

## **Simulation of the effects of oxygen on food consumption and growth of Nile tilapia, *Oreochromis niloticus* (L.)**

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### **Abstract**

Fish need oxygen for aerobic generation of energy for body maintenance, locomotion, feeding and biosynthesis. The rate of oxygen uptake of most fish is limited by diffusion through the gills, and gill surface area grows at a slower rate than body mass. We hypothesize, therefore: (1) that the maximum rate of feed intake is related to the capacity to take in oxygen for processing of this feed; and (2) that the maximum rate of feed intake relative to body size decreases with increasing body size to a point where growth is zero. An oxygen limitation module based on this theory was incorporated into an existing dynamic simulation model for the Nile tilapia, *Oreochromis niloticus* (L.).

The module calculates the maximum potential oxygen supply to the fish on the basis of Fick's law of diffusion and the allometric relationship between body weight and gill surface area. Total oxygen demand of the fish is computed as the sum of routine metabolism, feeding metabolism and energy needed for biosynthesis. In the module, the feeding rate is limited to a level where total oxygen demand does not exceed the potential supply.

The model is used to simulate feeding and growth of *O. niloticus*. Simulation results provide strong support for the oxygen limitation theory. Hence, the model can be used for the analysis of fish growth as affected by feed amount, feed composition, as well as environmental conditions (temperature, dissolved oxygen concentration). It also explains differences in

final size between fish species, and within species under different conditions.

### **Introduction**

Oxygen is an important water quality factor in fish production. In most post-larval fishes, oxygen enters the body through the gill surface. Because a surface does not grow as fast as a volume, the maximum oxygen supply per gram body weight can be expected to decrease as the fish grows (assuming that the efficiency of uptake does not change with body size). This concept can be translated into a balanced oxygen equation (analogous to the balanced energy equation; Brett & Groves 1979): oxygen available for growth equals oxygen entering the body minus oxygen needed for metabolism (Pauly 1981; Longhurst & Pauly 1987). As the fish grows bigger, oxygen supply limits the amount of energy that is available for growth. Eventually, the fish can consume just enough oxygen for its maintenance requirements. Body and gills cease to grow and the fish has attained its maximum size. These concepts were summarized in a generalized von Bertalanffy Growth Function (VBGF) (Pauly 1981).

Although the VBGF has a theoretical basis, it does not allow for an analysis of the effects of changes in oxygen supply to and demand of the fish. Apart from metabolic losses, fish growth is determined by the quantity and quality of the food. These aspects are

covered in a dynamic simulation model for *Clarias gariepinus* (Burchell 1822) (referred to here as the Fish Growth Simulator 1: FGS1) proposed by Machiels and co-workers (Machiels & Henken 1986, 1987; Machiels & van Dam 1987; Machiels 1987). With this model, oxygen demand can be calculated from the major biochemical reaction equations of the intermediary metabolism, in relation to feed composition and quantity.

In an earlier paper, a modified version of FGS1 was parameterized for rainbow trout, *Oncorhynchus mykiss* (Walbaum), and Nile tilapia, *Oreochromis niloticus* (L.), and called FGS2 (van Dam & Penning de Vries 1995). The objective of this study is to assess quantitatively the effect of oxygen limitation by incorporating a mechanism for oxygen limitation.

## Materials and methods

### General

An oxygen limitation module, developed below, was incorporated into FGS2. The simulation results of this adjusted model (called FGS3) were assessed using data from published reports (details below).

First, the model was used to simulate oxygen consumption in the absence of oxygen limitation. All parameter values were set as in FGS2 (van Dam & Penning de Vries 1995). Then, two situations were evaluated: (1) oxygen supply limitation by reduced water oxygen pressure; (2) oxygen supply limitation when the fish reaches its maximum size. All simulations were done in Professional Dynamo Plus (Pugh-Roberts 1986). To obtain a fairly constant level of feeding over a wide range of fish sizes, feeding levels were expressed in terms of metabolic fish weight (dimension:  $\text{kg}^{0.8}$ ; 0.8 is the exponent from the relationship between fish weight and routine metabolism) (Winberg 1956; Becker & Fishelson 1990).

### Data sources and parameterization

For evaluation of oxygen demand simulation, data from Osman (1988) were used. These experiments involved *O. niloticus* fed around maintenance level (data set OSM3, 0.5–4.0  $\text{g kg}^{-0.8} \text{ day}^{-1}$ ) and at higher feeding levels (data set OSM4, 14–24  $\text{kg}^{-0.8} \text{ day}^{-1}$ ). We converted the total amount of feed for each tank into 42 daily rations and computed the average oxygen consumption for OSM3 and OSM4 ( $\text{g O}_2 \text{ kg}^{-0.8} \text{ h}^{-1}$ ) for

each week of the experiment.

