, non-breeding females have growth patterns similar to those of males. Bramick *et al.* (1995) studied triploid *O. niloticus* and found no difference in growth between diploid and triploid sibs up to the onset of reproduction in diploids. Thereafter, growth in diploid females declined immediately relative to their later maturing triploid sibs. Growth in diploid males only declined after large numbers of fry occurred in the experimental ponds, suggesting that the decline in growth was linked to increased competition rather than the energetic costs of reproduction.

(e) Individual variability and genetics

Individual variability in growth may have important implications for the dynamics and life history evolution of populations, and consequently for their management (Lomnicki, 1988; De Angelis and Gross, 1992; Tyler and Rose, 1994; Mangel, 1996; Stamps *et al.*, 1998). Variability in growth may be due to phenotypic plasticity as well as genetically determined growth potential. In laboratory situations, tilapias may exhibit a high degree of individual variability in growth linked to hierarchical interactions. Fernandes and Volpatro (1993) show how hierarchical interactions lead to increased heterogeneity in growth, related largely to metabolic differences between dominant

and subordinate fish. The question to what extent individual variability in growth has a genetic basis is of obvious relevance for selective breeding programmes, as well as the selective exploitation of natural populations. A comparative study of the growth of different strains of *O. niloticus* under a range of farming conditions has shown that strain effects were significant, but only accounted for a low proportion (1.5 %) of the overall observed variation in growth rates (Eknath *et al.*, 1993). The proportion of variation explained by genetic differences is, of course, expected to be higher if only populations within a single environment are considered. Silliman (1975) subjected laboratory populations of *O. mossambicus* to selective and unselective fishing over a period of about four generations, and subjected groups of mature fish from both treatments to growth experiments under similar conditions. He found no difference in the growth of females, while males from the unselectively fished population grew larger than those from the selectively fished one. The result is therefore somewhat inconclusive, as well as of questionable validity. The growth tests have been carried out using large fish that had experienced different conditions during husbandry prior to the test, rather than individuals of the following generation reared under identical conditions.

6.2.2 Mortality

Despite of its obvious importance to life history evolution, ecology and management, mortality has been studied far less than growth or reproduction, being more difficult to measure in field situations and considered less controllable in culture.

(a) Describing mortality

Traditionally, mortality is described as proportional survival over a culture period in aquaculture, and as an instantaneous rate in fisheries ecology (for a discussion see Hopkins and Pauly, 1993). The development of population numbers over time under the influence of a constant instantaneous mortality rate is described by

$$N_t = N_0 e^{-Zt} \quad (\text{Eq. 6.5})$$

where N_t is the population abundance at time t , N_0 is the initial number at time $t=0$, and Z is the instantaneous mortality rate. Proportional survival S from $t=0$ to t is defined by

$$S = N_t / N_0 \quad (\text{Eq. 6.6})$$

Consequently, S and Z are related by

$$S = e^{-Zt} \quad (\text{Eq. 6.7})$$

Among the advantages of using instantaneous mortality are that they are independent of the study period and can therefore be compared easily, and that they are additive. In fisheries ecology, the total mortality rate Z is often written as the sum of the mortality rate F caused by fishing, and the natural mortality rate M due to all other causes (e.g. predation, parasitism, or adverse environmental conditions):

$$Z = M + F \quad (\text{Eq. 6.8})$$

(b) Comparative information on mortality rates

An overview of the range and median of total mortality rates determined for some tilapia populations in different habitats is given in Fig. 6.5. Data for natural populations are from Table 6.1, and reflect mortality due to fishing as well as natural causes. Data for pond and cage culture have been extracted from Lorenzen (1996b), and reflect natural mortality during the on-growing period in culture, i.e. excluding the final, catastrophic event of fishing mortality characteristic of stocks in single cohort aquaculture. Total mortality rates in the natural populations range from 0.4 to 5.8, with median values of 1.8/year in lakes (> 100 ha), 0.8/year in rivers, and 2.1/year in small water bodies of less than 100 ha in area. Sample sizes in all categories are too small to provide anything more than a rough indication, but it is worth noting that some populations suffer extremely high total mortality rates, and that there is no obvious relationship between (natural) habitat type and total mortality rate. The highest degree of variation is evident in small water bodies, which account for the lowest and well as the highest recorded values. Mortality rates in pond and cage culture are comparatively low, ranging from 0.01/year to 1.4/year, with a median of 0.2/year. This category includes many ponds that are not unlike natural small water bodies in terms of fluctuations of physico-chemical parameters etc., but there are no instances of particularly high mortality. Mortality rates in small water bodies are particularly variable, but there is no evidence to suggest that they are different on average from those in larger water bodies.

[Figure 6.5 about here]

Certain methods of fisheries assessment (dynamic pool models, see Section 6.3.4) require the separation of total mortality into its components due to fishing and due to natural causes. Unfortunately, the natural mortality rate of an exploited population is difficult to assess, and there is only one well-documented estimate of natural mortality in a wild tilapia population, for *O. esculentus* in Lake Victoria in the late 1950s (Garrod, 1963). Pauly (1980) developed a multiple regression model predicting natural mortality from growth parameters and mean environmental temperature, which has been widely used to provide estimates of natural mortality in assessments of tilapia (as well as many other) stocks. Pauly's original data set included Garrod's natural mortality estimate for *O. esculentus* as the only estimate for tilapiines.

(c) Size dependence

Natural mortality rates in fish are strongly size-dependent, and can be described by a power function of the form

$$M_W = M_u W^b \quad (\text{Eq. 6.9})$$

where M_W is the natural mortality at weight W , M_u is then natural mortality at unit weight, and b is the allometric exponent of the relationship. A comparative analysis of mortality-weight relationships across a wide range fish species (Lorenzen, 1996b) showed that natural ecosystems are characterised by a common natural mortality-weight relationship with an allometric exponent of $b = -0.29$. Natural mortality in aquaculture systems was lower overall than in natural ecosystems, but more strongly weight-dependent with an allometric exponent of $b = -0.43$.

The study by Lorenzen (1996b) included 36 natural mortality estimates for tilapias in pond and cage culture, spanning a range of mean weights from 0.45 to 330 g. These data are shown in Fig. 6.6, together with the corresponding mortality-weight relationship estimated by non-parametric (Theil) regression (Sprent, 1989). The parameters (with 90% CI) of the relationship for tilapia pond and cage culture are $b = -0.60$ [-0.67, -0.45] and $M_u = 2.9$ [2.3, 3.7] /year. These parameters are not significantly different from those estimated for the full set of pond and cage culture data, including or excluding the tilapia data analysed here. This suggests that in tilapias, too, natural mortality rates in aquaculture are more strongly size dependent than in wild stocks. Consequently, natural mortality rates of large/mature are far lower in culture than in natural stocks. There are no data on mortality-weight relationships in wild tilapia populations, but these relationships have been found to be quite consistent among other populations (Lorenzen 1996b) and there is no reason to expect very different patterns in the tilapias.

[Figure 6.6 about here]

Size-dependence in mortality has important ecological and life history implications, because it provides a direct link between growth and survival. In the context of the “stunting” problem, it is worth noting that populations characterised by a low maximum size can be expected to show reduced longevity compared to large growing populations, simply as a result of size-dependent mortality.

(d) Factors determining mortality rates

Mortality rates are determined by a combination of environmental factors (e.g. temperature, presence of predators), and factors rooted in the behaviour, physiology and genetics of the individual organism (e.g. choice of habitat, predator avoidance behaviour). These factors and their interaction are poorly understood, and have been little studied in the tilapias. However, a study on the influence of salinity on mortality in cultured tilapia illustrates the potential usefulness of systematic mortality studies to management. Hopkins and Pauly (1993) showed that in pure *O. niloticus* stocks, mortality increases with increasing salinity, while *O. niloticus* x *O. mossambicus* hybrid stocks show the opposite trend. Further quantitative studies on mortality in culture and in wild populations could lead to significant improvements in management, and may also provide insights into fundamental ecological questions (see e.g the discussion on predation mortality in Lorenzen 1996b).

6.2.3 Reproduction

The tilapias have certain reproductive strategies that set them apart from the vast majority of fish species. All tilapias normally build and spawn in nests, around which they defend territories. Spawning is followed by guarding of the brood by both parents in the Genus *Tilapia*, female mouthbrooding of eggs and fry in *Oreochromis*, and bi-parental mouthbrooding of eggs only in *Sarotherodon*. Relative gonad weight in tilapias rarely exceeds 6 % of body weight, and is therefore near the lower limit observed for teleost fish (Peters, 1963; Iles, 1973). Overall, tilapias are characterised by a very high fertility: 150 adult fish have been reported to have produced 15 000 fry in less than four months (Hickling, 1963). Fecundity (the number of eggs produced) is approximately proportional weight, or the third power of length, in the substrate spawning

tilapias, but scales with the second power of length in mouthbrooders (Welcomme, 1967; Jalabert and Zohar, 1982).

Reproductive biology is covered in depth by Turner (this volume), and the discussion here focuses on aspects of particular interest to population dynamics and life history analysis: size and age at maturity.

(a) Describing size and age at maturity

In physiological terms, the onset of the maturation process may be distinguished from a phase of final maturation, and the two phases appear to be influenced by different cues (Brummett, 1995). The maturation process may be described in terms of maturity stages, based on gonadal morphology (e.g. Nikolsky 1969), and “late” stages may be distinguished from “early” stages in order to classify organisms as mature or immature. The age and length at maturity is usually expressed as the age/length at which 50% of the population are mature (i.e. in late stages of gonadal development), determined by fitting a logistic function to proportional maturity data (King, 1995). Where information based on gonadal morphology is not available, other indicators of maturity may be used as a proxy, for example coloration (e.g. Lowe (McConnell), 1958).

(b) Variation in reproductive traits

The tilapias are renowned for their variability in reproductive traits, in particular the age and size at maturity. Length at maturity L_m has been shown to vary from 35 mm (Hecht and Zway, 1984) to 275 mm (James and Bruton, 1992) in *O. mossambicus*, or from 100 mm (Bolivar *et al.*, 1993) to 390 mm (Lowe (McConnell), 1958) in *O. niloticus*. Information on age at maturity is less easily available, but *O. niloticus* have been shown to mature at an age of 3 months in tanks (Bolivar *et al.*, 1993), and possibly over 2 years in large lakes (Gwahaba, 1973; Kolding, 1993). In general, size and age at maturity are correlated, i.e. tilapias mature either early and small, or late and large (Duponchelle and Panfili 1998; section 6.4 this chapter). However, there are also examples of populations with a low maximum size where maturation appears to be delayed or suppressed completely (Silliman, 1975; Eyeson, 1983). In such populations, small mature fish may be quite old. Different sizes at maturity are associated with differences in fecundity and brood frequency, with small maturing individuals being relatively more fecund and breeding more frequently than large maturing ones (Iles, 1973).

The observation that the largest maturing tilapia populations are found in large lakes and river systems suggests that length at maturity may be related to the size of the water body in which a population lives. Empirical relationships between length at maturity and water body area have been established by Lowe (McConnell) (1958) for African lakes, by De Silva (1986) for Sri Lankan reservoirs, and by Duponchelle and Panfili (1998) for reservoirs in Ivory Coast. However, a plot of length at maturity in *O. mossambicus* populations against water body size, covering several orders of magnitude, suggests that such relationships exist within sets similar water bodies, but not globally (Fig. 6.7).

[Figure 6.7 about here]

A comparative analysis across African lakes also suggests a negative correlation between the condition factor of fish and the onset of maturation, i.e. populations in poor condition appear to

mature at a smaller size than those in a good condition (Lowe (McConnell), 1958). There are a number of possible explanations for this correlation, e.g: poor condition causes maturation at small size, maturation at small size causes poor condition, or poor condition limits somatic growth so that fish mature small but not necessarily early. Additional data on growth are required to resolve this problem.

(c) Mechanisms underlying variation in reproductive traits

Is the observed variation in reproductive traits a reflection of phenotypic plasticity, or the result of genetic selection? Many observations, such as life history comparisons between long established populations, are indeed consistent with either mechanism, but there is compulsive evidence from natural environments, transfer experiments and population genetics that the observed differences are primarily phenotypic in origin. Lowe (McConnell) (1958) and Welcomme (1970) observed maturation at small size in temporarily isolated lagoons of large lakes. In the early days of tilapia culture, transfers of specimens from large-maturing African lake populations to ponds or aquaria were common, and led to immediate reductions in size at maturity to values around 100 mm, far outside the range (200-300 mm) observed in the lake populations. Although these experiments are not well documented, they are regularly referred to in the earlier literature (see e.g. Cridland, 1961; Iles, 1973, Fryer and Iles, 1972). Such drastic and immediate changes in maturity traits can not be explained by genetic selection and must be phenotypic in origin. In a recent study, Duponchelle *et al.* (1998) subjected groups of *O. niloticus* from two reservoir populations with very different reproductive characteristics to a common environment, and found that the differences disappeared within five months. Further evidence for the phenotypic nature of variation in size at maturity is the failure of population genetics studies to detect any differences between small and large maturing feral *O. mossambicus* populations of single origin (Bluehdorn and Arthington 1990).

Having established that the observed variation in age and size at maturity in tilapias is primarily phenotypic in nature, the question remains: how is the expression of this plasticity controlled? There are two main lines of thought in this respect, one that interprets plasticity in terms of the individual organism's physiological responses to environmental stimuli, and another that sees intraspecific interactions as a key factor.

The main physiological hypotheses focus on (1) unspecific stress, (2) the oxygen regime, and (3) other physical or chemical cues. Several authors have linked early maturation in tilapias to unspecific stress, related to factors such as strong fluctuations in physico-chemical parameters, high rates of mortality due to catastrophic events or predation, and extreme reduction in living space in periods of draught (Lowe-McConnell 1982; this volume; Kolding, 1993). However, the stress hypothesis is difficult to evaluate because stress is defined in terms of consequences, not causes. Indeed, it is not uncommon in the literature to find descriptions of early maturing populations that are considered stressed simply because they mature early. Unless the level of stress can be established independently (e.g. by physiological indicators such as levels of stress hormones), the stress hypothesis is little more than a circular argument. Even if a correlation between independent indicators of stress and early maturation could be established, this would be of limited practical use unless the underlying causes of stress could be isolated.

The relationship between mortality and reproductive traits is explored in section 6.4. In established, self-sustaining populations age at maturity is inversely related to the mortality rate, while the relationship between size at maturity and mortality is more complex. However, in situations of demographic dis-equilibrium, such as aquaculture facilities stocked only with juveniles, maturation may occur very early even though mortality rates are extremely low (cf. section 6.2.2).

Pauly (1984) proposed a theory that the transition to maturity is induced by declining oxygen availability, due to the geometric constraints on gill surface area as fish grow. He hypothesised further that the (as yet to be discovered) physiological mechanism inducing maturation in response to oxygen levels could be triggered off prematurely under conditions of fluctuating ambient oxygen concentrations, or stress-related increases in oxygen consumption within the organisms itself. The latter point would provide a mechanistic basis for the stress hypothesis, including a potentially measurable stress indicator (elevated oxygen consumption). Empirical evidence for a link between low or fluctuating oxygen levels and early maturation at a small size is anecdotal. Undoubtedly, early maturation has been observed under conditions associated with low or strongly fluctuating oxygen levels, such as in shallow lagoons or highly productive ponds (see also Lowe-McConnell, this volume). However, there is no evidence that high and stable oxygen saturation alone would cause a substantial delay in maturation (see e.g. Horstgen-Schwark and Langholz, 1998, who maintained oxygen saturation within narrow limits, close to 100%). Also, there is evidence for suppressed or delayed reproduction in some populations maintained under a lower degree of saturation. In Silliman's 1975 study, little reproduction was observed in the *O. mossambicus* population over a long period while oxygen saturation barely exceeded 50%. Also, Eyeson's (1983) *S. melanotheron* population showed low reproductive activity while maintained in a shallow outdoor tank, a habitat most likely associated with low and fluctuating oxygen saturation.

Environmental factors or "cues" affecting tilapia reproduction have recently been reviewed by Brummett (1995), who identified temperature, light intensity, quantity and quality of food, and certain water quality parameters as important environmental cues. Food supply in particular may be expected to have a strong influence on reproduction. In experiments with *O. niloticus* x *O. aureus* hybrids, low feeding levels reduced the proportion of mature fish, weight at maturity, and fecundity (Siddiqui *et al.*, 1997). However, fecundity per unit weight of females was highest in the fish fed the lowest ration. Coward and Bromage (1999) show that under prolonged food restriction, *T. zillii* will sacrifice somatic growth to maintain reproductive investment. These observations suggest a complex relationship between food supply and reproductive traits, possibly involving a high degree of individual variability in responses. This area calls for further investigation. Manipulations in food supply have been successful in influencing maturation in other species, e.g. salmonids (Bagenal, 1969; Thorpe *et al.*, 1990).

Intraspecific interactions may have a strong influence on final maturation and reproduction in tilapias. Extreme crowding may completely suppress final maturation and reproduction (Coward *et al.*, 1998). Under moderately crowded conditions, dominance hierarchies and territorial behaviour may restrict reproduction to a small fraction of the population. Van Someren and Whitehead (1959) describe aquarium experiments in which only a limited number of males show breeding coloration at any one time, and if these males are removed others will take their place.

Behavioural studies of tilapias and other cichlids show that body size is a key determinant of the outcomes of conflicts about territories (Baerends and Baerends-van Roon, 1950; Oliveira and Almada, 1996), although this may be modulated by other factors such as gonad size (Neat *et al.*, 1998). These observations suggest competition for breeding territories, with small/inferior individuals queuing for territories, as a mechanism influencing maturation size. This hypothesis has been clearly formulated by Moriarty (1982). Deferred maturation as a consequence of territoriality has been described in many bird populations (Sutherland, 1996), and has been analysed theoretically by Ens *et al.* (1995).

The stress and oxygen hypotheses have been formulated to explain the occurrence of small and early maturation, while large and late maturation has been considered “normal” and therefore not in need of an explanation. The opposite view that early maturation is the norm, but may be delayed if the fish is unable to acquire the resources necessary for successful reproduction, is embodied e.g. in the territorial behaviour hypothesis. While there is no *a priori* reason to prefer one perspective over the other, the latter perspective is supported by the fact that early maturation has been observed under a very wide range of conditions (e.g. high as well as low mortality, low and fluctuating as well as high and fairly stable levels of oxygen saturation). The delay perspective is also supported by studies in other species (e.g. Policansky, 1983; Thorpe, 1994) and has been applied fruitfully in the analysis of life history plasticity (Thorpe *et al.*, 1998). The interpretation of observed reproductive patterns is complicated by the fact that maturation takes several months to complete (Jalabert and Zohar, 1982), which implies that conditions preceding actual maturation by at least a few months are likely to be of key importance.

In conclusion, the mechanisms controlling maturation and reproduction in tilapias are still poorly understood, and there is no clear support for any of the main hypotheses advanced in this respect. The stress hypothesis is poorly defined and therefore not readily testable. A link does exist between mortality and maturation, but this link is more complex than is generally appreciated (see section 6.4). The oxygen hypothesis is consistent with field data in the sense that early maturation has been observed under conditions of low or fluctuating oxygen availability, but this could be purely coincidental and there is no indication that high/stable oxygen availability alone is sufficient to induce late maturation. This hypothesis is, however, eminently testable. Likewise, the degree to which maturation can be controlled by behavioural interactions should be explored further in experiments. Given the ubiquitous occurrence of early maturation under culture conditions, convincing evidence for control of maturation by a particular factor would require a demonstration that the factor in question can substantially delay maturation.

(d) Individual variability and genetics

There is evidence of considerable within-population variation in age and size at maturity. This is obvious from maturity-at-age or at-length curves derived for natural populations (e.g. De Silva, 1986; Duponchelle and Panfili, 1998). In a long-term experiment with *O. niloticus*, 28% of the females matured within 60 days and a further 15% between 61 and 210 days, while 57% of the females had not matured by the end of the experiment at 210 days (Bolivar *et al.*, 1993). The basis of this variation has not been evaluated; possibilities include genetic, as well as phenotypic factors such as behavioural interactions.

Whereas a high degree of phenotypic plasticity is evident in reproductive traits, this does not imply the absence of a genetic component: several studies have indicated a high degree of heritability (around 0.5) for age and/or size at maturity (Lester *et al.*, 1988; Kronert *et al.*, 1989; Oldorf *et al.*, 1989). This suggests that, although the observed variation between populations is primarily phenotypic in origin, selection for late maturity may bring about a delay sufficient to allow completion of a culture cycle of 4-6 months without reproduction.

6.3 DYNAMICS AND MANAGEMENT OF POPULATIONS

The section starts with a brief overview of the structural diversity of tilapia populations and their responses to exploitation. This is followed by a review of the dynamics and management of wild and farmed populations, and the dynamics of invasions. Farmed populations are defined here as those subject to management intervention other than harvesting. The degree of intervention defines culture intensity as extensive (stocking and harvesting only, production based on natural aquatic productivity), semi-intensive (natural productivity enhanced by fertilisation and some feeding), and intensive (production based mainly on complete feeds). However, it must be remembered that even farmed tilapia populations may show many of the dynamic features of wild populations and that on the other hand, many small-scale tilapia aquaculture systems entail little manipulation other than harvesting of a largely self-sustaining pond population.

6.3.1 The diversity of tilapia populations

Many tilapia species can form breeding populations in habitats ranging from large lakes to small aquaria, and may be exploited and manipulated at wide range of intensities. Different conditions give rise to different patterns of growth, mortality and reproduction, which have been reviewed in the previous section. These patterns translate into populations of widely different age and size structure.

A further aspect of population structure that deserves attention for its dynamic and management implications is spatial structure. Large water bodies usually offer a diversity of habitats that differ in terms of the physical environment (e.g. temperature, turbidity), the resources available (e.g. types and abundance of food, spawning substrate), and the intensity of intra and interspecific interactions (e.g. competition for food, predation risk). Individuals choose habitats on the basis of their requirements and competitive abilities, and it has been shown that in general, the resulting pattern of habitat use maximises the individual's fitness (see Tyler and Rose, 1994). Different life history stages of fishes differ in their requirements and competitive abilities, and therefore tend to occupy different habitats. In tilapia populations in larger water bodies, juveniles remain in near-shore areas at first and gradually move towards deeper, open waters as they grow (Fryer and Iles, 1972). Large individuals appear to be the most cosmopolitan, occupying open waters as well as the shallow near-shore areas. Breeding is generally limited to particular areas of relatively shallow water. This general pattern of spatial structure seems to hold even in relatively small water bodies, as demonstrated in a small (200 ha) reservoir in Sri Lanka (Pet and Piet, 1993). However, spatial structure necessarily becomes less pronounced in very small water bodies such as ponds that offer little habitat diversity. A similar situation can arise when shallow areas of larger water bodies are cut off from the main water body, and all life stages are forced to share the same habitat (Welcomme, 1970). Breeding for example is no longer confined to particular areas in uniform water bodies, but occurs over the whole bottom area (see e.g. Huet, 1978). Most tilapias are

flexible in their habitat requirements and able to complete their life cycle within a single habitat, even if it lacks any of the features normally preferred by different stages such as cover or substrate suitable for building nests. It is clear, however, that confinement to a single, uniform habitat greatly increases the interaction between size/age groups, and reduces the opportunity for individuals to escape limiting conditions by moving to a different habitat. The implications of differences in habitat diversity for the dynamics of tilapia populations have received little explicit attention, but this area may well be of key importance to the understanding of life history variation (section 6.4). Tyler and Rose (1994) review approaches to the modelling of spatial heterogeneity in fish populations. The diversity of tilapia populations makes them ideally suited for an empirical analysis, and the testing of models that may help to unravel the proximate basis of habitat choice and the resulting population dynamics.

6.3.2 Population regulation and responses to exploitation

Population regulation by density-dependent processes is an important factor in the long-term persistence of populations, and the regulatory processes also determine the levels of exploitation to which a population can be subjected on a sustainable basis. It is therefore important to understand the main mechanisms by which tilapia populations are regulated and respond to exploitation.

Several potential regulatory mechanisms have been identified in the previous section. Density-dependence in growth, mediated by competition for resources, is well-established (section 6.2.1). Combined with size dependent mortality (section 6.2.2), density-dependence in growth also generates density dependence in mortality. Competition for breeding territories and suppression of maturation in fish unable to defend territories (section 6.2.3) suggests a mechanism for density-dependent, behavioural control of reproduction. Observations of density-dependent responses in wild populations are limited, not least because environmental variability often obscures density-dependent responses. However, it is worth noting Gwahaba's (1973) observation that increasing exploitation (as suggested by increasing yields) of the *O. niloticus* stock in Lake George was associated with declining length at maturity. A comparative analysis of life history responses to exploitation is given in section 6.4.

Perhaps the most detailed information on responses to exploitation in a tilapia stock has been obtained in a long-term laboratory experiment. Silliman (1975) maintained a population of *O. mossambicus* for more than six years, in an 850 l tank under constant feed supply and environmental conditions, and subjected the stock to different levels of harvesting. The pattern of total (natural and fishing) mortality, and the resulting patterns of numerical abundance, biomass, maximum individual length, and recruitment are shown in Fig. 6.8. Natural mortality in the experiment can be assessed as total mortality prior to exploitation, i.e. $M=Z=0.1/\text{year}$. The population was then subjected to fishing mortality rates of $F=0.5/\text{year}$ and $F=1.1/\text{year}$ in addition to the natural mortality, leading to the total mortality schedule shown in Fig. 6.8(a). Population abundance (Fig. 6.8(b)) was stable at around 240 individuals in the beginning, but dropped to a lower level of about 180 as a result of a catastrophic mortality event linked to equipment failure (indicated by an arrow in Figs. 6.8(b) and (c)) at the end of year 2. The onset of exploitation at $F=0.5/\text{year}$ in year 3 did not lead to an immediate change in abundance, but there was a recruitment-related increase later in the year followed by continuous decline to about 120 at the

beginning of year 6. The higher level of exploitation at $F=1.1$ /year from the beginning of year 6 was again linked to initial increases in abundance as a result of recruitment, followed by a decline to the lowest level of 100 at the end of the experiment. Population biomass (Fig. 6.8(c)) increased sharply as result of individual growth until the end of year 2 and remained at a stable level of about 10 kg until the middle of year 4, but declined subsequently under the influence of exploitation. Maximum individual length (Fig. 6.8(d)) in the catch was stable at about 220 mm until the end of year 4, but increased markedly thereafter as population abundance and biomass declined. Recruitment (Fig. 6.8(e)) increased markedly with increasing levels of exploitation and the associated reduction in abundance and biomass. The evidently high degree of variability in recruitment per sampling period is a consequence of the demographic stochasticity inherent in a very small population, but a strong and consistent increase in the level of recruitment with increasing exploitation becomes evident when recruitment is aggregated over the experimental phases. The experimental population was tightly regulated, there is clear evidence for density dependence in the level of recruitment, as well as in the somatic growth of adults.

[Figure 6.8 about here]

Unfortunately, Silliman (1975) reported no detailed observations on reproductive traits in the experimental population, so that it is impossible to ascertain the mechanisms involved in the regulation of recruitment. However, Eyeson (1983) studied a similarly confined tank population of *S. melanotheron* and found reproductive activity to be suppressed to a very low level. Coward *et al.* (1998) show that crowding can lead to complete suppression of spawning, associated with low levels of sex steroids, in *T. zillii*.

6.3.3 Fishery yields and ecosystem properties

Environmental conditions such as ecosystem productivity define fundamental limits to the productivity of populations and the yields obtainable from their exploitation. This is evident in the strong correlations found between indicators of productivity/trophic levels and average tilapia yields in different water bodies. In Sri Lankan reservoirs, for example, commercial fish yields (dominated by the introduced *O. mossambicus*) are strongly correlated with the concentration of chlorophyll a, an indicator of primary production (Fig. 6.9; from Moreau and De Silva, 1991). The tilapias generally occupy low trophic levels in the food webs of tropical aquatic ecosystems, and are correspondingly efficient at transforming primary production into fish yield. Turner (1995) compared transfer efficiencies of primary production into fish yield in twenty African lakes, and found that the tilapia-dominated lakes in the set had significantly higher transfer efficiencies than lakes with fisheries dominated by the predatory *Lates*. More detailed trophic ecosystem models have been constructed for some ecosystems with significant tilapia stocks, e.g. Lake George (Moreau *et al.*, 1993) and lake Kinneret (Walline *et al.*, 1993). Trophic ecosystem models provide a framework to synthesise ecological data and evaluate the relationship between ecosystem properties and the yield and biomass of populations (Christensen and Pauly, 1993).

[Figure 6.9 about here]

Relationships between average yields and ecosystem properties can provide a deceptively static picture of populations that are in fact highly dynamic. Yields from many tilapia fisheries have been highly variable in the medium term, due to environmental factors as well as exploitation. Examples

of yield variation in tilapia fisheries from three African lakes are shown in Fig. 6.10. In Lake Naivasha, a high altitude rift valley lake, *O. leucosticus* and *T. zillii* have been introduced in the 1960. Following an initial surge with a peak yield of over 1000 t in the late 60s, annual yield of the combined tilapia fishery has varied between 20 and 530 t from 1970 to 1996. Yield variation in the established fishery has been related primarily to fluctuations in the water level, the extent of macrophyte vegetation, and high but variable fishing effort in the 1980s (Muchiri and Hickley, 1991; Muchiri, 1997). Lake Malombe is a large, shallow inundation of the Shire River in southern Malawi. Yield from the indigenous “Chambo” (*Oreochromis* sp.) fishery was high and only moderately variable between 1976 and 1986, but declined drastically thereafter. The rapid decline in the Chambo fishery has been attributed to the development of a seine net fishery for small Haplochromines, with a large bycatch of juvenile *Oreochromis* sp. (FAO 1993). Lake Turkana is a large rift valley lake that supports a productive fishery based primarily on *O. niloticus*. The variation in *O. niloticus* yield has been linked primarily to change in water levels, although changes in exploitation may also play a role (Kolding, 1993; Muchiri, 1997). These examples illustrate the high degree of variation experienced in tilapia fisheries even in large water bodies.

[Figure 6.10 about here]

6.3.4 Quantitative assessment of exploitation

The aim of quantitative stock assessment is to evaluate effects of alternative exploitation regimes on variables of management interest such as yield or catch rates. The quantitative approaches that have been used in the assessment of tilapia fisheries fall into three broad categories: empirical yield models, production models, and dynamic pool models.

(a) Empirical yield models

Empirical yield models are single or multiple regression models relating yield to, for example, indicators of productivity (e.g. the morphoedaphic index, chlorophyll a concentration, primary production), fishing effort, and/or water level. While no empirical models have been developed explicitly for tilapia fisheries, a number of such models have been developed for fisheries in which tilapias account for a large proportion of the catch. Empirical models for Sri Lankan reservoirs, where commercial catches are dominated by introduced *O. mossambicus*, predict yields from the ratio of catchment to reservoir area, chlorophyll a concentration, and fishing effort (Moreau and De Silva, 1991). Empirical yield models make no assumptions regarding the mechanisms underlying patterns in yields, and their predictions should not be extrapolated beyond the range for which data are available. Empirical models are most useful in situations where data are available for a wide range of conditions, such as for example yield, effort and trophic status indicators for a number of different water bodies. This makes empirical models ideal tools for the assessment of small water body fisheries with their high potential for replication. However, there are problems and potential pitfalls in the assessment of exploitation regimes using empirical yield models. Often, for example, water body productivity and fishing effort are correlated (the more productive water bodies attract more fishers). This can give rise to an apparently linear relationship between yield and effort, which however does not imply that the fisheries are underexploited but merely reflects underlying differences in water body productivity.

(b) Production models

Production models are based on elementary ideas of production ecology, and are commonly used to estimate optimal effort levels from time series of catch and effort data (overview in Hilborn and Walters, 1992; Hilborn and Mangel, 1997). Such data are relatively easy to collect at least in principle, and production models therefore hold good potential for the assessment of fisheries for which more detailed information is lacking. However, the measurement of fishing effort can be a major problem where many different gear types are used and fishing methods change over time. Production models have been used to assess the Chambo (*Oreochromis* sp.) fishery of Lake Malawi (Alimoso, 1991), and the *O. leucosticus* dominated gill net fishery of Lake Naivasha (Muchiri and Hickley, 1991). In both cases the traditional, equilibrium method of fitting the production model has been used. The method assumes that each annual yield estimate represents the equilibrium yield corresponding to the fishing effort exerted in that year. This assumption is clearly questionable in fisheries undergoing rapid change, and its violation can lead to severe overestimation of the sustainable level of fishing effort (see e.g Hilborn and Walters, 1992). It is therefore strongly recommended to fit production models using dynamic (non-equilibrium) approaches. This may appear more mathematically demanding than the equilibrium approach at first, but can in fact be accomplished relatively easily in computer spreadsheets (see Hilborn and Mangel, 1997). The dynamic approach is also true to the ecological production concept underlying the formulation of production models, whereas equilibrium fitting is not principally different from the use of empirical yield (regression) models.

(c) Dynamic pool models

Dynamic pool approaches to stock assessment break down abundance and biomass dynamics into the component processes of growth, mortality and reproduction, and allow the assessment of management options formulated at a high level of technical detail (e.g mesh size regulations). A problem with the application of dynamic pool approaches to tilapias and other fish in the tropics species is that these fish are difficult to age, making it difficult to analyse age-dependent aspects such as growth or mortality. This has prompted the development of a variety of approaches to estimating growth and mortality parameters from length composition data (Pauly and Morgan, 1987; Rosenberg and Beddington, 1988). Most of the commonly used methods establish a growth function (usually the VBGF, see section 6.2.1) to relate length to age, and then proceed to conduct further analysis in an essentially age-based framework. Growth studies of tilapias using length composition data include those of Getabu (1987), Amarasinghe and De Silva (1992), and Blay and Asabere-Ameyaw (1993).

Most tilapia fisheries are exploited predominantly by gill nets. The size-selectivity of gill nets implies that, unless a very wide range of mesh sizes is used, the length structure of catches does not reflect that of the population. This makes gill net catch data difficult to interpret, as illustrated by Amarasinghe and De Silva (1992): their use of catch length distributions obtained from relatively unselective seine nets resulted in a drastic re-assessment of growth patterns determined in an earlier study using gill nets only (De Silva and Senaratne, 1988). The problem of gill net selectivity can be addressed by using a wide range of mesh sizes, and correcting catch length distributions for gill net selectivity. Gill net selectivity has been estimated for several tilapia species, e.g. *O. esculentus* (Garrod, 1961); *O. mossambicus* (De Silva and Sirisena, 1987; Pet *et al.*, 1995); *O. niloticus* (Pet *et al.*, 1995); and *O. shiranus* (Mattson, 1994). The selectivity

models developed in these studies may be used to calculate approximate selectivity curves for tilapia fisheries where no specific experiments have yet been carried out, and may indicate to what extent fishery samples are representative of the population.

Conventional dynamic pool models are based on the assumption that fish populations are regulated at the pre-recruit stage, while growth and mortality in the adult population are considered to be constant (density-independent). This implies that the optimal exploitation of the growth potential of a recruited cohort is independent of the level of recruitment, and can be assessed in a yield-per-recruit analysis even if the level of recruitment is not known. Yield per recruit analysis identifies optimal combinations of gear selectivity and fishing effort to exploit stocks of known growth and natural mortality parameters. Such analyses have been used for example in Sri Lanka to determine the optimal size of first capture in the commercial fisheries for *O. mossambicus* (Amarasinghe and De Silva, 1992). As mentioned earlier (and again in section 6.4), there is strong evidence for density-dependence in individual growth in tilapias, and in principle this violates a key assumption of conventional yield-per-recruit analyses. The implication of density-dependent growth is that, due to its compensatory nature, changes in exploitation will lead to smaller changes in yield than predicted from analyses assuming constant growth.

The second element of dynamic pool models, apart from yield-per-recruit analysis, is the analysis of the relationship between spawning stock and recruitment. In general, such studies are based on analyses of catch-at-age data to reconstruct past cohort size and thereby recruitment as well as stock biomass. Unfortunately, both recruitment and stock size are difficult to measure in tilapias and other tropical species that reproduce over an extended period and are difficult to age. Consequently, there are no tilapia stocks for which a stock recruitment relationship has been determined. The tank experiment using *O. mossambicus* reviewed earlier (section 6.3.2) shows that recruitment in tilapias can be very strongly density-dependent, with very low recruitment when stock levels are high. This suggests a Ricker-type stock-recruitment relationship with a clear maximum at intermediate stock sizes.

The spatial structure of tilapia populations can have important implications for management and may need to be considered explicitly in certain situations. The tendency of young *O. mossambicus* to stay in near-shore areas while larger size groups venture into midwater implies that small mesh gill nets can be used in midwater to catch small species without affecting the tilapia stock. This was first realised and investigated by De Silva and Sirisena (1987). A dynamic pool model for a Sri Lankan reservoir fishery with explicit consideration of size-dependent habitat occupation has been developed by Pet *et al.* (1996b). The model confirmed that a subsidiary gillnet fishery for the small cyprinids could be established in open waters if small mesh gill nets of about 15 mm were used, while larger mesh nets of 30 mm would cause major damage to the *O. mossambicus* fishery.

(d) Accounting for environmental variation and life history plasticity

The various conventional methods of fish stock assessment applied to tilapia stocks have clearly provided useful information for management, and in some cases this information has been used to identify management measures such as mesh size limits (e.g. in Sri Lankan reservoirs). However, certain features of tilapia fisheries, such as large environmental variations and a high degree of plasticity in maturation and growth pose limitations to the use of conventional models. In spite of the wide recognition of these factors in the literature, little attempt has been made at incorporating

them into quantitative assessments. This is a key area for future research in stock assessment, of tilapias as well as other species.

6.3.5 Culture fisheries

Culture fisheries, i.e. fisheries based at least in part on the regular stocking of farm-produced (or occasionally wild caught) seed fish, are at the interface between capture fisheries and aquaculture (Lorenzen, 1995; see also Welcomme and Bartley, 1998, for a review of enhancements). Culture fisheries should be distinguished from other forms of management that may also involve stocking, for example for introductions with the aim of establishing a self-sustaining population (see section 6.3.9; and Cowx, 1998, for a review of stocking strategies). Tilapia culture fisheries are widespread in the tropics (Sugunan, 1997), although their precise extent is difficult to determine due to their position between the statistical reporting categories. Also, due to the tendency of tilapias to form breeding populations within a few months of stocking, the distinction between culture fisheries and introductions is somewhat difficult. The direct contribution of stocking to yields is most obvious in seasonally dry water bodies, but is difficult to assess, and may possibly be negligible in permanent water bodies where breeding populations of tilapias exist. Yields from tilapia culture fisheries can be up to 3 t/ha/year in productive water bodies (Lorenzen *et al.*, 1998b).