For evaluation of the simulation of the effect of low ambient oxygen pressure (PAMB), data from Tsadik & Kutty (1987) were used. There were five tanks and three PAMBs: TSAD1 and TSAD2 (PAMB  $\approx$  150 mm Hg); TSAD3 (PAMB  $\approx$  70 mm Hg); and TSAD4 and TSAD5 (PAMB  $\approx$  25 mm Hg). In the experiments, fish were fed to satiation and the amount consumed was recorded. For the simulations, we converted the total amount consumed in the high-oxygen tanks (TSAD1 and TSAD2) to a feeding regime with a constant feeding level (about 20  $\text{g dry feed kg}^{-0.8} \text{ day}^{-1}$ ). For the lower-oxygen tanks (TSAD3, TSAD4 and TSAD5) we adopted the same feeding regime, but in the simulations oxygen limitation resulted in only partial consumption of the daily rations. The predicted total amount of feed consumed and final fresh weight were compared with the observed values. The initial fat percentage was assumed to be 3% of fresh weight.

To evaluate the simulation of maximum fish size, we use the largest reported size of *O. niloticus* as a lead: 63 cm (Lowe-McConnell 1982) or 5700 g (Palomares 1991) in Lake Turkana. Bluegreen algae (*Spirulina* spp., *Anabaena spiroides*, *Chroococcus* spp. and *Microcystis*) and diatoms dominated the diet and were consumed in a diurnal feeding rhythm. A fish of 137 g ingested 1.282 g of dry weight per day (Harbott 1976) which we converted to a feeding level of 6.29  $\text{g kg}^{-0.8} \text{ day}^{-1}$ . The proximate composition of the bluegreen *Aphanizomenon flos-aquae* was taken as the diet composition (Yurkowski & Tabachek 1979). Average temperature was 30°C (Palomares 1991). Growth of a fish of 5 g initial weight was simulated for 5000 days. The effects of changes in gill size, feeding level and feed composition on fish growth were evaluated.

A glossary of parameter and variable names is given in Table 1. Simulation conditions are summarized in Table 2.

## Oxygen limitation module formulation

### Oxygen demand

Most of the total oxygen demand (O2NEED, in  $\text{g day}^{-1}$ ) is needed for aerobic energy generation through amino acid oxidation (1.25  $\text{g O}_2$  per  $\text{g amino acid}$ ) and lipid oxidation (2.9  $\text{g O}_2$  per  $\text{g lipid}$ ). The remaining oxygen is used for gluconeogenesis (0.68  $\text{g O}_2$  per  $\text{g amino acid}$ ) and lipid synthesis from glucose (0.22  $\text{g O}_2$  per  $\text{g glucose}$ ) (Machiels & Henken 1986; Fig. 1). Oxygen demand is therefore computed as:

**Table 1** Glossary of variable and parameter names

Name	Variable	Dimension
AAFDGL	Proportion of digested protein used for gluconeogenesis	
AAGLUC	Rate of gluconeogenesis	g amino acid day <sup>-1</sup>
AALIRAT	Proportion of energy supplied by fat	
AAOX	Amino acid oxidation rate	g day <sup>-1</sup>
DIGCA	Carbohydrate digestibility	%
DIGLI	Lipid digestibility	%
DIGPR	Protein digestibility	%
DP	Gill oxygen pressure gradient	mm Hg
DT	Time step of integration	day
EFGSIZ	Effective gill surface area	m <sup>2</sup>
FEEDCA	Feed carbohydrate	% in dry matter
FEEDDAY	Daily ration	g
FEEDDM	Feed dry matter	% of fresh weight
FEEDEN	Feed energy content	kJ g <sup>-1</sup>
FEEDLI	Feed lipids	% in dry matter
FEEDMX1	Feeding rate limited by O <sub>2</sub>	g d <sup>-1</sup>
FEEDMX2	Feeding rate limited by feed	g d <sup>-1</sup>
FEEDPR	Feed protein	% in dry matter
FEEDRT	Actual feeding rate	g dry matter d <sup>-1</sup>
FEEMET	Feeding metabolism	mole ATP d <sup>-1</sup>
GARF	Gill area reduction factor	
GILCOR	Effective gill surface area correction factor	
GLULIP	Rate of lipid synthesis from glucose	g d <sup>-1</sup>
GSCF	Coefficient of TAGSIZ–W relationship	m <sup>2</sup> g <sup>-1</sup>
GSEX	Exponent of TAGSIZ–W relationship	–
K	Krogh's permeability coefficient	g d <sup>-1</sup> m <sup>-1</sup> (mm Hg) <sup>-1</sup>
LIATCO	Cost of lipid synthesis	mole ATP g <sup>-1</sup>
LENGTH	Length of simulation	day
LIPOX	Lipid oxidation rate	g d <sup>-1</sup>
OLEF	Empirical coefficient of O <sub>2</sub> MAX–W relationship	d <sup>-1</sup>
O2FCP	Scope for food consumption and processing	g d <sup>-1</sup>
O2FMG	Oxygen cost of feeding metabolism	g O <sub>2</sub> (g feed m <sup>-1</sup> )
O2FDG	Oxygen cost of 1 g feed dry matter*	g O <sub>2</sub> (g feed dm) <sup>-1</sup>
O2LIG	Oxygen cost of lipid synthesis*	g O <sub>2</sub> (g feed dm) <sup>-1</sup>
O2MAX	Maximum oxygen supply rate	g d <sup>-1</sup>
O2NEED	Total oxygen demand rate	g d <sup>-1</sup>
O2PRG	Oxygen cost of protein in synthesis*	g O <sub>2</sub> (g feed dm) <sup>-1</sup>
OXYCAL	Oxycaloric equivalent	kJ (g O <sub>2</sub> )
PAMB	Ambient oxygen pressure	mm Hg
PROLEV	Protein feeding level	g protein kg <sup>-0.8</sup> d <sup>-1</sup>
PRATCO	Cost of protein synthesis	mole ATP g <sup>-1</sup>
ROUMET	Routine metabolism	mole ATP d <sup>-1</sup>
SYNMET	Biosynthesis metabolism	mole ATP d <sup>-1</sup>
TAGSIZ	Total anatomical gill surface area	m <sup>2</sup>
TEMP	Temperature	°C
TIMFED	Feeding period	day
WBD	Water–Blood distance	m
W	Fish fresh weight	g

\* dm, dry matter.

Parameter variable	Data set1		
	OSM3/4	TSAD1-5	Turkana
Feed composition			
FEEDDM	89 <sup>a</sup>	87 <sup>b</sup>	7 <sup>c</sup>
FEEDPR	40	45	48
FEEDCA	37	27	21
FEEDLI	10	10	14
Digestibility <sup>d</sup>			
DIGPR	80	80	80
DIGCA	50	50	50
DIGLI	50	50	50
Gills			
GSEX <sup>e</sup>	—	0.75	0.75
GSCF <sup>e</sup>	—	5.76 x 10 <sup>-4</sup>	5.76 x 10 <sup>-4</sup>
GARF <sup>f</sup>	—	0.65	0.65
K <sup>g</sup>	5 x 10 <sup>-6</sup>	5 x 10 <sup>-6</sup>	5 x 10 <sup>-6</sup>
WBD <sup>h</sup>	3.6 x 10 <sup>-6</sup>	3.6 x 10 <sup>-6</sup>	3.6 x 10 <sup>-6</sup>
Initial weight			
IW	25/7 <sup>a</sup>	8 <sup>b</sup>	5
Environment			
TEMP	26.5 <sup>a</sup>	28 <sup>b</sup>	30
Simulation			
LENGTH	42 <sup>a</sup>	35 <sup>b</sup>	5000
DT	0.125	0.125	0.125

**Table 2** Parameter settings and simulation conditions for simulation of *Oreochromis niloticus* growth in three different situations

<sup>1</sup>Sources: a, Osman (1988); b, Tsadik & Kutty (1987); c, Yurkowski & Tabachek (1979); d, van Dam & Penning de Vries (1995); e, Fernandes & Rantin (1986); f, Hughes (1966); g, Randall & Daxboeck (1984); h, Hughes & Morgan (1973).

$$O2NEED = 1.25 \times AAOX + 2.90 \times LIPOX + 0.68 \times AAGLUC + 0.22 \times GLULIP \quad (1)$$

### Oxygen supply

All processes involved in oxygen transport from the ventilation water to fish tissues (i.e. gill ventilation with water, oxygen diffusion through the gills, oxygen binding to haemoglobin in blood, and transport to the tissues) are geared to the respiratory needs of the fish in relation to its ecology. Surveys of gill area show that active species generally have larger gill surface areas than sluggish species (de Jager & Dekkers 1975; Hughes 1984) and that the oxygen affinity of fish haemoglobin is related to the oxygen tension of the water (Powers 1980). For the model, we assume that diffusion is the limiting step in the respiratory-circulatory route. There is experimental evidence for this: trout with damaged gills showed a reduction in metabolic scope (Duthie & Hughes 1982). Also, experiments with carps and eels have shown that the rate of oxygen binding to haemoglobin is fast compared with diffusion (Hills, Hughes & Koyama 1982).