Although culture fisheries may generate benefits even in the absence of any systematic management, benefits are maximised if stocking and harvesting regimes are carefully co-ordinated and adapted to the natural conditions of the water body. The most comprehensive analysis of management options is possible with population dynamics models, while empirical yield models often allow a rapid assessment of key variables using comparative data from sets of culture fisheries. The population dynamics of fisheries based entirely on stocking, with density-dependent growth and size-dependent mortality of the type demonstrated for tilapias in section 6.2, has been studied theoretically by Lorenzen (1995), and an example of a practical assessment using the methodology is given in Lorenzen *et al.* (1997). However, the tilapias' tendency to reproduce in almost any environment means that, in contrast e.g. to the major carps, pure culture fisheries for tilapias are rare and limited to the stocking of monosex fry (see below). There is as yet no model to adequately capture the dynamics of the more common culture-enhanced tilapia fisheries where natural reproduction as well as stocking must be considered. Empirical models of culture fisheries involving tilapias have been derived by Lorenzen *et al.*, (1998b) for village fisheries in NE Thailand; and Quiros (1998) for larger reservoirs in Latin America. Lorenzen *et al.*, (1998b) show that if stocked in combination with major carp species, *O. niloticus* develop dominant breeding populations in highly productive water bodies, while the stocked carp will dominate water bodies of low to intermediate productivity. Although tilapia dominated culture fisheries therefore appear to be more productive than carp-dominated ones; this may reflect the underlying productivity of the water body more than an inherently higher trophic efficiency of tilapias.

Van der Mheen (1994) discusses practical aspects of stocking small water bodies with wild caught, mixed tilapia seed and also derives some empirical models to predict catches from stocking densities. Stocking of wild caught tilapia seed has been carried out on a large scale and with formal government support in e.g. in Zimbabwe, but such transfers are also common in rural areas of Asia, often on an entirely informal basis (Lorenzen pers. obs.).

Culture fisheries constitute an investment into fish stocks, often held in some form of common property. Such investment may precipitate changes in the access regime to, and exploitation of the fishery. In small water bodies in Laos for example, tilapia stocking appeared to facilitate the development of community management systems with active effort regulation. A comparative study by Lorenzen *et al.* (1998a) indicates that this management regime resulted in substantial standing stocks and yields of tilapias (based on a combination of regular stocking and natural recruitment), and also had a positive effect on the abundance of indigeneous stocks. The latter impact was unexpected and is rooted in changes to the exploitation regime precipitated by culture fisheries development. This illustrates that there is more to culture fisheries than stocking, and that prediction of outcomes of culture fisheries development requires an approach integrating the analysis of biological and institutional dynamics with a strong element of adaptive learning (Lorenzen and Garaway, 1998).

6.3.6 Dynamics and management of isolated cohorts

In commercial tilapia culture, reproduction is controlled as far as possible, and the different stages of the rearing cycle are separated in hatcheries, nurseries and grow-out (as is common in the culture of most non-tilapiine species). The isolated cohort is therefore the dominant population structure in commercial growout, and the management of such populations deserves explicit attention.

Annual yields from isolated cohorts can be in the same order as those from culture fisheries in extensive systems without fertilisation or feeding, but can be far higher in semi-intensive and intensive systems (see the respective chapters in this book). Empirical analyses of yield in relation to management inputs using multivariate statistical methods or multiple regression (Draper and Smith, 1981; Manly, 1994) can provide useful information for management without the need to obtain detailed data on population processes such as growth or mortality. In an analysis of commercial polyculture systems in Israel, Milstein (1995) shows that the highest yields are achieved in systems where tilapia (*O. niloticus* x *O. aureus* hybrids) is the main species, and also evaluated the relationship between input levels and yields.

Cohort growth and mortality models allow a more detailed evaluation of management options than empirical yield models, and are increasingly being used in bio-economic analyses of fish farms (for an introduction see Bjørndal, 1990). Springborn *et al.* (1992) used a population model based on the VBGF and an exponential mortality equation to predict the economically optimal harvesting time for *O. niloticus* cohorts in pond culture under two different fertilisation regimes. The two regimes analysed gave rise to very different growth patterns, with consequent large differences in the optimal harvesting time of 105 vs. 191 days. The analysis did not, however, account for the rotation problem: in order to maximise returns per unit time it is usually optimal to harvest before the time that maximises the production or profit from the individual cohort, because the cohort can be replaced them with faster growing young fish (see e.g. Bjørndal, 1990).

A constraint on the use of simple models such as the conventional VBGF and constant mortality is that the parameters for these models must be estimated separately from experiments for each different level of management inputs. It is therefore desirable to develop growth and possibly mortality models that incorporate explicit terms for management inputs. For example, the density-

dependent growth model and the mortality-weight relationship discussed in section 6.2 can be used to evaluate stocking density and size as well as harvesting regimes in extensive culture (Lorenzen, 1995; Lorenzen *et al.*, 1997). The multiple regression models of fish growth described by Pauly *et al.* (1993) and Prein and Pauly (1993) allow analysis of a wide range of management impacts on growth, and may aid the improvement of semi-intensive and intensive husbandry systems. Prein (1993a,b) describe the application of these models to the analysis of tilapia growth in pond culture. For integrated farms in the Philippines, for example, the analysis showed positive effects of solar radiation, pond area, and manure loading rate, and negative effects of stocking density and early morning oxygen saturation on growth. Oxygen saturation was negatively correlated with pond productivity, and overall the positive effect of productivity overrides the negative effect of low morning oxygen saturation. This example illustrates the potential to derive useful generalisations from the analyses of experimental and commercial data using growth models that can account for management impacts. However, there are also potential pitfalls associated with the statistical design of experiments that have not been rigorously planned to provide data adequate for the purpose of model development (see e.g. Riley and Darmi, 1995).

The potential of population and related modelling approaches to aid planning, and substantially reduce the experimental effort required to improve culture systems, has not been fully appreciated among aquaculture practitioners. The further development of modelling approaches and a more rigorous application of statistical principles in experimental design and analysis (Riley and Darmi, 1995; Knud-Hansen, 1997) are likely to yield increasingly more useful and reliable generalisations. This will require an increasingly close collaboration between practitioners, experimentalists and modellers.

6.3.7 Controlling reproduction and “stunting” in culture

Although most commercial culture systems are designed to raise single, isolated cohorts, the tendency of tilapias to breed within a few months of stocking means that this ideal is not easily achieved. Reproduction can quickly turn fast growing single cohorts into dense populations dominated by small recruits, with consequent decline in the growth of stocked fish. The absolute production of such “stunted” pond populations may be extremely high, but there is often a lower limit to the size at which tilapias can be marketed profitably, and therefore “stunting” is considered a problem in commercial farms. However, uncontrolled reproduction in culture is not universally a problem: recent research shows that subsistence-oriented fish farmers may value reproduction as positive, and that markets for “undersized” tilapias exist and cater mainly for the poor (Little and Hulata this volume; Cheftel and Lorenzen 1999).

(a) Approaches to the problems of reproduction and “stunting”

Four different approaches to the problems arising from early maturation in cultured tilapias can be distinguished: (1) complete control of reproduction through culture of mono-sex or sterile populations; (2) stock or environmental manipulations aimed at delaying maturation; (3) the use physical means or predators to minimise survival of offspring; or (4) increased feeding to minimise the impact of recruits on the growth of the parent stock. Approach 1 is perhaps the most widely used in commercial culture of tilapias, and methods for the production of mono-sex stocks are discussed elsewhere in this book. Attempts at delaying maturation by means of stock or environmental manipulations (approach 2) have not so far been very successful (cf. section. 6.2.3),

and no such manipulations are routinely used in culture. Approach 3 is associated with two main methods: cage culture and predator stocking. While cage culture does not prevent breeding altogether, but the eggs are lost from the cage at the time spawning (Pagan-Font, 1975). Predator stocking is discussed in more detail below. Approach 4, increasing food supply to offset consumption by new recruits, is likely to be a widespread response by farmers, and has been shown to be potentially effective (De Graaf *et al.*, 1996). Although it has been argued that increased feeding exacerbates the underlying problem of early maturation and prolific breeding (e.g. Noakes and Balon 1982), experimental evidence reviewed in section 6.2.3 suggests that tilapias tend to respond to resource scarcity with increased relative allocation to reproduction, and that therefore reproductive traits are not very sensitive to manipulations of feed supply within the constraints set by practical fish culture. The economics of feeding decisions in this context are, however, intriguing, and worthy of further analysis.

(b) Predator-prey culture

A complex approach of particular interest in the context of population dynamics is the stocking of predators to control recruitment. This approach probably originated with the experiments of Swingle (1960), who extended his previous work on the creation of predator-prey systems in American farm ponds to tilapias. Predator stocking has since been practised and reported widely throughout the world (Dunseth and Bayne, 1978; McGinty, 1984, 1985; Bedavi, 1985; Ofori, 1988; El Gamal, 1992; Fisher and Grant, 1994; Lazard and Oswald, 1995; DeGraaf *et al.*, 1996). Predator stocking undoubtedly works well in principle, and the approach has often succeeded in producing market-size fish. However, careful selection of the species, size and number of predators stocked is essential to produce the desired results. If predators are too small, too few or feed on a wide spectrum of fish and invertebrate prey, recruitment control may be ineffective and stunting may result despite the presence of predators (Lazard and Oswald, 1995). Conversely, if predators are too large and numerous, they may decimate the stocked fish and cause loss of production. Predator stocking is thus complex, given that both the stocked tilapia and the predator grow in the course of the culture cycle and adequate size ratios and predation pressures must be maintained throughout the cycle. Some predators have themselves a tendency to reproduce and thus create a mixed-size predator population (e.g. Dunseth and Bayne, 1978). Even once these complexities have been mastered, the system remains sensitive to variations in the growth of either species, which may often be impossible to avoid. Overall this has given the predator approach to recruitment control the reputation to be somewhat unreliable, if effective in principle (Huet, 1978). The development of population models for predator-prey system in pond culture has great potential to advance the understanding and aid the management of such systems, as illustrated by Fisher and Grant's (1994) model of a Nile tilapia (*O. niloticus*)-tucunare (*Cichla ocellaris*) system.

Avian predators are often considered a nuisance if not a major problem by fish culturists. In the case of tilapia farming, these predators may contribute to limiting unwanted recruitment and therefore have a beneficial effect. This was suggested in a study by Ashkenazi and Yontov (1996), who argue that stocked fingerlings in the size range susceptible to heron predation are available in Israeli fish farms for only short period (six weeks), and that the largest part of heron predation occurs on unwanted recruits.

6.3.8 Tilapia as invaders

Originating from Africa, tilapias are now found in the tropical and sub-tropical regions of all continents. Two species, *O. mossambicus* and *O. niloticus*, in particular must be regarded as some of the most successful invaders among the fishes (Welcomme, 1988; FAO, 1998). The following, brief review of tilapias as invaders is structured according to the conceptual framework of Williamson (1996), recognising the attributes of arrival and establishment, spread, and equilibrium and effects.

(a) Arrival and establishment

Virtually all recent arrivals of tilapias in new habitats can be traced back to human importations, mostly for the purpose of fish culture but also for the enhancement of capture fisheries (Welcomme, 1988). Studies of insect, bird and mammalian introductions have shown the probability of establishment to be strongly related to the number of arrivals of that species in a habitat (Beirne, 1975; Newsome and Noble, 1986; Griffith *et al.*, 1989). Williamson (1996) postulates as a general rule that propagule pressure, the number of arrivals, has a strong influence on establishment success. Most tilapia introductions have been conducted on a large scale either through the establishment of breeding centres distributing fry to a large number of farms, or through extensive movement of live fry between countries. This implies widespread and repeated arrivals of tilapias in the geographic range where they have been introduced, and may account at least in part for the apparently high degree of success in establishment. There are also, however, cases where successful establishment has occurred following accidental releases, for example in Australia where the escape of aquarium fish is thought to be responsible for all invasions by *O. mossambicus* (Arthington and Bluehdorn, 1994).

A number of species characteristics have been suggested as possible predictors of invasion success and will be reviewed briefly in the context of tilapias: high rate of population growth, wide distribution in native habitat, and the existence of a “vacant niche” (Williamson, 1996). Tilapias are capable of achieving very high rates of population growth, due to the reproductive traits discussed in section 6.2.3. For populations to persist, equilibrium rates of population growth must equal mortality rates, and both are related to body size (Beverton and Holt, 1959; Fenchel, 1974; Pauly, 1980; Lorenzen, 1996b). Analysing a large set of data on individual introductions, Pullin *et al.* (1997) showed that establishment success in fish was indeed inversely related to their maximum length. About 80% of introductions of fish with a maximum length of 10 cm lead to establishment, compared to only 40% in fish of 110 cm. Tilapias occupy an intermediate place in the maximum length range. The more commonly introduced tilapia species show establishment success rates between 60 and 95%, with the most successful being *O. mossambicus* at about 95%.

The most widely introduced tilapias, *O. mossambicus* and *O. niloticus*, are widely distributed in their native habitats (see e.g. Philippart and Ruwet, 1982), and thus conform to Williamson’s (1996) second above mentioned criterion for successful invaders.

Some tilapia introductions, particularly for fisheries enhancement, have been conducted to fill perceived “vacant niches” in aquatic ecosystems (Fernando and Holcik, 1991; Coates, 1993). The concept of the “vacant niche” itself has been the subject of controversy. Herbold and Moyle (1986) have argued that the concept was fundamentally flawed, because the niche is a property of

the organism, not the ecosystem and a niche can not therefore be vacant. Instead, they argued that introductions invariably compress the realised niches of existing species. While this is true in principle, many ecologists find the “vacant niche” concept useful and apply a slightly different, if possibly less rigorous definition. Williamson (1996) summarises this view as “a species occupying a vacant niche is one that plays an entirely new functional role in a community, not one that does not use any resources previously used by other species”. In fisheries ecology, a similarly broad but more explicitly utilitarian definition has been used. Fernando and Holcik (1991) and Coates (1993) identify “vacant niches” in Sri Lankan reservoirs and the Sepik river system (Papua New Guinea) using two criteria: a comparatively low fish yield, and a relatively low diversity of indigenous species due to the absence of truly lacustrine species in Sri Lanka, and the generally low number of freshwater species in the geologically young Sepik-Ramu basin. Introductions of tilapias in these systems where “vacant niches” had been identified have indeed led to successful establishment.

Tilapias have invaded highly diverse fish communities such as that of lake Victoria (Twongo, 1995), as well as low-diversity communities in river systems of New Guinea and Australia (Coates, 1993; Arthington and Bluehdorn, 1994). This seems to suggest that the invasibility of communities by tilapias is not strongly related to diversity, although no quantitative assessment has been conducted. The question whether communities differ in their invasibility has generated much ecological debate, but the overall conclusion appears to be that there is no relation (Williamson, 1996), and this is consistent with observations on tilapias.

(b) Spread

The spread of tilapias within a habitat has rarely been monitored, and the patterns of natural spread may be difficult to disentangle from those linked to repeated arrivals. An exception is the spread of *O. mossambicus* through the Gascoyne river system of Western Australia: the species is believed to have been released accidentally near the mouth of the river, and has colonised the approximately 500 mile long river system within ten years (Arthington and Bluehdorn, 1994).

(c) Equilibrium and effects

The “equilibrium” state and effects of fish introductions must be evaluated in terms of both, the fishery and the wider ecosystem. Many tilapia introductions (particularly of *O. mossambicus* and *O. niloticus*) have led to the development of commercial fisheries (De Silva 1988; De Silva and Senaratne, 1988; Fernando and Holcik, 1991; Sreenivasan, 1991; Coates, 1993; Muchiri *et al.*, 1995; Twongo, 1995). Increases in commercial yields and the rapid expansion of some commercial fisheries following tilapia introductions (e.g. De Silva 1988) may be regarded as indicators of the economic success of introductions. However, increases in commercial fish yields may greatly overestimate ecological production benefits from introductions: in a Sri Lankan reservoir for example, the introduced tilapias accounted for over 80% of the commercial yield, but barely 10% of the ecological fish production (Pet *et al.* 1996a). Due to its tendency to form dense, stunted populations *O. mossambicus* is regarded as a pest in many of the countries where it was intentionally introduced (Welcomme, 1988), but this view is by no means universal (De Silva and Senaratne, 1988).

The major ecological impacts of fish species introductions may involve genetic effects such as hybridisation with indigenous species or between exotic species and strains, habitat alterations, competition, predation and the introduction of exotic parasites and pathogens (Courtenay and Stauffer, 1984; Moyle *et al.*, 1986; Arthington, 1991; Carvalho and Hauser, 1995). Hybridisation may occur between closely related species, and is therefore most likely in habitats that already contain endemic or previously introduced tilapias. Ogutu-Ohwayo and Hecky (1991) suggest that hybridisation with introduced species was at least partly responsible for the disappearances of *O. spilurus* from Lake Naivasha, and *O. esculentus* and *O. variabilis* from Lake Victoria. However, in the absence of genetic investigations, the relative importance of hybridisation and competition is difficult to ascertain. Hybridisation is also common between *O. mossambicus* and *O. niloticus* where both species have been introduced (Amarasinghe and De Silva, 1996).

Habitat alterations and competition are key mechanisms by which some introduced tilapias have compressed the realised niches of existing species. Habitat alterations by tilapia have been reported primarily for the macrophytophagous *O. aureus*, *T. rendalli* and *T. zillii*, which have sometimes proved highly destructive to established vegetation (Philippart and Ruwet, 1982). Competition for spawning habitat has been reported between introduced *T. zillii* and the endemic *O. variabilis* in Lake Victoria, to the detriment of the latter (Welcomme, 1988).

A survey of perceived impacts of *O. niloticus* introductions in several Asian countries suggests no overly destructive effects (Pullin *et al.*, 1997). However, there is surprisingly little reliable information on ecological impacts of tilapia introductions other than those in the African lakes. Ecological impacts of introductions are often difficult to assess due to a lack of pre-introduction data and the effects of confounding factors. This problem can be overcome through spatially replicated studies, particularly in small and medium sized water bodies where sufficient replicates and controls can usually be identified. This approach was used by Lorenzen *et al.* (1998a) to assess the effects of tilapia stocking and fishing restrictions on small water body fisheries in Laos. The combination of *O. niloticus* stocking and fishing restrictions significantly increased total standing stocks, while *O. niloticus* stocking in itself had no impact on the standing stocks of wild fish. Possible effects of *O. niloticus* stocking on wild fish diversity could not be assessed conclusively, due to a high degree of variation between replicates. Further studies with larger numbers of replicates are urgently required to provide solid baseline data on the ecological effects of the most widely introduced tilapias.

It is now widely accepted that proposals for fish introductions should be evaluated very carefully, particularly where new introductions into a watershed are concerned (it may be rather impractical, at least in developing countries, to evaluate every single transfer within a watershed!). Coates (1998) reviews experiences with the use of codes of practice for introduction proposals. An example of the application of the EIFAC/ICES code of practice for introductions (Turner, 1988) is the evaluation of introductions to the Sepik River basin in Papua New Guinea (Coates, 1993; 1995).

6.4 LIFE HISTORY VARIATION AND “STUNTING”

The tilapias display considerable variation in life-history traits between species, between populations of the same species, and between individuals within populations. Variation in individual traits has been explored in section 6.2. The present section focuses on relationships between life history traits, illustrating at first the existence of some broad patterns of symmetry in tilapia life histories, before considering the nature of “stunting”, and finally outlining approaches towards a quantitative understanding and prediction of life history variation.

6.4.1 Tilapia life history variation

Relationships between life history traits arise because of fitness trade-offs. In the fishes, such relationships have been analysed extensively using both, comparative empirical approaches and theoretical optimality models (e.g. Beverton and Holt, 1959; Roff, 1992; Beverton, 1992; Charnov, 1993; Mangel, 1996). The aims of these studies were both theoretical and practical: to understand the evolution of life histories, and to establish relationships that can be used to estimate population parameters that are difficult to measure (e.g. the natural mortality rate M) from more easily measured parameters (e.g. asymptotic length) (e.g. Pauly 1980).

Most empirical studies have been conducted on populations close to their natural, undisturbed (unexploited) state in order to relate life history patterns to the conditions under which they have evolved through natural selection (Beverton, 1992). The empirical analysis of life history patterns in populations that have undergone recent changes in mortality or other environmental factors is complicated by the fact that observed patterns reflect immediate phenotypic responses within the genetic constraints shaped over evolutionary time scales. Such is the case in the following exploration of tilapia life histories, because most data are from populations that are heavily exploited and/or have only recently been introduced into new habitats. Moreover, information on mortality rates is limited to total mortality.

Some relationships between life history parameters among the tilapia populations included in Table 6.1 are explored in Fig. 6.11. Note logarithmic scales on both axes. Power relationships of the form $\log Y = \beta_0 + \beta_1 \log X$ have been estimated using non-parametric (Theil) regression; relationships with exponents β_1 of 1 or -1 imply proportional or inversely proportional relationships between the untransformed variables. There is a significant and approximately linear (β_1 not significantly different from 1) relationship between L_m and L_∞ (Fig. 6.11(a)). Although there is an apparent tendency for K to decline with increasing L_4 , the relationship is not significant (Fig. 6.11(b)). The relationship between K and Z is significant and positive, but a slope β_1 significantly less than 1 indicates a non-linear relationship, with K increasing less than in proportion to Z (Fig. 6.11(c)). Age at maturity A_m is inversely related to Z (β_1 not significantly different from -1 , Fig. 6.11(d)). These patterns are broadly consistent with patterns of symmetry known as the “Beverton and Holt invariants” (Charnov 1993), which have been found to exist in many taxonomic groups of fishes (Beverton and Holt, 1959; Beverton, 1992; Charnov, 1993) and have been investigated theoretically by Charnov (1993), Mangel (1996), and Jensen (1996). The invariants are: the ratio between length at maturity and asymptotic length ($L_m/L_\infty=C_1$), the ratio between natural mortality and VBGF growth rate K ($M/K=C_2$); and age at maturity A_m is inversely proportional to the adult natural mortality rate M ($A_m M=C_3$). The L_m/L_∞ and $A_m M$ invariants appear to hold in exploited tilapia populations (substituting Z for M), although it will be

shown later that L_m/L_∞ is not strictly speaking an invariant, but depends strongly on Z . The M/K invariant does not hold for total mortality in exploited populations, because K does not increase as strongly with Z mortality as would be expected from comparative studies of unexploited populations or ultimate life history models.

[Figure 6.11 about here]

6.4.2 “Stunting”

“To stunt”, according to Chamber’s Twentieth Century Dictionary, means “to hinder for growth, dwarf”. By definition, therefore, “stunted” fish populations are made up of individuals that are small relative to their conspecifics elsewhere. “Stunting” is a common phenomenon in freshwater fish and has been studied extensively for more than fifty years, but its mechanisms are still poorly understood. Unfortunately, studies on the “stunting” of tilapias have been little informed by the work conducted on other populations of freshwater fish, or by comparative studies on larger sets of tilapia life history data. This has led to the perception that stunting in tilapias is a special or even unique phenomenon, and given rise to some misleading interpretations. Iles (1973) suggested that tilapia stunting may be understood as a unique response to conditions of high mortality, and identified early maturation was key mechanism responsible for stunting. He further suggested that stunted populations were characterized by early maturation at a small size even relative to the asymptotic size, and consequently identified the L_m/L_∞ ratio as an indicator of “stunting” (with values below 0.7 characterizing a “stunted” population). However, the following review shows that (a) the patterns of stunting in tilapias are not unlike those found in other species, and that (b) different life histories may be associated with the “stunting”, and the phenomenon can not be interpreted simply as a response to high mortality rates.

(a) Life history variation within species

The data assembled in Table 6.1 contain sufficient information on life history variation in *O. mossambicus* to merit an exploratory analysis of “stunting” in this species. The relationship between L_m and L_∞ is shown in Fig. 6.12(a), where the solid line indicates the median L_m/L_∞ ratio of 0.54. The populations represent a wide range of L_m and L_∞ . Overall, L_m and L_∞ are correlated, and there is no obvious relationship between L_∞ and the ratio of L_m/L_∞ : “stunted” populations with a L_∞ below 300 mm show a similar range of L_m/L_∞ values as those growing to 400 mm or more. Hence the L_m/L_∞ ratio is not an indicator of “stunting”. However, both the L_m/L_∞ ratio and the age at maturity A_m do decline with increasing total mortality rate (Fig. 6.12(b),(c)), as predicted by Iles (1973) and more recent life history models (see Roff, 1992). A better understanding of the responses involved can be obtained by looking separately at the relationships of L_m and L_∞ to Z separately (rather than their ratio). As shown in Fig. 6.12(d), L_m declines slightly with increasing Z , but there is also an apparently more pronounced increase in L_∞ . Hence the decline in L_m/L_∞ with Z reflects primarily an increase in growth combined with a decline in and A_m . This shows that L_m/L_∞ ratios can not be understood in terms of plasticity of L_m alone, but must be considered in context of two highly plastic life history traits. Further comparative analyses of tilapia life histories are required in order to assess whether the patterns apparent in the limited set of *O. mossambicus* data are generalisable. It is interesting to note, however, that the patterns

are not inconsistent with responses to exploitation observed in marine fish stocks. In a comparative study of 77 stocks, Rochet (1998) concludes that exploitation leads to earlier age and increased size at maturity.

[Figure 6.12 about here]

The occurrence of stunted populations has been reported for many families of fish other than the chichlids, for example percids (Eschmeyer, 1936; Alm, 1946; Jansen, 1996), cyprinids (Burrough and Kennedy, 1979; Linfield, 1979; Piironen and Holopainen, 1988; Holopainen *et al.*, 1997), coregonids (Healey, 1980; Ridgeway and Chapleau, 1994), salmonids (Alm, 1959; Leggett and Power, 1969; Hindar and Jonsson, 1982; Donald and Alger, 1989; Amundsen *et al.*, 1993). Alm (1959) pointed out that the low maximum size characteristic of stunted populations may be combined with either early (see also e.g. Ridgeway and Chapleau, 1994; Jansen, 1996; Doyon *et al.*, 1998), or late maturation (see also e.g. Donald and Alger, 1989). The same is true for tilapias: while the occurrence of early maturation has been widely reported (e.g. in Iles 1973), there are also examples of stunted populations where maturation appears to be delayed or suppressed, e.g. in Silliman (1975) or Eyeson (1983). Note that the populations in the latter studies were also characterized by comparatively high L_m/L_{∞} ratios (Table 6.1). Stunted populations are characterized by a low maximum size and will necessarily show a low absolute size at maturity as well, even if maturity is delayed relative to “normal” populations. The relationship between “stunting” and mortality is complex. Stunted populations may be characterized by reduced longevity (i.e. higher mortality) compared to non-stunted populations of the same species (Roff, 1992; Jansen, 1996). This increased mortality suffered by some “stunted” populations may well be a consequence of “stunting” and size-dependent mortality, rather than a cause of “stunting”. Further increases in mortality through experimental exploitation have often been shown to increase growth and “rehabilitate” stunted populations (Donald and Alger, 1989; Amundsen *et al.*, 1993).

If the patterns of life history variation and “stunting” in tilapias are not substantially different from those exhibited by other species, is the degree of variation exceptionally great? Table 6.2 summarises the coefficients of variation of asymptotic length, length at maturity and their ratio for populations of *O. mossambicus* and *O. niloticus*, as well as for four non-tilapiines, herring (*Clupea harengus*), cod (*Gadus morhua*), walleye (*Stizostedion vitreum*) and lake trout (*Salvelinus namaycush*). The tilapiines do indeed show relatively high degree of life history variation, which is however on par with that found in cod and walleye. It appears, then, that tilapia life history variation is neither qualitatively nor quantitatively unique.

(b) Phenotypic response or genetic selection?

It has already been established in section 6.2 that the growth and reproductive traits implicated in “stunting” are highly plastic, and this suggests that tilapia “stunting” is also primarily a phenotypic response. This conclusion is further supported by the rapid emergence of “stunted” phenotypes following isolation of sub-populations from non-stunted populations (e.g. Welcomme, 1970). Also, a transfer experiment (Duponchelle *et al.*, 1998) and a population genetics study (Bluehdorn and Arthington, 1990) failed to provide evidence for genetic differentiation between “stunted” and “normal” populations of tilapias.

Many studies on “stunting” in other species have likewise pointed to a phenotypic response, reversible by experimental manipulations such as transfers or reductions in density (e.g. Heath and Roff 1987; Donald and Alger, 1989; Amundsen *et al.*, 1993). However, there are also examples where a degree of genetic differentiation is apparent (Svedaeng, 1990; Taylor and Bentzen 1993; Szczerbowski *et al.*, 1997). Genetic differentiation is likely to occur when “stunted” and “normal” forms persists in isolation for prolonged periods of time. Hence the occurrence of genetic differentiation between the life history forms is likely to reflect local conditions more than a property of particular species.

(c) Environmental characteristics associated with “stunting”

A survey of the literature points to certain environmental conditions that are often associated with “stunting”, even though the phenomenon itself is not identified with a uniform life history strategy. The conditions that seem most regularly associated with stunting in tilapias and in other fishes are: small water bodies, isolated populations, and a low diversity of the local fish community. None of these conditions necessarily lead to stunting, they merely characterise situations where stunting is likely to occur and may aid the identification of underlying mechanism.

The association of “stunting” with small water bodies has often been made in the literature on tilapias as well as other species (see e.g. this chapter for tilapias; Holopainen *et al.*, 1997 for crucian carp). Many records of stunted populations are from ponds or small lakes (e.g. Pechlaner, 1984; Ridgeway and Chapleau, 1994; Holopainen *et al.*, 1997). However, not all populations of species known to “stunt” necessarily do so in small water bodies: there are examples of “stunted” and “normal” populations of the same species in water bodies of similar size, or even the same water body (e.g. Fenderson, 1964; Doyon *et al.*, 1998). Neither is the occurrence of “stunting” limited to the smallest of water bodies: “stunted” populations have been reported from lakes of more than 1000 ha area (e.g. Amundsen, 1988; Amundsen *et al.*, 1993), although “stunting” in such large lakes tends to be less severe than in smaller water bodies.

Isolation of a population is a factor that often coincides with its occurrence in a small water body. However, there are situations where isolation can be identified as a key factor in its own right, for example in landlocked populations of anadromous species such as salmon (e.g. Leggett and Power, 1969; Gibson *et al.*, 1996). There is an obvious similarity between isolation in anadromous species and populations in small water bodies in that in both cases, fish are prevented from migrating into open waters to escape the intense competition characteristic of shallow littoral areas (Hanson and Leggett, 1985), or extremes of physical conditions. However, isolated populations may also show “normal” growth patterns, either naturally or in response to experimental exploitation (see e.g. Pechlaner, 1984; Donald and Alger, 1989).

Another factor often associated with stunting is a low diversity of the resident fish community, sometimes to the extent that the “community” is monospecific (Welcomme, 1970; Johnson, 1983; Ridgeway and Chapleau, 1994; Holopainen *et al.*, 1997). A low diversity is in itself a characteristic of small water bodies (e.g. Minns, 1989), and the independent significance of this factor is therefore not easy to assess. A very low diversity is certainly not a necessary condition for “stunting”, as the occurrence of “stunted” populations in lakes of moderate diversity shows (e.g. Heath and Roff, 1996).

(d) Conclusion

The term “stunting” has long been used, and will likely continue to be used as a descriptor of populations characterised by a low maximum size. However, “stunting” is not identified with a particular life history strategy, but rather describes a variety of life histories united in but one trait: a low maximum size. The perception that stunting in tilapias is unique and does represent a particular life history strategy (Iles, 1973; Noakes and Balon, 1982) is not borne out in a comparative perspective. The “stunting indicator” proposed in this context, the L_m/L_{∞} ratio, is unrelated to “stunting” as it is commonly understood (as a low L_{∞}). Use of this indicator is, in fact, misleading as the following examples illustrate. Mattson and Kaunda (1997) compared two populations of *O. shiranus* in small waterbodies, with L_m/L_{∞} ratios of 0.59 and 0.48 (see also Table 6.1). While the indicator would suggest that the latter population was the more “stunted”, it was actually characterised by much higher growth and overall productivity than the former. Another example is given by the two *S. melanotheron* populations included in Table 6.1. The tank population (Eyeson, 1983) with an L_{∞} of 86 mm is clearly “stunted”, but its L_m/L_{∞} ratio of 0.58 is far higher than the value of 0.37 found in the larger growing ($L_{\infty} = 161$ mm) lagoon population. In both these examples, as in the *O. mossambicus* data explored before, L_m varied less between populations than L_{∞} .

If “stunting” is not synonymous with a particular life history strategy, but rather a collective descriptor for a variety of strategies, then it is unlikely that “stunting” can be understood in terms of a single factor such as “a high mortality rate”. As discussed elsewhere in this chapter, such “blanket” explanations appear to fail even when “stunting” is re-defined to describe a particular life history strategy or individual trait. The problem is thus one of understanding life history plasticity in general, rather than the ill-defined phenomenon of “stunting”. This is likely to require a far more detailed analysis of responses in individual traits and their interactions than has so far been attempted in the search of explanations for “stunting”.

6.4.3 Towards a mechanistic understanding of life history plasticity

There is little doubt that the remarkable life history plasticity of tilapias is the legacy of their evolution in variable habitats (Lowe-McConnell, 1982; Noakes and Balon, 1982). What is less clear, but of immense theoretical and practical importance, is the question: how is the expression of this plasticity controlled?

Examination of life history data from established tilapia populations shows patterns of symmetry consistent with ultimate considerations of life history theory, i.e. maximisation of some measure of fitness. However, an understanding the proximate basis life history plasticity, i.e. the mechanisms that animals use to achieve optimum life history patterns (Thorpe *et al.*, 1998) is required in order to manage this plasticity in cultured and exploited stocks. The challenge this involves is illustrated in the example of *O. mossambicus* life history plasticity discussed in section 6.4.2. Comparative examination of the data shows a decline in the L_m/L_{∞} ratio and in A_m with increasing Z , a pattern consistent with predictions from ultimate life history models for optimal age and size at maturity (e.g. Roff, 1992). However, this response involves plasticity in several traits (primarily an increase in L_4), which is difficult to accommodate with the common life history models predicting

optimal age and size at maturity from externally determined growth and mortality patterns (Roff, 1992; Stearns, 1992; but see Stamps *et al.*, 1998 for an alternative approach). The problem is that there are several highly plastic traits, and it is not clear *a priori* which of these traits would respond and to what extent. This problem can not be solved by re-writing ultimate models, for example to predict optimal L_{∞} subject to L_m . A dynamic framework is required that allows to analyse and predict development paths on the basis of state dependent, proximate responses to environmental factors.

Such a dynamic framework must accommodate processes that are more or less continuous in nature (e.g. growth, mortality), as well as others that involve discrete “switches” (e.g. maturation, ontogenic shifts in habitat use). Continuous processes tend to be easier to understand and model, for example growth may be modelled on the basis of the acquisition of resources and their allocation to maintenance metabolism, somatic growth and reproduction. Processes involving switches are less well understood and more difficult to model. Perhaps the most promising approach is to interpret switches as determined by the organism’s present physiological state and rate of change, in relation to a genetically determined threshold (Roff, 1996; Thorpe *et al.*, 1998). Thorpe *et al.* (1998) have used this approach in the development of a first, proximate life history model to predict quantitatively the occurrence of smolting and maturation in Atlantic salmon.

A comparative analysis of the wealth of information now available from field studies on tilapia populations could generate a matrix of conditions associated with alternative life histories, which may be used to test the predictions from proximate models. Much of the detailed information on state-dependent responses in development paths required to construct such models in the first place, however, will have to be gained from experimentally manipulated populations, not least in aquaculture.

6.5 CONCLUDING REMARKS

Tilapia populations are being exploited and otherwise manipulated in an extraordinarily wide range of habitats, and have been studied extensively under a wide range of conditions. This has resulted in a wealth of information pertinent to their population dynamics and life histories, the significance of which is most fully appreciated in a comparative perspective integrating across wild and cultured populations. This chapter aims to develop such an integrated perspective, but much remains to be done.

The analysis of growth and reproductive traits has shown a high degree phenotypic plasticity in both. The mechanisms governing plasticity in growth are relatively well understood at least in qualitative terms, and through a set of different but largely complementary quantitative models. By contrast, little is known about the mechanisms governing plasticity in reproductive traits, and the existing hypotheses are either inconsistent with the data or too loosely defined to be of real value. Recent developments in evolutionary ecology, analysing maturation in terms of the organism’s status relative to genetically defined thresholds, may be promising to explore. Patterns of mortality have been relatively little explored, in spite of their importance to management, ecology and evolution.

Population dynamics approaches have substantial potential to aid the management of wild as well as farmed tilapia stocks, as illustrated in a range of examples throughout this chapter. This

potential has not been realised as much as it deserves to be, but it is hoped that this chapter will provide a new impetus. Many of the approaches and methods discussed are easily transferable. However, most of the studies reviewed use conventional stock assessment models, which do not account for the plasticity of life history traits found in the tilapias (as well as many other species of fish). This indicates a need to develop new approaches that can account for such plasticity, particularly in the assessment of management strategies for populations that can be subjected to a high level of manipulation. Density-dependent growth appears to be a particularly pervasive aspect of plasticity, and is relatively easy to incorporate into assessment models.

“Stunting” in tilapias is a reflection of the plasticity in life history traits already discussed. However, “stunting” in tilapias is neither qualitatively nor quantitatively unique: similar patterns are found in many species of freshwater fish. “Stunting” is a collective term applied to a variety of life history forms characterised by a common trait, a low maximum size. The variety of life histories associated with a low maximum size and of the underlying causes for their expression defies a simple definition and causal explanation. In particular, the widespread use of the L_m/L_∞ ratio as stunting indicator in tilapias is misleading and should be abandoned. While “stunting” may be used as a descriptor of populations characterised by a low maximum size, an understanding of the underlying mechanisms will most likely emerge from an appreciation of the underlying variety of life histories. Understanding the proximate causes of life history variation is perhaps the greatest challenge in tilapia population biology. This understanding will most likely emerge from a combination of quantitative modelling with laboratory and field experiments: it will rely on a close integration of the study of wild and farmed stocks, and ultimately benefit the management of both.

Comparative information suggests that life history variation in tilapias is not as unique as it has often been considered to be, and this implies that tilapias may serve as useful model to explore life history plasticity in fish in general.

ACKNOWLEDGEMENTS

Comments on a draft version of this chapter by Malcolm Beveridge, Marc Mangel, Sampsa Vilhunen and Robin Welcomme have substantially improved the manuscript. Needless to say, the author takes full responsibility for any remaining errors of fact or interpretation. Work on this chapter was partially supported by the by the Nuffield Foundation (NUF-NAL), and by the UK Department for International Development (DFID, Fisheries Management Science Programme). The views expressed are not necessarily those of the DFID.

REFERENCES

- AIT (1990). Assessment and trial of alternative feed options for project fry nursing recommendations in nylon hapas. *AIT Aquaculture Outreach Report*.
- Alimoso, S.B. (1991) Catch effort data and their use in the management of fisheries in Malawi, in *Catch Effort Sampling Strategies*, (ed. I.G. Cowx), Fishing News Books, Oxford, pp. 393-403.
- Alm, G. (1946) Reasons for the occurrence of stunted fish populations. *Reports of the Institute of Freshwater Research Drottningholm* **25**, 1-146.
- Alm, G. (1959) Connection between maturity, size and age in fishes. *Reports of the Institute of Freshwater Research Drottningholm* **40**, 1-145.
- Amarasinghe, U.S. (1996) Stock assessment in Sri Lankan reservoirs, in *Stock Assessment in Inland Fisheries* (ed. I.G. Cowx), Fishing News Books, Oxford, pp. 345-356.
- Amarasinghe, U.S. and De Silva, S.S. (1992) Population dynamics of *Oreochromis mossambicus* and *O. niloticus* (Cichlidae) in two reservoirs in Sri Lanka. *Asian Fisheries Science* **5**, 37-61.
- Amarasinghe, U.S. and De Silva, S.S. (1996) Impact of *Oreochromis mossambicus* x *O. niloticus* (Pisces: Cichlidae) hybridisation on population reproductive potential and long-term influence on a reservoir fishery. *Fisheries Management and Ecology* **3**, 239-250.
- Amundsen, P.A. (1988) Effects of an intensive fishing programme on age structure, growth and parasite infection of stunted whitefish (*Coregonus lavaretus* L.) in Lake Stuorajarvi, northern Norway. *Finnish Fisheries Research* **9**, 425-434.
- Amundsen, P.A., Klemetsen, A. and Grotnes, P.E. (1993) Rehabilitation of a stunted population of Arctic char by intensive fishing. *North American Journal of Fisheries Management* **13**, 483-491.
- Arthington, A.H. (1991) Ecological and genetic impacts of introduced and translocated freshwater fishes in Australia. *Canadian Journal of Fisheries and Aquatic Sciences* **48** (Supplement 1), 33-43.
- Arthington, A.H. and Bluehdorn, D.R. (1994) Distribution, genetics, ecology and status of the introduced cichlid, *Oreochromis mossambicus*, in Australia. *Mitteilungen des Internationalen Vereins fuer Limnologie* **24**, 53-62.
- Ashkenazi, S. and Yomtov, Y. (1996) Herons and fish farming in the Huleh valley, Israel - conflict or mutual benefit? *Colonial Waterbirds* **19**, 143-151.
- Baerends, G.R. and Baerends-Van Roon, J.M. (1950) An introduction to the study of ethology of cichlid fishes. *Behaviour*, Supplement 1, 1-242.

- Bagenal, T.B. (1969) The relationship between food supply and fecundity in brown trout *Salmo trutta* L. *Journal of Fish Biology* **1**, 167-182.
- Bedavi, R.M. (1985) Recruitment control and production of market-size *Oreochromis niloticus* with predator *Lates niloticus* in Sudan. *Journal of Fish Biology* **26**, 459-464.
- Beirne, B.P. (1975) Biological control attempts by introductions against pest insects in the field in Canada. *Canadian Entomologist* **107**, 225-236.
- Beverton, R.J.H. (1992) Patterns of reproductive strategy and parameters in some marine teleost fishes. *Journal of Fish Biology* **41** (Supplement B), 136-160.
- Beverton, R.J.H. and Holt, S.J. (1957) On the dynamics of exploited fish populations. Fishery Investigations, Series II. Ministry of Agriculture, Fisheries and Food. HMSO, London.
- Beverton, R.J.H. and Holt, S.J. (1959) A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics, in *Ciba Foundation Colloquia on Ageing*, Vol. 5, (ed. G.E.W. Wolstenholme and M. O'Connor), Churchill, London, pp. 142-177.
- Bjorndal, T. (1990) *The Economics of Salmon Aquaculture*. Blackwell, London.
- Blay, J. and Asabere-Ameyaw, E. (1993) Assessment of the fishery of a stunted population of the cichlid, *Sarotherodon melanotheron* (Rueppel), in a Aclosed@ lagoon in Ghana. *Journal of Applied Ichthyology* **9**, 1-11.
- Bluehdorn, D.R and Arthington, A. (1990) The incidence of stunting in Australian populations of the introduced Cichlid *Oreochromis mossambicus* (Peters), in *The Second Asian Fisheries Forum* (eds. R. Hirano and I Hanyu). Asian Fisheries Society, Manila, pp. 41-44.
- Bolivar, R.B., Eknath, A.E., Bolivar, H.L. and Abella, T.A. (1993) Growth and reproduction in individually tagged Nile tilapia (*Oreochromis niloticus*) of different strains. *Aquaculture* **111**, 159-169.
- Bowen, S.H. (1979) A nutritional constraint on detritivory by fishes: the stunted population of *Sarotherodon mossambicus* in Lake Sibaya, South Africa. *Ecological Monographs* **49**, 17-31.
- Bramick, U., Puckhaber, B., Langholz, H.J. and Horstgen-Schwank, G. (1995) Testing of triploid tilapia (*Oreochromis niloticus*) under tropical pond conditions. *Aquaculture* **137**, 343-352.
- Brummett R.E. (1995) Environmental regulation of sexual maturation and reproduction in tilapia. *Reviews in Fisheries Science* **3**, 231-248.
- Burrough, R.J. and Kennedy, C.R. (1979) The occurrence and natural alleviation of stunting in a population of roach, *Rutilus rutilus* (L.). *Journal of Fish Biology* **15**, 93-109.
- Carvalho, G.R. and Hauser, L. (1995) Genetic impacts of fish introductions: a perspective on

African lakes, in: *The Impact of Species Changes in African Lakes* (eds. T.J. Pitcher and P.J.B. Hart). Chapman and Hall, London, pp. 457-493.

Charnov, E.L. (1993) *Life History Invariants*, Oxford University Press, Oxford.

Cheftel, J. and Lorenzen, K. (1999) An appraisal of the potential uptake of genetically male tilapia by small-scale fish farmers in Nueva Ecija, Central Luzon, Philippines. Research Report, Huxley School, Imperial College, London. 86 pp.

Chen, F.Y. and Prowse G.A. (1964) The effect of living space on the growth rate of fishes. *Ichthyologica* **3**, 11-20.

Christensen, V. and Pauly, D. (eds.) (1993) *Trophic Models of Aquatic Ecosystems*, ICLARM, Manila.

Coates, D. (1993) Environmental management implications of aquatic species introductions: a case study of fish introductions into the Sepik-Ramu Basin, Papua, New Guinea. *Asian Journal of Environmental Management* **1**, 39-49.

Coates, D. (1995) Implementing the EIFAC/ICES code of practice: experiences with the evaluation of international fish transfers into the Sepik River Basin, Papua New Guinea, in *Proceedings of the World Fisheries Congress* (ed. C. W. Voigtlander). Oxford and IBH Publishing, New Delhi. pp. 159-173.

Coates, D. (1998) Codes of practice for the stocking and introduction of fish, in *Stocking and Introduction of Fish*. (ed. I.G. Cowx). Fishing News Books, Oxford. pp. 383-396.

Colby, P.J. and Nepszy, S.J. (1981) Variations among stocks of walleye (*Stizostedion vitreum vitreum*): management implications. *Canadian Journal of Fisheries and Aquatic Science* **38**, 1814-1822.

Colby, P.J., McNicol, R.E. and Ryder, R.A. (1979) Synopsis of biological data on the walleye *Stizostedion v. vitreum* (Mitchell 1818). *FAO Fish Synopsis* **119**.

Costa-Pierce, B.A. & Hadikusumah, H.Y. (1990). Research on cage aquaculture systems in the Saguling Reservoir, West Java, Indonesia, in *Reservoir Fisheries and Aquaculture Development for Resettlement in Indonesia*, (ed. B.A. Costa-Pierce), ICLARM Technical Report 23, pp. 112-217.

Courtenay, W.R. and Stauffer, J.R. (eds.) (1984) *Distribution, Biology, and Management of Exotic Fishes*. Johns Hopkins University Press, Baltimore.

Coward, K. and Bromage, N.R. (1999) Spawning frequency, fecundity, egg size and ovarian histology in groups of *Tilapia zillii* maintained upon two distinct food ration sizes from first-feeding to sexual maturity. *Aquatic Living Resources* **12**, 11-22.

Coward, K., Bromage, N.R. and Little, D.C. (1998) Inhibition of spawning and associated

suppression of sex steroid levels during confinement in the substrate-spawning *Tilapia zillii*. *Journal of Fish Biology* **52**, 152-165.

Cowx, I.G. (1999) An appraisal of stocking strategies in the light of developing country constraints. *Fisheries Management and Ecology* **6**, 21-34.

Cridland, C.C. (1961) Laboratory experiments on the growth of *Tilapia* spp. The reproduction of *Tilapia esculenta* under artificial conditions. *Hydrobiologia* **18**, 177-184.

Cruz, E.M. & Ridha, M. (1991). Production of the tilapia *Oreochromis spilurus* Guenther stocked at different densities in sea cages. *Aquaculture* **99**, 95-103.

Day, T. and Taylor, P.D. (1997) Von Bertalanffy's equation should not be used to model age and size at maturity. *American Naturalist* **149**, 381-393.

DeAngelis, D.L. and Gross, L.J. (1992) (eds.) *Individual-based Models and Approaches in Ecology: Populations, Communities and Ecosystems*. Chapman and Hall, London.

DeGraaf, G., Galemoni, F. and Banzoussi, B (1996) Recruitment control of Nile tilapia, *Oreochromis niloticus*, by the African catfish, *Clarias gariepinus* (Burchell 1822), and the African snakehead, *Ophiocephalus obscuris*. 1. A biological analysis. *Aquaculture* **146**, 85-100.

De Silva, S.S. (1986) Reproductive biology of *Oreochromis mossambicus* populations of man-made lakes in Sri Lanka: a comparative study. *Aquaculture and Fisheries Management* **17**, 31-47.

De Silva, S.S. (1988) Reservoirs in Sri Lanka and their fisheries. *FAO Fisheries Technical Paper* **298**.

De Silva, S.S. and Senaratne, K.A.D.W (1988) *Oreochromis mossambicus* is not universally a nuisance species: the Sri Lankan experience, in *The Second International Symposium on Tilapia in Aquaculture* (eds. R.S.V. Pullin, T. Bhukaswan, K Tonguthai and J.L. MacLean), ICLARM, Manila, pp. 445-450.

De Silva, S.S. and Sirisena, H.K.G. (1987) New fish resources in Sri Lanka: feasibility of introduction of a subsidiary gillnet fishery for minor cyprinids. *Fisheries Research* **6**: 17-34.

Diana, J.S. (1997) Feeding strategies, in *Dynamics of Pond Aquaculture* (edited by H.S. Egna and C.E. Boyd), CRC, Boca Baton, pp. 245-262

Diana, J.S. & Lin, C.K. (1991). Tilapia and *Clarias* polyculture, in *Aquaculture/Pond Dynamics Collaborative Research Support Program: Ninth Annual Administrative Report*, Oregon State University, Corvallis, pp. 45-48.

Donald, D.B. and Alger, D.J. (1989) Evaluation of exploitation as a means of improving growth in a stunted population of brook trout. *North American Journal of Fisheries Management* **9**, 177-183.

- Doyon, J.F., Schetagne, R. and Verdon, R. (1998) Different mercury bioaccumulation rates between sympatric populations of dwarf and normal lake whitefish (*Coregonus clupeaformis*) in the La Grande complex watershed, James Bay, Quebec. *Biogeochemistry* **40**, 203-216.
- Draper, N.R. and Smith, H. (1981) *Applied Regression Analysis*, 2nd Edn., Wiley, New York.
- Dudley, R.G. (1974) Growth of *Tilapia* on the Kafue floodplain Zambia: predicted effects of the Kafue Gorge Dam. *Transactions of the American Fisheries Society* **103**, 281-291.
- Dunseth, D.R. and Bayne, D.R. (1978) Recruitment control and production of *Tilapia aurea* (Steindachner) with the predator *Cichlasoma managuense* (Guenther). *Aquaculture* **14**, 383-390.
- Duponchelle, F. and Panfili, J. (1998) Variations in age and size at maturity of female Nile tilapia, *Oreochromis niloticus*, populations from man-made lakes of Cote d'Ivoire. *Environmental Biology of Fishes* **52**, 453-465.
- Duponchelle, F., Pouyaud, L. and Legendre, M. (1998) Evidence of environmental effects on reproductive characteristics of Nile tilapia (*Oreochromis niloticus*) populations from man-made lakes of Ivory Coast. *Aquatic Living Resources* **11**, 137-144
- El Gamal, A.A. (1992) Predation by Nile perch *Lates niloticus* (L.) on *Oreochromis niloticus* (L.), *Cyprinus carpio* (L.), *Mugil* sp. and its role in controlling tilapia recruitment in Egypt. *Journal of Fish Biology* **40**, 351-358.
- Eknath, A.E., Tayamen, M.M. Palada-de Vera, M.S., Danting, J.C., Reyes, R.A. Dionisio, E.E., Capili, J.B., Bolivar, H.L., Abella, T.A., Circa, A.V., Bentsen, H.B., Gjerde, B., Gjedrem, T. and Pullin, R.S.V.P. (1993) Genetic improvement of farmed tilapias: the growth performance of eight strains of *Oreochromis niloticus* tested in different farm environments. *Aquaculture* **111**, 171-188.
- Ens, B.J., Weissing, F.J. and Drent, R.H. (1995) The despotic distribution and deferred maturity: two sides of the same coin. *American Naturalist* **146**, 625-650.
- Eschmeyer, R.W. (1936) Some characteristics of a population of stunted perch. *Michigan Academy of Science, Arts and Letters* **22**, 613-678.
- Eyeson, K.N. (1983) Stunting and reproduction in pond reared *Sarotherodon melanotheron*. *Aquaculture* **31**, 257-267.
- FAO (1993) Fisheries management in the south-east arm of Lake Malawi, the Upper Shire River and Lake Malombe, with particular reference to the fisheries on chambo (*Oreochromis* spp.) *CIFA Technical Paper* **21**. FAO, Rome.
- FAO (1998) Database on introductions of aquatic species. Accessible via the world wide web: <http://www.fao.org/WAICENT/FAOINFO/FISHERY/statist/fisoft/dias/index.htm>.

- Fenchel, T. (1974) Intrinsic rate of natural increase: the relationship with body size. *Oecologia* **14**, 317-326.
- Fenderson, O.C. (1964) Evidence of sub-populations of lake Whitefish, *Coregonus clupeaformis*, involving a dwarf form. *Transactions of the American Fisheries Society* **93**, 77-94.
- Fernandes, M.D and Volpatro, G.L. (1993) Heterogeneous growth in the Nile tilapia-social stress and carbohydrate-metabolism. *Physiology and Behaviour* **54**, 319-323.
- Fernando, C.H. and Holcik, J. (1991) Some impacts of fish introductions into tropical freshwaters, in *Ecology of Biological Invasions in the Tropics* (ed. P.S. Ramakrishnan), International Science Publications, New Delhi, pp. 103-129.
- Fisher, G.W. and Grant, W.E. (1994) Use of a native predator to control overcrowding in warm-water polyculture ponds: simulation of a tucunare (*Cichla monoculus*) - tilapia (*Oreochromis niloticus*) system. *Ecological Modelling* **72**, 205-227.
- Fryer, G. and Iles D.T. (1972) *The Cichlid Fishes of the Great Lakes of Africa*, Oliver and Boyd, Edinburgh.
- Garrod, D.J. (1959) The growth of *Tilapia esculenta* Graham in Lake Victoria. *Hydrobiologia* **12**, 268-298.
- Garrod, D.J. (1961) The selection characteristics of nylon gill nets to *T. esculenta* Graham. *Journal du Conseil Permanent International pour l'Exploration de la Mer* **26**, 191-203.
- Garrod, D.J. (1963) An estimation of the mortality rates in a population of *Tilapia esculenta* Graham (Pisces, Cichlidae) in Lake Victoria, East Africa. *Journal of the Fisheries Research Board of Canada* **20**, 195-227.
- Getabu, A. (1987) Aspects of Lake Victoria Fisheries with emphasis on *Oreochromis niloticus* and *Alestes sadleri* from Nyanza Gulf. *FAO Fisheries Report* **389**, 416-431.
- Gibson, R.J., Williams, D.D., McGowan, C. and Davidson, W.S. (1996) The ecology of dwarf fluvial Atlantic salmon, *Salmo salar* L., cohabiting with brook trout, *Salvelinus fontinalis* (Mitchill), in southeastern Newfoundland. *Polskie Archiwum Hydrobiologii* **43**, 145-168.
- Griffith, B., Scott, M.J., Carpenter, J.W., and Reed C. (1989) Translocation as a species conservation tool: status and strategy. *Science* **245**, 477-480.
- Gwahaba, J.J. (1973) Effects of fishing on the *Tilapia nilotica* population in L. George, Uganda, over the past twenty years. *East African Wildlife Journal* **11**, 317-328.
- Hanson, J.M. and Leggett, W.C. (1985) Experimental and field evidence for inter- and intraspecific competition in two freshwater fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 280-286.

- Harding, D. (1965) Research on Lake Kariba, 1962-1963. *Fisheries Research Bulletin Zambia* 1962/63, 38-55.
- Healy, M.C. (1980) Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. *Journal of the Fisheries Research Board of Canada* **37**, 255-267.
- Heath, D. and Roff, D.A. (1987) A test of genetic differentiation in growth of stunted and non-stunted populations of perch and pumpkinseed. *Transactions of the American Fisheries Society* **116**, 98-102.
- Heath, D.D and Roff, D.A. (1996) The role of trophic bottlenecks in stunting: a field test of an allocation model for growth and reproduction in yellow perch, *Perca flavescens*. *Environmental Biology of Fishes* **45**, 53-63.
- Hecht, T. and Zway, P. (1984) On the stunted Mocambique tilapia *Oreochromis mossambicus* (Peters, 1852) (Pisces: Cichlidae) of the Matiovila Hot Spring, Kruger National Park. *Koedoe* **27**, 25-38.
- Herbold, B. and Moyle, P.B. (1986) Introduced species and vacant niches. *American Naturalist* **128**, 751-760.
- Hickling, C.F. (1963) The cultivation of tilapia. *Scientific American* **208**, 143-152.
- Hilborn, R. and Walters, C.J. (1992) *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*, Chapman and Hall, London.
- Hilborn, R., and Mangel, M. (1997) *The ecological detective: confronting models with data*, Princeton University Press, Princeton.
- Hindar, K. and Jonsson, B. (1982) Habitat and food segregation of the dwarf and normal arctic char (*Salvelinus alpinus*) from Vangsvtnet Lake, Western Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **93**, 1030-1045.
- Holopainen, I. J., Tonn, W.M. and Paszkowski, C.A. (1997) Tales of two fish: the dichotomous biology of crucian carp (*Carassius carassius* (L.)) in nortyhern Europe. *Annales Zoologici Fennici* **34**, 1-22.
- Hopkins, K.D. and Pauly, D. (1993) Instantaneous mortalities and multivariate models: application to tilapia culture in saline waters, in *Multivariate Methods in Aquaculture Research: Case Studies of Tilapias in Experimental and Commercial Systems* (eds. M. Prein, G. Hulata and D. Pauly), ICLARM, Manila.
- Horstgen-Schwark, G. and Langholz, H.J. (1998) Prospects of selecting for late maturity in tilapia (*Oreochromis niloticus*) III. A selection experiment under laboratory conditions. *Aquaculture* **167**, 123-133.

- Huet, M. (1978) *Textbook of Fish Culture*. 2nd edn. Fishing News Books, Oxford.
- Iles, T.D. (1973) Dwarfing or stunting in the genus *Tilapia* (Cichlidae): a possibly unique recruitment mechanism. *Rapports et proces-verbaux de la Conseil International d'Exploration de la Mer* **164**, 247-254.
- Inland Fisheries Project (1977). *Progress Report* (Report No. 10). Diliman: College of Fisheries, University of the Philippines.
- Jalabert, B. and Zohar, Y. (1982) reproductive physiology in cichlid fishes, with particular reference to *Tilapia* and *Sarotherodon*, in *The Biology and Culture of Tilapias* (eds R.S.V. Pullin and R.H. Lowe-McConnell), ICLARM, Manila, 129-140.
- James, N.P.E. and Bruton, M.N. (1992) Alternative life-history traits associated with reproduction in *Oreochromis mossambicus* (Pisces: Cichlidae) in small water bodies of the eastern Cape, South Africa. *Environmental Biology of Fishes* **34**, 379-392.
- Jansen, W.A. (1996) Plasticity of maturity and fecundity of yellow perch, *Perca flavescens* (Mitchill): comparison of stunted and normal-growing populations. *Annales Zoologici Fennici* **33**, 403-415.
- Jensen, A.L. (1996) Beverton and Holt life history invariants result from optimal trade-offs of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 820-822.
- Jensen, A.L. (1997) Origin of the relation between K and L_{inf} and synthesis of relations among life history parameters. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 987-989.
- Johnson, L. (1983) Homeostatic characteristics of single species fish stocks in Arctic lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **40**, 987-1024.
- Kapetsky, J.M. (1974) Growth, mortality, and reproduction of five fish species of the Kafue River floodplain, Zambia. PhD Thesis, University of Michigan.
- King, M. (1985) *Fisheries Biology, Assessment and Management*, Fishing News Books, Oxford.
- Knut-Hansen, C.F. (1997) Experimental design and analysis in aquaculture, in *Dynamics of Pond Aquaculture* (eds. H.S. Egna and C.E. Boyd), CRC Press, Boca Baton, pp. 325-376.
- Kolding, J. (1993) Population dynamics and life-history styles of Nile tilapia, *Oreochromis niloticus*, in Ferguson's Gulf, Lake Tūkana, Kenya. *Environmental Biology of Fishes* **37**, 25-46.
- Kronert, U., Horstgen-Schwark, G. and Langholz, H.J. (1989) Prospects of selecting for late maturity in tilapia (*Oreochromis niloticus*) I: family studies under laboratory conditions. *Aquaculture* **77**, 113-121.
- Lazard, J. & Oswald, M. (1995) Association silure africain – tilapia: polyculture ou controle de la reproduction? *Living Aquatic Resources* **8**, 445-463.

- Leggett, W.J. and Power, G. (1969) Differences between two populations of landlocked Atlantic salmon (*Salmo salar*) in Newfoundland. *Journal of the Fisheries Research Board of Canada* **35**, 1585-1596.
- Lester, L.T., Aballa, T.A., Palada, M.S. and Keus, H.J. (1988) Genetic variation in size and sexual maturation of *Oreochromis niloticus* under hapa and cage culture conditions, in *The Second International Symposium on Tilapia in Aquaculture* (eds. R.S.V. Pullin, T. Bhukaswan, K Tonguthai and J.L. MacLean), ICLARM, Manila, pp. 223-230.
- Linfield, R.S. (1979) Changes in the rate of growth in a stunted roach, *Rutilus rutilus*, population. *Journal of Fish Biology* **15**, 275-289.
- Liu, K.M. & Chang, W.Y.B (1992) Bioenergetic modelling of effects of fertilisation, stocking density, and spawning on the growth of the Nile tilapia, *Oreochromis nilotica*. *Aquaculture and Fisheries Management* **22**: 291-301.
- Lomnicki, A. (1988) *Population Ecology of Individuals*. Princeton University Press, Princeton.
- Lorenzen, K. (1995) Population dynamics and management of culture-based fisheries. *Fisheries Management and Ecology* **2**, 61-73.
- Lorenzen, K. (1996a) A simple von Bertalanffy model for density-dependent growth in extensive aquaculture, with an application to common carp (*Cyprinus carpio*). *Aquaculture* **142**, 192-205.
- Lorenzen, K. (1996b) The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *Journal of Fish Biology* **49**, 627-647.
- Lorenzen, K. and Garaway, C.J. (1998) How predictable is the outcome of stocking? *FAO Fisheries Technical Paper* **347**, 133-152.
- Lorenzen, K., Garaway, C.J., Chamsingh, B. & Warren, T.J. (1998a) Effects of access restrictions and stocking on small water body fisheries in Laos. *Journal of Fish Biology* **53** (Supplement 1) 345-357.
- Lorenzen, K., Juntana, J., Bundit, J. & Tourongruang, D. (1998b) Assessing culture fisheries practices in small water bodies: a study of village fisheries in Northeast Thailand. *Aquaculture Research*. **29**: 211-224.
- Lorenzen, K., Xu, G., Cao, F., Ye, J. & Hu, T. (1997) Analysing extensive fish culture systems by transparent population modelling: bighead carp, *Aristichthys nobilis* (Richardson 1845), culture in a Chinese reservoir. *Aquaculture Research* **28**: 867-880.
- Lowe (McConnell), R.H. (1958) Observations on the biology of *Tilapia nilotica* in L. Victoria, E. Africa. *East African Fisheries Research Organisation Supplementary Publication* **1**, 1-72.

- Lowe-McConnell, R.H. (1982) Tilapias in fish communities, in *The Biology and Culture of Tilapias* (eds R.S.V. Pullin and R.H. Lowe-McConnell), ICLARM, Manila, 83-113.
- McGinty, A.S. (1984) Effects of predation by tucunare (*Cichla ocellaris*) on *Tilapia nilotica* in ponds. *Journal of the Agricultural University of Puerto Rico* **68**, 101-105.
- McGinty, A.S. (1985) Effects of predation by largemouth bass in fish production ponds stocked with *Tilapia nilotica*. *Aquaculture* **46**, 269-274.
- Mangel, M. (1996) Life history invariants, age at maturity and the ferox trout. *Evolutionary Ecology* **10**, 249-263.
- Manly, B.F.J. (1994) *Multivariate Statistical Methods: a Primer*. 2nd edn. Chapman and Hall, London.
- Mattson, N.S. (1994) Direct estimates of multi-mesh gillnet selectivity to *Oreochromis shiranus chilwae*. *Journal of Fish Biology* **45**, 997-1012.
- Mattson, N.S. and Kaunda, E.K.W.H. (1997) Population dynamics of *Oreochromis shiranus* in two small water bodies in Malawi. *Journal of Fish Biology* **50**, 592-607.
- Milstein, A. (1995) Fish-management relationships in Israeli commercial fish farming. *Aquaculture International* **3**, 292-314.
- Minns, C.K. (1989) Factors affecting fish species richness in Ontario lakes. *Transactions of the American Fisheries Society* **118**, 533-545.
- Moreau, J. and De Silva, S.S. (1991) Predictive yield models for lakes and reservoirs of the Philippines, Sri Lanka and Thailand. *FAO Fisheries Technical Paper* **319**.
- Moreau, J., Bambino, C. and Pauly, D. (1986) A comparison of four indices of overall fish growth performance, based on 100 tilapia populations (Fam. Cichlidae), in *The First Asian Fisheries Forum*, Asian Fisheries Society, Manila, pp. 201-206.
- Moreau, J., Christensen, V. and Pauly, D. (1993) A trophic ecosystem model of Lake George, Uganda, in *Trophic Models of Aquatic Ecosystems*, (ed. V. Christensen and D. Pauly), ICLARM Conference Proceedings **26**, 124-129.
- Moriarty, D.J.W. (1982) Physiology: chairman's overview, in *The Biology and Culture of Tilapias* (eds R.S.V. Pullin and R.H. Lowe-McConnell), ICLARM, Manila, 115-117.
- Moyle, P.B., Li, H.W. and Barton, B.A. (1986) The Frankenstein effect: impact of introduced fishes on native fishes in North America, in *Fish Culture in Fisheries Management* (ed. R.H. Stroud), American Fisheries Society, Bethesda, pp. 415-426.

- Muchiri, S.M. (1997) Fluctuations in the fisheries of Kenya's Rift Valley Lakes: causes and prospects for the future, in *Developing and Sustaining World Fisheries Resources, 2nd World Fisheries Congress* (eds. D.A. Hancock, D.C. Smith, A. Grant and J.P. Beumer), CSIRO, Collingwood, pp. 90-97.
- Muchiri, S.M. and Hickley, P. (1991) The fishery of Lake Naivasha, Kenya, in *Catch Effort Sampling Strategies* (ed. I.G. Cowx), Fishing News Books, Oxford, pp. 382-392.
- Muchiri, S.M., Hart, P.J.B. and Harper, D.M. (1995) The persistence of two introduced tilapia species in Lake Naivasha, Kenya, in the face of environmental variability and fishing pressure, in *The Impact of Species Changes in African Lakes* (eds. T. Pitcher and P.J.B. Hart), Chapman and Hall, London, pp. 299-319.
- Neat, F.C., Huntigford, F.A. and Beveridge, M.C.M. (1998) Fighting and assessment in male cichlid fish: the effects of asymmetries in gonadal state and body size. *Animal Behaviour* **55**, 883-891.
- Newsome, A.E. and Noble, I.R. (1986) Ecological and physiological characteristics of invading species, in *Ecology of Biological Invasions: an Australian Perspective* (eds. R.H. Groves and J.J. Burdon), Australian Academy of Science, Canberra, pp. 1-20.
- Nikolsky, G.V. (1969) *Fish Population Dynamics as the Biological Background for the Rational Exploitation and Management of Fishery Resources*, Oliver and Boyd, Edinburgh.
- Noakes, D.L.G and Balon, E.K. (1982) Life histories of tilapias: an evolutionary perspective, in *The Biology and Culture of Tilapias* (eds R.S.V. Pullin and R.H. Lowe-McConnell), ICLARM, Manila, pp. 61-82.
- Ofori, J.K. (1988) The effect of predation by *Lates niloticus* on overpopulation and stunting in mixed sex culture of tilapia species in ponds, in *The Second International Symposium on Tilapia in Aquaculture* (eds. R.S.V. Pullin, T. Bhukaswan, K. Tonguthai and J.L. McLean), ICLARM, Manila, pp. 69-73.
- Oldorf, W., Kronert, U., Balarin, J., Haller, R., Horstgen-Schwark, G. and Langholz, H.J. (1989) Prospects of selecting for late maturity in tilapia (*Oreochromis niloticus*) II. Strain comparisons under laboratory and field conditions. *Aquaculture* **77**, 123-133.
- Oliveira, R.F. and Almada, V.C. (1996) On the (in)stability of dominance hierarchies in the cichlid fish *Oreochromis mossambicus*. *Aggressive Behaviour* **22**, 37-45.
- Ogutu-Ohwayo, R. and Hecky, R.E. (1991) Fish introductions in African and some of their implications. *Canadian Journal of Fisheries and Aquatic Sciences* **48** (Supplement 1), 8-12.
- Pagan-Font, F.A. (1975) Cage culture as mechanical method for controlling reproduction of *Tilapia aurea* (Steindachner). *Aquaculture* **6**, 243-247.

Papotsoglou, S.E. & Tziha, G. (1996) Blue tilapia (*Oreochromis aureus*) growth rate in relation to dissolved oxygen concentration under recirculated water conditions. *Aquacultural Engineering* **15**, 181-192.

Pauly, D. (1980) On the interrelationship between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil Permanent internationale pour l'Exploration de la Mer* **39**, 175-192.

Pauly, D. (1981) The relationship between gill surface area and growth performance in fish: a generalisation of von Bertalanffy's theory of growth. *Berichte der Deutschen Wissenschaftlichen Kommission fuer Meeresforschung* **28**, 251-282.

Pauly, D. (1984) A mechanism for the juvenile to adult transition in fishes. *Journal du Conseil Permanent internationale pour l'Exploration de la Mer* **41**, 280-284.

Pauly, D. and Morgan, G.P. (eds.) (1987) *The Theory and Application of Length-Based Methods of Stock Assessment*, ICLARM, Manila.

Pauly, D., Moreau, J. and Prein, M. (1988) A comparison of overall growth performance of tilapia in open water and in aquaculture, in *The Second International Symposium on Tilapia in Aquaculture* (eds. R.S.V. Pullin, T. Bhukaswan, K. Tonguthai and J.L. McLean), International Center for Living Aquatic Resources Management, Manila, pp. 469-479.

Pauly, D., Prein, M. and Hopkins, K.D. (1993) Multiple regression analysis of aquaculture experiments based on the "extended Gulland and Holt plot", in *Multivariate Methods in Aquaculture Research: Case Studies of Tilapias in Experimental and Commercial Systems* (eds. M. Prein, G. Hulata and D. Pauly), International Center for Living Aquatic Resources Management, Manila, pp. 13-23.

Pechlaner, R. (1984) Dwarf populations of Arctic charr in high-mountain lakes of the Alps resulting from under-exploitation, in *Biology of Arctic charr* (eds. L. Johnson and B.L. Burns), University of Manitoba Press, Winnipeg, pp. 319-327.

Pet, J.S. and Piet, G.J. (1993) The consequences of habitat occupation and habitat overlap of the introduced tilapia *Oreochromis mossambicus* and indigenous fish species for fishery management in a Sri Lankan reservoir. *Journal of Fish Biology* **43** (Supplement A), 193-208.

Pet, J.S., Pet-Soede, C. and Densen, W.L.T. van (1995) Comparison of methods for the estimation of gillnet selectivity to tilapia, cyprinids, and other species of Sri Lankan reservoir fish. *Fisheries Research* **24**, 141-164.

Pet, J.S., Gevers, G.J.M., Densen, W.L.T. van and Vijverberg, J. (1996a) Management options for a more complete utilisation of the biological production in Sri Lankan reservoirs. *Ecology of Freshwater Fish* **5**, 1-14.

- Pet, J.S., Machiels, M.A.M. and Densen, W.L.T. van (1996b) A size-structured simulation model for evaluating management strategies in gillnet fisheries exploiting spatially differentiated populations. *Ecological Modelling* **88**, 195-214.
- Peters, H.M. (1963) Eizahl, Eigewicht und Gelegetwicklung in der Gattung *Tilapia* (Cichlidae, Teleostei). *Internationale Revue der gesamten Hydrobiologie* **48**, 547-576.
- Philippart, J.C. and Ruwet, J.C. (1982) Ecology and distribution of tilapias, in *The Biology and Culture of Tilapias*, (eds R.S.V. Pullin and R.H. Lowe-McConnell), ICLARM, Manila, pp. 15-59.
- Piironen, J. and Holopainen, I.J. (1988) Length structure and reproductive potential of crucian carp (*Carassius carassius*(L.)) populations in some small forest ponds. *Annales Zoologici Fennici* **25**,
- Policansky, D. (1983) Size, age and demography of metamorphosis and sexual maturation in fishes. *American Zoologist* **23**, 57-63.
- Prein, M. (1993a) Multiple regression and path analysis of Nile tilapia growth in integrated livestock-fish culture in the Philippines, in *Multivariate Methods in Aquaculture Research: Case Studies of Tilapias in Experimental and Commercial Systems* (eds. M. Prein, G. Hulata and D. Pauly), ICLARM, Manila, pp. 50-66.
- Prein, M. (1993b) Multivariate analysis of tilapia growth experiments in Israel, Zambia and Peru, in *Multivariate Methods in Aquaculture Research: Case Studies of Tilapias in Experimental and Commercial Systems* (eds. M. Prein, G. Hulata and D. Pauly), ICLARM, Manila, pp. 75-87.
- Prein, M. and Pauly D. (1993) Two new approaches to examining multivariate aquaculture growth data: the "extended Bayley plot" and path analysis, in *Multivariate Methods in Aquaculture Research: Case Studies of Tilapias in Experimental and Commercial Systems* (eds. M. Prein, G. Hulata and D. Pauly), ICLARM, Manila. Pp, 32-49.
- Pullin, R.S.V, Palomares, M.L., Casal, C.V., Dey, M.M. & Pauly, D. (1997) Environmental impacts of tilapias, in *Proceedings of the Fourth International Symposium on Tilapia in Aquaculture*, Vol. 2 (ed. K. Fitzsimmons), Northeast Regional Agricultural Engineering Service Cooperative Extension, Ithaca, pp. 554-570.
- Quiros, R. (1998) Reservoir stocking in Latin America, an evaluation. *FAO Fisheries Technical Paper* **347**, 91-117.
- Ridgeway, L.L. and Chapleau, F. (1994) Study of a stunted population of yellow perch (*Perca flavescens*) in a monospecific lake in Gatineau Park, Quebec. *Canadian Journal of Zoology* **72**, 1576-1582.
- Riley, J and Darmi, M. (1995) A survey of statistical use in aquaculture research. *Aquaculture Research* **26**, 95-101.

- Rochet, M.J. (1998) Short-term effects of fishing on life history traits of fishes. *ICES Journal of Marine Science* **55**, 371-391.
- Roff, D.A. (1983) An allocation model of growth and reproduction in fish. *Canadian Journal of Fisheries and Aquatic Sciences* **40**, 1395-1404.
- Roff, D.A. (1992) *The Evolution of Life Histories: Theory and Analysis*, Chapman and Hall, New York.
- Roff, D.A. (1996) The evolution of threshold traits in animals. *Quarterly Review of Biology* **71**, 3-35.
- Rosenberg, A.A. and Beddington, J.R. (1988) Length-based methods of fish stock assessment, in *Fish Population Dynamics* (ed. J.A. Gulland), Wiley, Chichester, pp. 83-103.
- Schreiber, S., Focken, U. and Becker, K. (1998) Individually reared female Nile tilapia (*Oreochromis niloticus*) can grow faster than males. *Journal of Applied Ichthyology* **14**, 43-47.
- Shuter, B.J., Jones, M.L., Korver, R.M. & Lester, N.P. (1998) A general, life history based model for regional management of fish stocks: the inland lake trout (*Salvelinus namaycush*) fisheries of Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 2161-2177.
- Siddiqui, A.Q., Al-Harbi, A.H. and Al-Hafedh, Y.S. (1997) Effects of food supply on size at first maturity, fecundity and growth of hybrid tilapia, *Oreochromis niloticus* (L.) x *Oreochromis aureus* (Steindachner), in outdoor concrete tanks in Saudi Arabia. *Aquaculture Research* **28**, 341-349.
- Silliman, R.P. (1975) Selective and unselective exploitation of experimental populations of *Tilapia mossambica*. *Fishery Bulletin* **73**, 495-507.
- Sprenst, P. (1989) *Applied Nonparametric Statistical Methods*. Chapman and Hall, London.
- Springborn, R.R., Jensen, A.L., Chang, W.Y.B., and Engle, C. (1992) Optimum harvest time in aquaculture: an application of economic principles to a Nile tilapia, *Oreochromis niloticus* (L.), growth model. *Aquaculture and Fisheries Management* **23**, 639-647.
- Sreenivasan, A. (1991) Transfers of freshwater fishes into India, in *Ecology of Biological Invasions in the Tropics* (ed. P.S. Ramakrishnan), International Science Publications, New Delhi. pp. 131-138.
- Stamps, J.A., Mangel, M. and Phillips, J.A. (1998) A new look at the relationship between size at maturity and asymptotic size. *The American Naturalist* **152**, 470-479.
- Stearns, S.C. (1992) *The Evolution of Life Histories*, Oxford University Press, Oxford.
- Sugunan, V.V. (1997) Fisheries management of small water bodies in seven countries in Africa, Asia and Latin America. *FAO Fisheries Circular* **933**.

- Sutherland, W.J. (1996) *From Individual Behaviour to Population Ecology*, Oxford University Press, Oxford.
- Svedaeng, H. (1990) Genetic basis of life-history variation of dwarf and normal Arctic charr, *Salvelinus alpinus* (L.), in Stora Roesjoen, central Sweden. *Journal of Fish Biology* **36**, 917-932
- Swingle, H.S. (1960) Comparative evaluation of two tilapias as pond fishes in Alabama. *Transactions of the American Fisheries Society* **89**, 142-148.
- Szczerbowski, A., Zakes, Z., Luczynski, M.J. and Szkudlarek, M. (1997) Maturation and growth of a stunted form of crucian carp *Carassius carassius* (L.) in natural and controlled conditions. *Polskie Archiwum Hydrobiologii* **44**, 171-180.
- Taylor, E.B. and Bentzen, P. (1993) Molecular genetic evidence for reproductive isolation between sympatric populations of smelt *Osmerus* in Lake Utopia, south-western New Brunswick, Canada. *Molecular Ecology* **2**, 345-357.
- Teichert-Coddington, D. and Green, B.W. (1993) Tilapia yield improvement through maintenance of minimal oxygen concentrations in experimental grow-out ponds in Honduras. *Aquaculture* **118**, 63-71.
- Thorpe, J.E. (1994) Reproductive strategies in Atlantic salmon, *Salmo salar* (L.). *Aquaculture and Fisheries Management* **25**, 77-87.
- Thorpe, J.E., Talbot, C., Miles, M.S. and Keay, D.S. (1990) Control of maturation in cultured salmon, *Salmo salar*, in pumped seawater tanks, by restricting food intake. *Aquaculture* **86**, 315-326.
- Thorpe, J.E., Mangel, M., Metcalfe, N.B., Huntingford, F.A. (1998) Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evolutionary Ecology* **12**, 581-599
- Trippel, E.A. (1993) Relations of fecundity, maturation, and body size of lake trout and implications for management in northwestern Ontario lakes. *North American Journal of Fisheries Management* **13**, 64-72.
- Tsadik, G.G. and Kutty, M.N. (1987) Influence of ambient oxygen on feeding and growth of the tilapia, *Oreochromis niloticus* (Linnaeus). Working Paper ARAC/87WP/10. African Regional Aquaculture Centre, Port Harcourt, Nigeria.
- Turner, G.E. (1988) Codes of practice and manual of procedures for consideration of introductions and transfers of marine and freshwater organisms. *EIFAC Occasional Paper* **23**. FAO, Rome.
- Turner, G.F. (1995) Maximisation of yields from African lakes, in *Stock Assessment in Inland Fisheries* (ed. I.G.Cowx). Fishing News Books, Oxford, pp. 465-481.

- Twongo, T. (1995) Impact of fish species introductions on the tilapias of Lakes Victoria and Kyoga, in: *The Impact of Species Changes in African Lakes* (eds. T.J. Pitcher and P.J.B. Hart). Chapman and Hall, London, pp. 457-493.
- Tyler, J.A. and Rose, K.A. (1994) Individual variability and spatial heterogeneity in fish population models. *Reviews in Fish Biology and Fisheries* **4**, 91-123.
- van Dam, A.A. and Pauly, D. (1995) Simulation of the effects of oxygen on food consumption and growth of the Nile tilapia, *Oreochromis niloticus* (L.). *Aquaculture Research* **26**, 427-440.
- Van der Mheen, H. (1994) Practical aspects of stocking in small water bodies: an example from Zimbabwe. *CIFA Technical Paper* **28**. FAO, Rome.
- van Someren, V.D. and Whitehead, P.J. (1959) The culture of *Tilapia nigra* (Guenther) in ponds. I. Growth after maturity in male *T. nigra*. *East African Agriculture and Forestry Journal* **25**, 42-46.
- van Someren, V.D. and Whitehead, P.J. (1960) The culture of *Tilapia nigra* (Guenther) in ponds. III. Early growth of males and females at comparable stocking rates, and the length-weight relationship. *East African Agriculture and Forestry Journal* **25**, 169-173.
- van Someren, V.D. and Whitehead, P.J. (1961) The culture of *Tilapia nigra* (Guenther) in ponds. V. The effect of progressive alterations in stocking density on the growth of male *T. nigra*. *East African Agriculture and Forestry Journal* **26**, 145-155.
- Von Bertalanffy, L. (1957) Quantitative laws in metabolism and growth. *Quarterly Reviews in Biology* **32**, 217-231.
- Walline, P.D., Pisanty, S., Gophen, M. and Berman, P. (1993) The ecosystem of Lake Kinneret, Israel, in *Trophic Models of Aquatic Ecosystems* (eds. V. Christensen and D. Pauly), ICLARM, Manila, pp. 103-109.
- Walters, C.J. and Post, J.R. (1993) Density-dependent growth and competitive asymmetries in size-structured fish populations: a theoretical model and recommendations for field experiments. *Transactions of the American Fisheries Society* **122**, 34-45.
- Welcomme, R.L. (1967) The relationship between fecundity and fertility in the mouthbrooding cichlid fish *Tilapia leucostica*. *Journal of Zoology, London* **151**, 453-468.
- Welcomme, R.L. (1970) Studies on the effects of abnormally high water levels on the ecology of fish in certain shallow regions of Lake Victoria. *Journal of Zoology, London* **160**, 405-436.
- Welcomme, R.L. (1988) International introductions of inland aquatic species. *FAO Fisheries Technical Paper* **294**.
- Welcomme, R.L. and Bartley, D.M. (1998) Current approaches to the enhancement of fisheries. *Fisheries Management and Ecology* **5**, 351-382.

Williamson, M. (1996) *Biological Invasions*, Chapman and Hall, London.

Yi, Y. (1998) A bioenergetics growth model for Nile tilapia (*Oreochromis niloticus*) based on limiting nutrients and fish standing crop in fertilised ponds. *Aquacultural Engineering* **18**: 157-173.

Table 6.1 Life history parameters of certain tilapia populations. These data are used for exploratory analyses in various places in the chapter. Values in brackets have been inferred indirectly and are not use in quantitative analyses. L_{∞} and L_m in total length.

Species	Water body	Area [ha]	Z [year]	K [year]	L_{∞} [mm]	L_m [mm]	L_m/L_{∞}	A_m [years]	Source
<i>O. andersonii</i>	Kafue Floodplain	430000	0.8	0.21	434	276c	0.64	4.0c	Kapetsky (1974); Dudley (1974)
<i>O. esculentus</i>	Lake Victoria	6863500	3.0	0.28	295	230	0.78	5.4a	Garrod (1959, 1963); Fryer and Iles (1972)
<i>O. karongae</i>	Lake Malawi	303000	0.81	0.18	413	285	0.69	6.5a	FAO (1993)
<i>O. lidole</i>	Lake Malawi	303000	0.85	0.18	432	285	0.66	6.0a	FAO (1993)
<i>O. macrochir</i>	Kafue Floodplain	430000	0.7	0.31	308	211c	0.69	3.0c	Kapetsky (1974); Dudley (1974)
<i>O. mossambicus</i>	Tank	0.0001	0.5		224 (>120)d		(>0.53)d		Silliman (1975)
<i>O. mossambicus</i>	Rufanes Pool	0.12			265	114	0.43	1.0b	James and Bruton (1992)
<i>O. mossambicus</i>	Kowie	0.6			275	217	0.79	3.0b	James and Bruton (1992)
<i>O. mossambicus</i>	Bradshaw's Mill Dam	0.75	1.2		256	177	0.69	2.0b	James and Bruton (1992)
<i>O. mossambicus</i>	Mill Farm Dam	8	0.4		358	264	0.74	2.5b	James and Bruton (1992)
<i>O. mossambicus</i>	Pimburettwa	834	2.4	0.34	393	205	0.52	2.2a	Amarasinghe (1996); De Silva (1986)
<i>O. mossambicus</i>	Parakrama	2262	1.7	0.26	380	170	0.45	2.3a	Amarasinghe (1996); De Silva (1986)
<i>O. mossambicus</i>	Kaudulla	2537	1.6	0.52	437	210	0.48	1.3a	Amarasinghe (1996); De Silva (1986)
<i>O. mossambicus</i>	Minneriyaa	2560	3.1	0.45	450	195	0.43	1.3a	Amarasinghe (1996); De Silva (1986)
<i>O. niloticus</i>	Kaudulla	2537	1.9	0.34	545	225	0.41	1.6a	Amarasinghe (1996); Amarasinghe and De Silva (1992)
<i>O. niloticus</i>	Minneriyaa	2560	3.6	0.43	545	210	0.39	1.1a	Amarasinghe (1996); Amarasinghe and De Silva (1992)
<i>O. niloticus</i>	Lake George	27000	3.2		450	205	0.46		Gwahaba (1973)
<i>O. niloticus</i>	Lake Tukana	854700			610	390	0.64		Lowe (McConnell) (1958)
<i>O. shiranus</i>	Chisombezi	2.2	2.1	0.67	238	140	0.59	1.3a	Mattson and Kaunda (1997)
<i>O. shiranus</i>	Mbvonihia	3.6	5.8	1.08	304	150	0.49	0.6a	Mattson and Kaunda (1997)
<i>O. squamipinnis</i>	Lake Malawi	303000	1.09	0.24	378	255	0.67	4.7a	FAO (1993)
<i>S. melanotheron</i>	Fosu Lagoon	61	5.0	0.82	161	60	0.37	0.6a	Blay and Asabere-Ameyaw (1993)
<i>S. melanotheron</i>	Tank	0.001	(0.2)e		86	50	0.58		Eyeson (1983)
<i>T. rendalli</i>	Kafue Floodplain	430000	1.4	0.31	364	248c	0.68	3.0c	Kapetsky (1974); Dudley (1974)

(a) Calculated from L_m and growth parameters, assuming $t_0=0$; (b) determined by direct ageing; (c) approximate A_m , L_m calculated using growth parameters; (d) based on minimum length at which sexes can be distinguished externally; (e) average Z in pond and cage culture.

Table 6.2 Comparison of coefficient of variation in length at maturity, asymptotic length, and their ratio between populations of tilapias and other fish species.

Species	CV			N	Source
	L4 ∞	Lm	Lm/L ∞		
<i>O. mossambicus</i>	21	21	25	8	Table 6.1
<i>O. niloticus</i>	11	30	21	4	Table 6.1
<i>Clupea harengus</i>	15	16	8	12	Beverton (1992)
<i>Gadus morhua</i>	20	28	20	17	Beverton (1992)
<i>Stizostedion vitreum</i>	22	9	25	13	Colby <i>et al.</i> (1979); Colby and Nepszy(1981)
<i>Salvelinus namaycush</i>	9	9	5	6	Shuter <i>et al.</i> (1998); Trippel (1993)

FIGURES

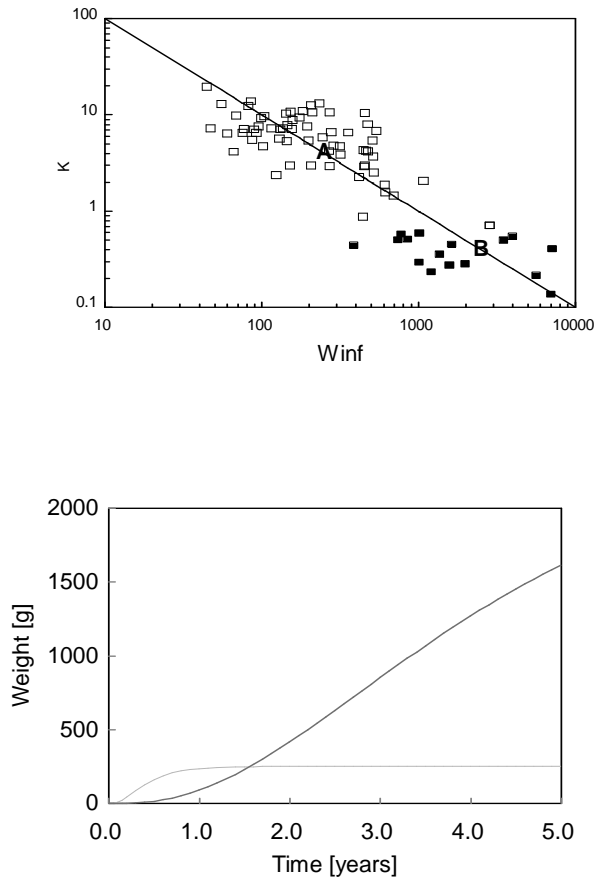


Fig. 6.1 Growth patterns in populations of *O. niloticus*. (a) VBGF parameters in wild (■) and farmed (□) populations. The solid line of slope -1 denotes equal growth performance index P . (b) Growth trajectories associated with points A and B. Both parameter combinations have the same growth performance index P (and therefore the same maximum growth rate), but lead to very different growth trajectories. Data from Moreau *et al.* (1986) and Pauly *et al.* (1988).

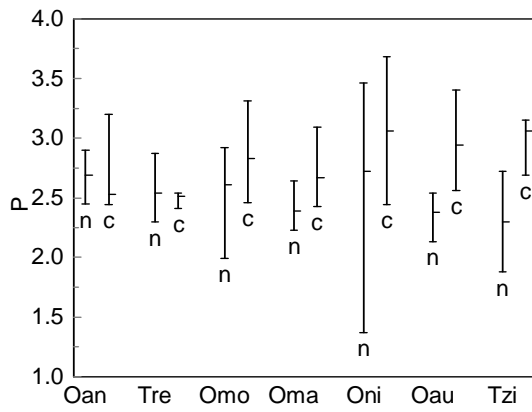


Fig. 6.2 Comparison of the growth performance index P between natural (n) and cultured (c) populations of *O. andersonii* (Oan), *T. rendalli* (Tre), *O. mossambicus* (Omo), *O. macrochir* (Oma), *O. niloticus* (Oni), *O. aureus* (Oau) and *T. zillii* (Tzi). Bars indicate the range and median. Based on data in Pauly *et al.* (1988).

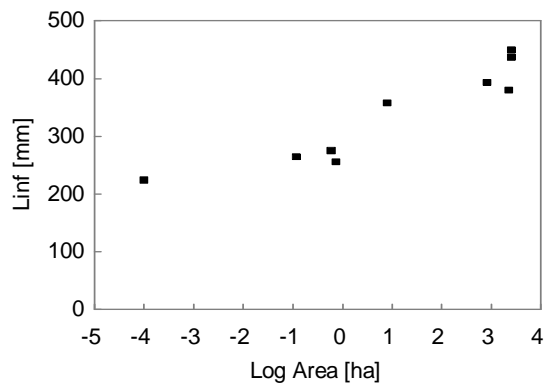


Fig. 6.3 Relationship between water body area and asymptotic size in populations of *O. mossambicus*. Data from Table 6.1.

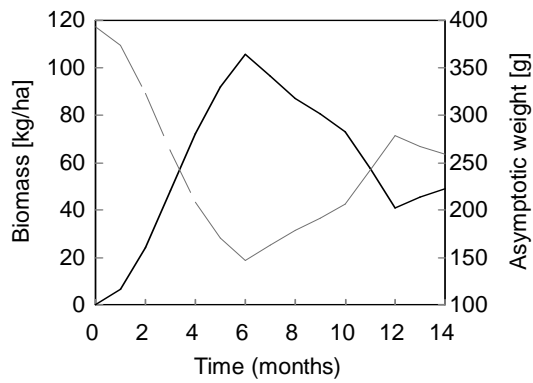
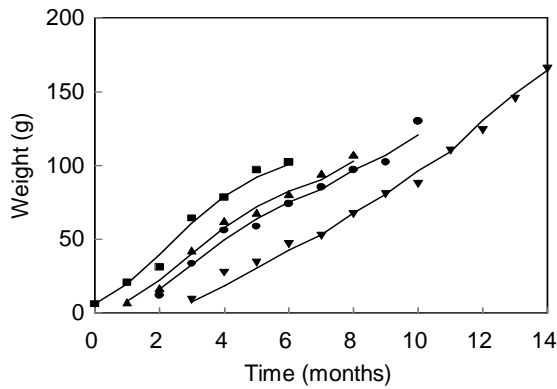


Fig. 6.4 Density-dependent growth of *O. spilurus niger* in extensive pond culture (without feeding). Four all-male cohorts were stocked and harvested in a staggered fashion. (a) Growth trajectories of the four cohorts, symbols denote observed weight and lines indicate predictions from a density-dependent VBGF (Eq. 6.4b) with parameters $W_{4L} = 394\text{g}$, $K=2.1$ /year, and $c=0.019\text{g}^{1/3}\text{ha/kg}$. (b) Population biomass B and corresponding asymptotic weight W_{4B} . Data from Van Someren and Whitehead (1961).

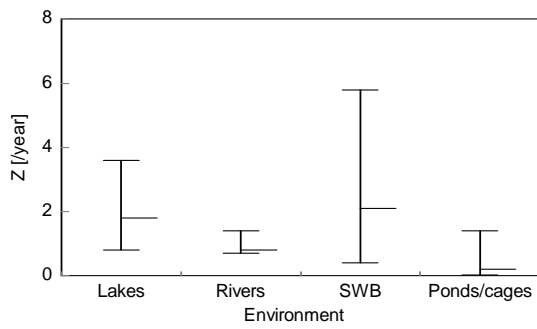


Fig. 6.5 Range and median of total mortality rates (Z) measured for tilapia populations in different environments: lakes (>100 ha); rivers; small water bodies (SWB, <100 ha); and pond and cage aquaculture. Data from Table 6.1; and Lorenzen (1996b). Numbers indicate sample size.

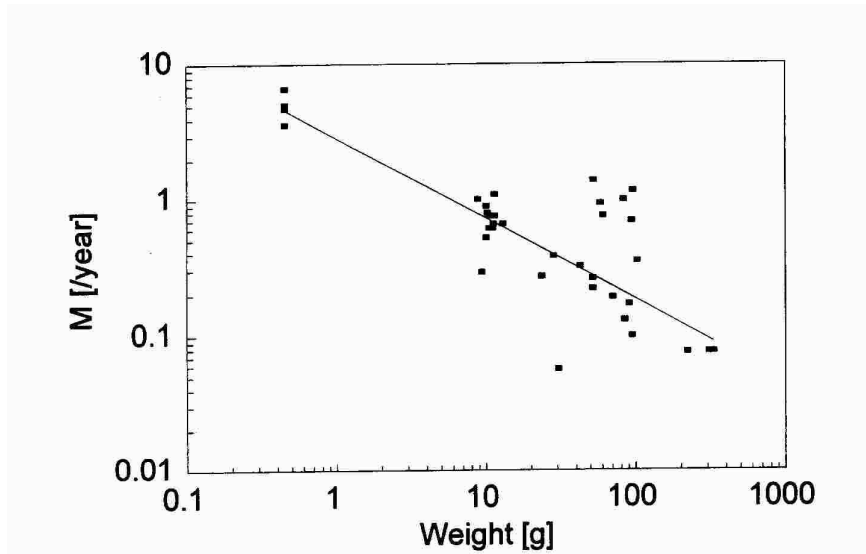


Fig. 6.6 Relationship between natural mortality and body weight in tilapia pond and cage culture. The solid line indicates a relationship (Eq. 6.9) determined by non-parametric (Theil) regression. The parameters $b = -0.60$ (90% CI [-0.67, -0.45]) and $\mu = 2.9$ (90% CI [2.3, 3.7]) are not significantly different from the overall means for pond and cage culture determined by Lorenzen (1996b). Data compiled by Lorenzen (1996b) from information in Inland Fisheries Project (1977); Williams *et al.* (1987); AIT (1990); Costa-Pierce and Hadikusuma (1990); Cruz and Ridha (1991) and Diana and Lin (1991).

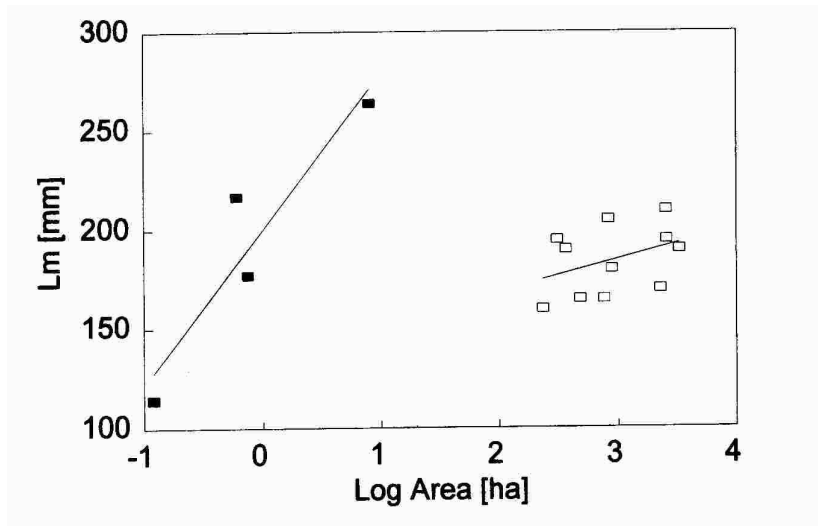


Fig. 6.7 Relationship between water body area and length at maturity in populations of *O. mossambicus* in South African (■) and Sri Lankan (□) reservoirs (Data from De Silva 1986; James and Bruton 1992).

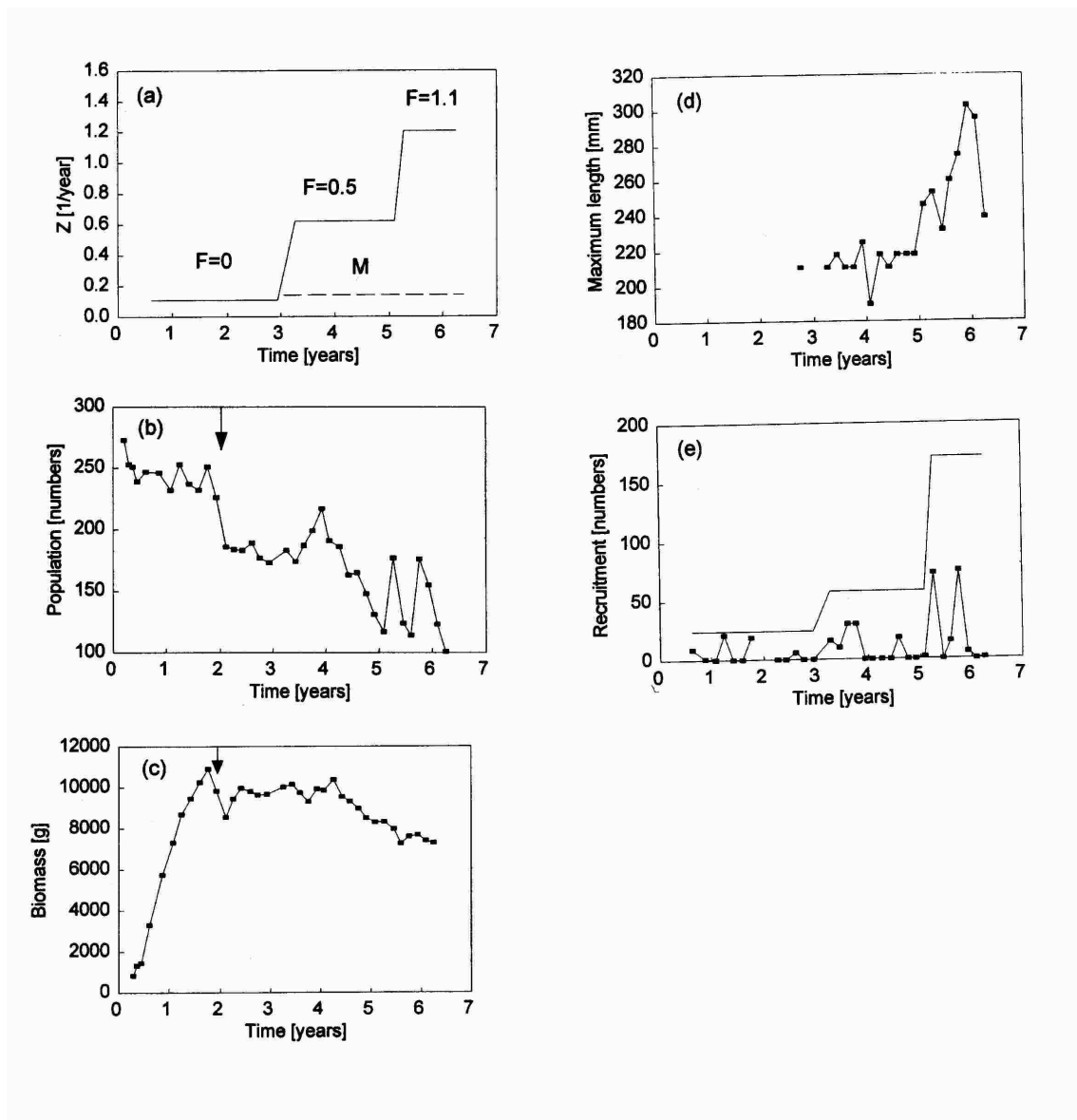


Fig. 6.8 Dynamics of an experimentally exploited population of *O. mossambicus*, maintained for over six years in a 850 l tank at constant feed supply (Silliman 1975). (a) Total mortality rate; (b) population; (c) biomass; (d) maximum length in catch; and (e) recruitment (squares: actual recruits per sampling period, line: cumulative recruits per year). Arrows indicate a catastrophic mortality event due to equipment failure.

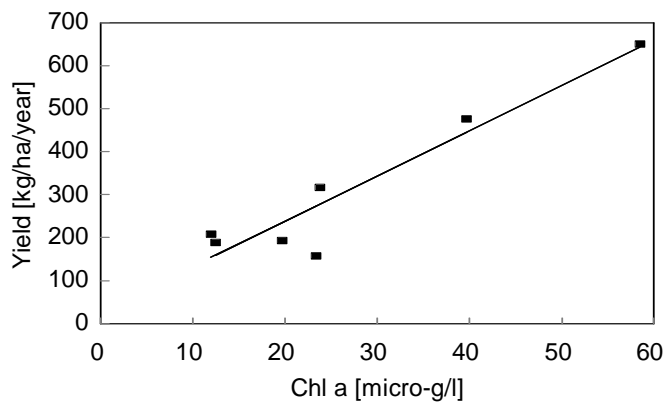


Fig. 6.9 Relationship between the trophic status indicator chlorophyll a and fish yield in *O. mossambicus*-dominated fisheries in Sri Lankan reservoirs (Moreau and De Silva 1991).

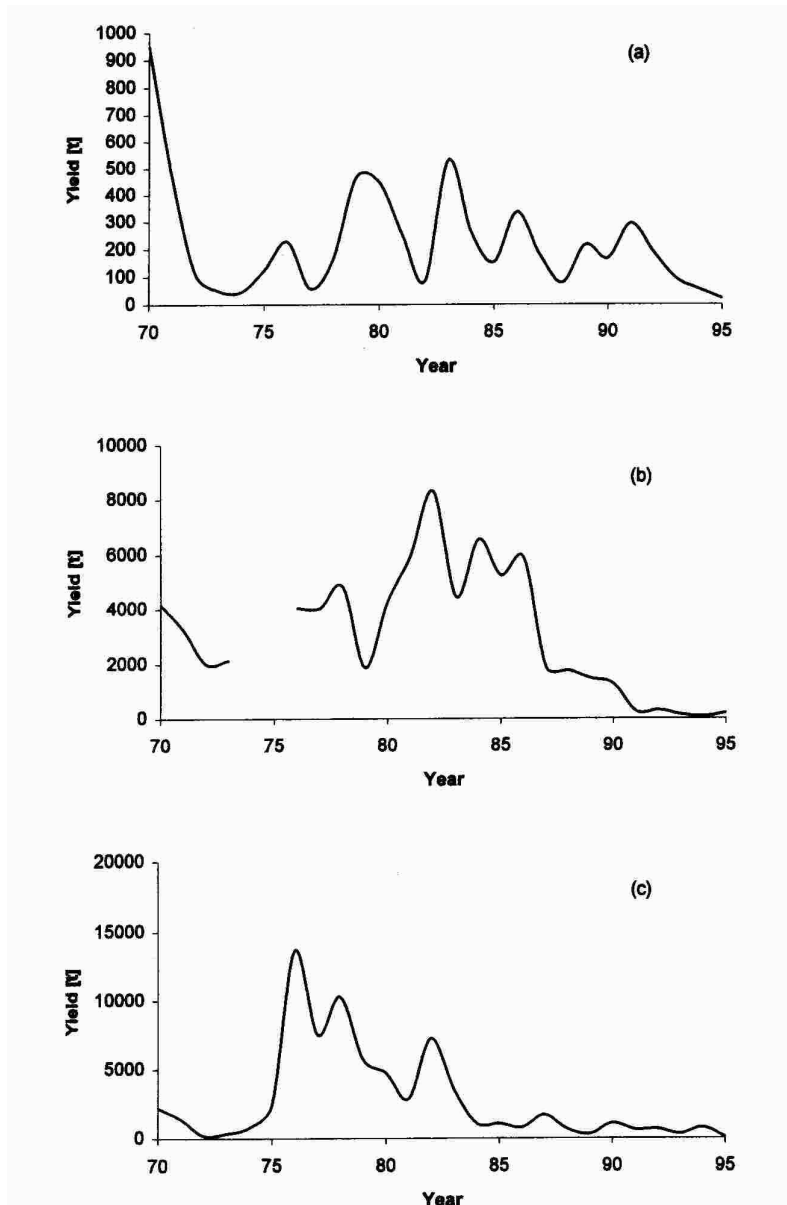


Fig.6.10 Variation in Yield in three tilapia fisheries: (a) Lake Naivasha (*O. leucostictus* and *T. zillii*), (b) Lake Malombe (*Oreochromis* sp., “Chambo”), and (c) Lake Turkana (mainly *O. niloticus*). Data from Muchiri (1997).

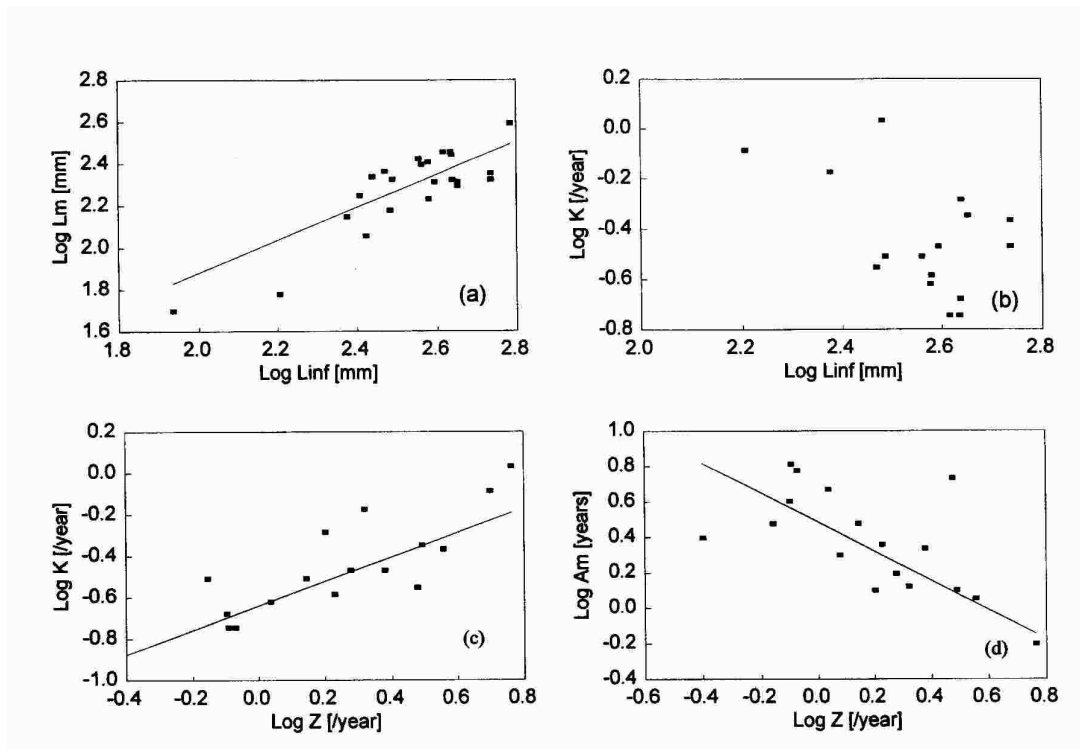


Fig. 6.11 Relationships between life history traits among the tilapia populations listed in Table 6.1. Where significant power relationships of the form $\log Y = \beta_0 + \beta_1 \log X$ exist, parameters are given with 90% confidence intervals. (a) Length at maturity L_m versus asymptotic length L_{∞} ; $\beta_0 = 0.33$ [-0.19, 1.19] and $\beta_1 = 0.78$ [0.44, 1.00]. (b) VBGF growth rate K versus L_{∞} ; no significant relationship. (c) VBGF growth rate K versus total mortality rate Z ; $\beta_0 = -0.64$ [-0.68, -0.60] and $\beta_1 = 0.59$ [0.38, 0.84]. (d) Age at maturity A_m versus total mortality rate Z ; $\beta_0 = 0.49$ [0.38, 0.58] and $\beta_1 = -0.83$ [-1.13, -0.50]. All relationships estimated by non-parametric (Theil) regression.

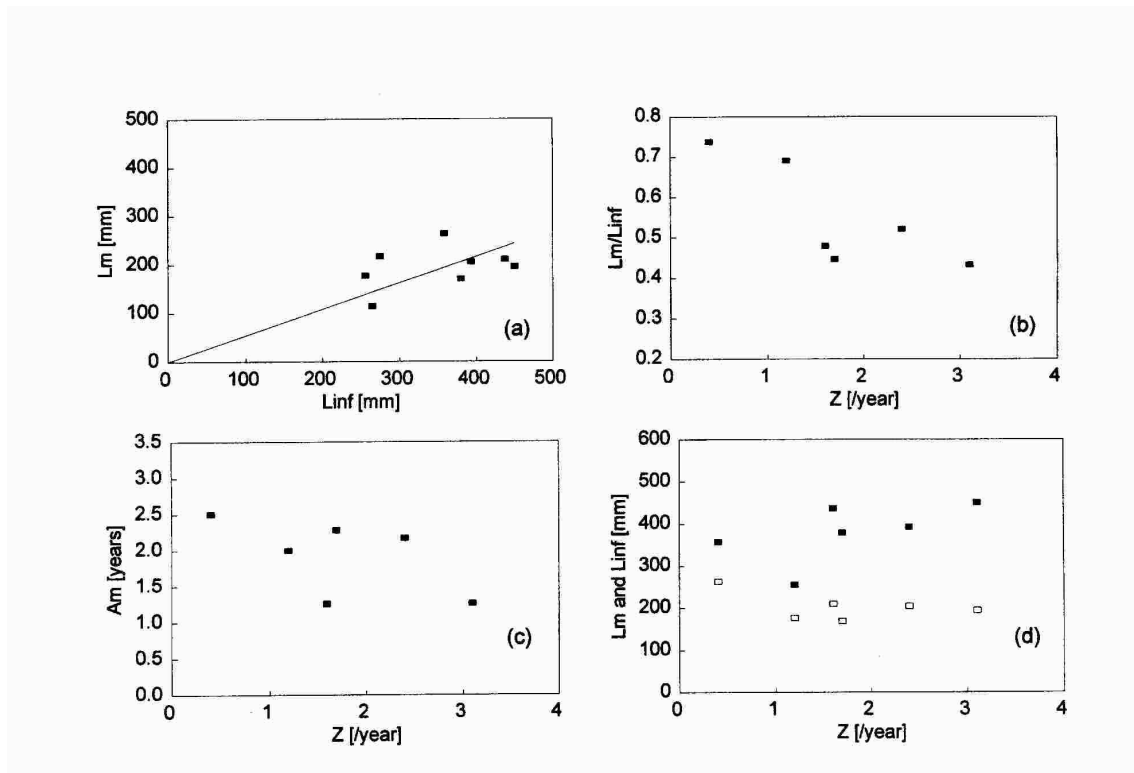


Fig 6.12 Relationship between life history traits in *O. mossambicus* populations. (a) Length at maturity L_m versus asymptotic length L_{∞} ; the line indicates the median L_m/L_{∞} ratio of 0.53. (b) L_m/L_{∞} ratio versus total mortality rate Z . (c) Age at maturity A_m versus Z . (d) L_m (open squares) L_{∞} (solid squares) versus Z . All data from Table 6.1.