When diffusion is the limiting process, maximum potential oxygen supply to the fish ( $O2MAX$  in g day<sup>-1</sup>) is given by Fick's law of diffusion:

$$O2MAX = \frac{DP \times K \times EFGSIZ}{WBD} \quad (2)$$

Where  $DP$  is oxygen pressure gradient (mm Hg),  $K$  is Krogh's diffusion constant (g day<sup>-1</sup> m<sup>-1</sup> (mm Hg)<sup>-1</sup>),  $EFGSIZ$  is effective surface area of the gills (m<sup>2</sup>), and  $WBD$  is anatomical water-blood distance (m).

$EFGSIZ$  is derived from the total anatomical gill surface area  $TAGSIZ$  (m<sup>2</sup>), which is related allometrically to fish body weight ( $W$ , in g):

$$TAGSIZ = GSCF \times W^{GSEX} \quad (3)$$

For a given species,  $GSCF$  and  $GSEX$  are computed from a regression of  $TAGSIZ$  on  $W$ .  $GSCF$  expresses the gill area of a fish of 1 g, and  $GSEX$  ranges from about 0.6 to 1.0 in a wide range of species (de Jager & Dekkers 1975; Hughes 1972, 1984).  $GSCF$  and  $GSEX$  are both positively related to the growth performance

of fishes (Pauly 1981, 1982).

Not the entire TAGSIZ is available for gaseous exchange as parts of the secondary lamella lie above the pillar cells (Hughes 1966). The diffusive surface depends on the activity of the fish: increased blood perfusion causes the lamellae to swell, resulting in a larger effective surface area (Randall & Daxboeck 1984). EFGSIZ (in m<sup>2</sup>) is therefore defined as:

$$EFGSIZ = GARF \times TAGSIZ \quad (4)$$

where GARF is a gill area reduction factor depending on the anatomy of the gill and swimming activity.

### Oxygen supply constraints

O2MAX defines how much oxygen can enter the fish for generation of energy for routine metabolism (ROUMET) and feeding metabolism (FEEMET) and for biosynthesis (SYNMET). ROUMET is defined to include all swimming activity of the fish. The difference between O2MAX and oxygen for ROUMET is the oxygen available for feeding and biosynthesis (O2FCP, in g O<sub>2</sub> day<sup>-1</sup>):

$$O2FCP = O2MAX - 5.81 \times ROUMET \quad (5)$$

where 5.81 converts routine metabolism from mole ATP day<sup>-1</sup> to g O<sub>2</sub> day<sup>-1</sup> (protein and fat oxidation both result in 0.172 mole ATP per g O<sub>2</sub> consumed).

The O<sub>2</sub> needs for consumption and processing of 1 g of feed dry matter (O2FDG, in g O<sub>2</sub> (g feed dm)<sup>-1</sup>) can be computed from the reaction equations of the intermediary metabolism and the assumptions for feeding metabolism and costs of biosynthesis (Machiels & Henken 1986; van Dam & Penning de Vries 1994). O2FDG is the sum of oxygen needed for protein synthesis (O2PRG), lipid synthesis (O2LIG) and feeding metabolism (O2FMG, all in g O<sub>2</sub> (g feed dm)<sup>-1</sup>):

$$O2FDG = O2PRG + O2LIG + O2FMG \quad (6)$$

where

$$O2PRG = 1.18 \times DIGPR \times (1 - AAFDGL) \times FEEDPR \times PRATCO \times 5.81 \quad (7)$$

$$O2LIG = (0.18 \times DIGPR \times FEEDPR \times AAFDGL + 0.32 \times DIGCA \times FEEDCA + 0.96 \times DIGLI \times FEEDLI) \times LIATCO \times 5.81 \quad (8)$$

$$O2FMG = \frac{0.045 \times FEEDEN}{OXYCAL} \quad (9)$$

The maximum feeding rate under an oxygen constraint (FEEDMX1, in g day<sup>-1</sup>) is then given by:

$$FEEDMX1 = O2FCP / O2FDG \quad (10)$$

Without oxygen supply limitations, the feeding rate is determined by the amount of feed offered or available. When a daily ration (FEEDDAY, in g) is consumed during a period TIMFED (in d), the feeding rate FEEDMX2 (g day<sup>-1</sup>) can be expressed as:

$$FEEDMX2 = FEEDDAY / TIMFED \quad (11)$$

Oxygen permitting, the fish consumes the amount of feed offered (FEEDMX2); otherwise, it consumes as much as can be processed based on oxygen availability (FEEDMX1) (Fig. 1). This is achieved by always choosing the lower feeding rate:

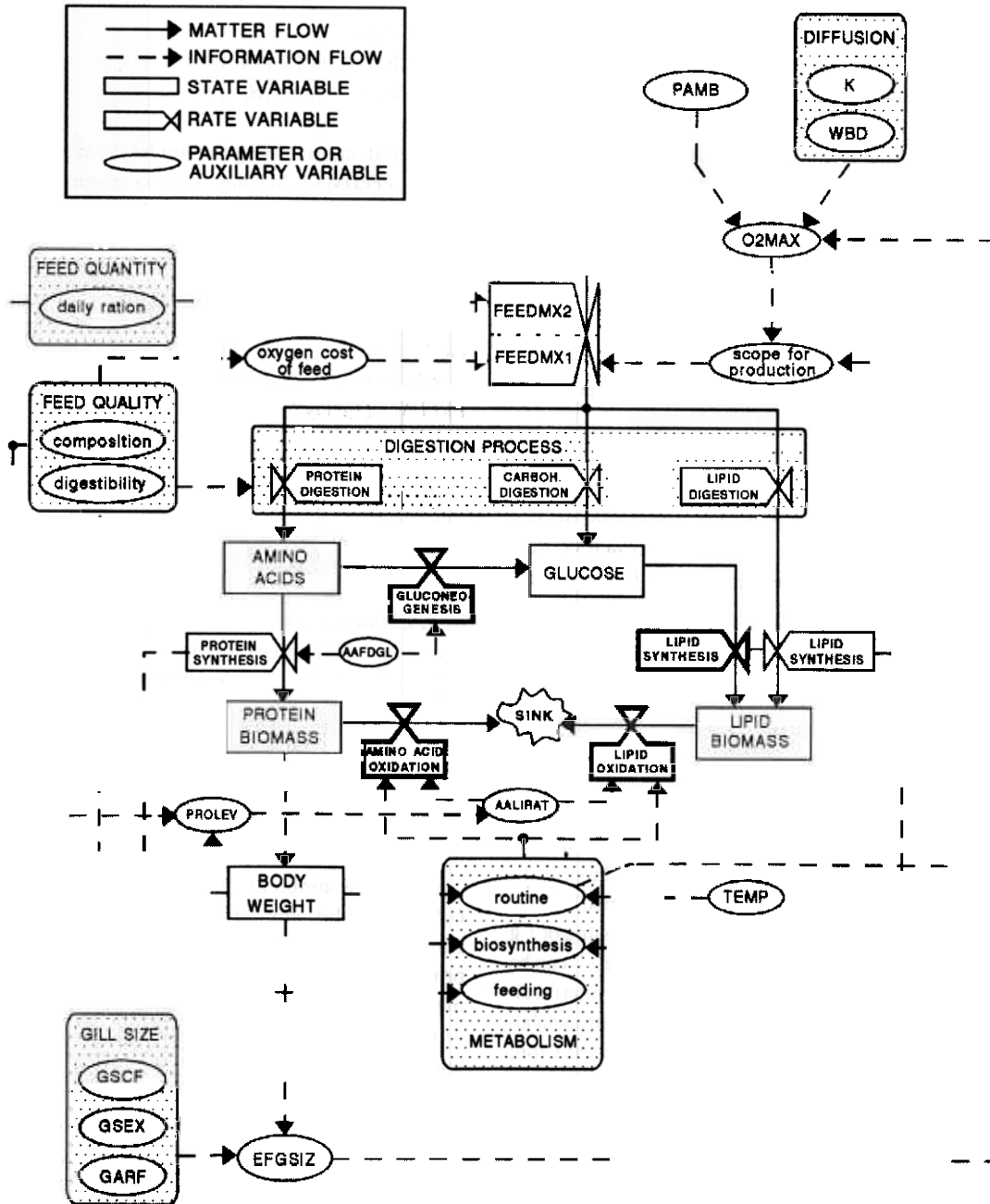
$$\begin{aligned} FEEDRT &= FEEDMX1 \text{ when } FEEDMX1 < FEEDMX2 \\ &= FEEDMX2 \text{ when } FEEDMX1 > FEEDMX2 \end{aligned} \quad (12)$$

Under low ambient oxygen pressure (PAMB), O2FCP can become zero: available oxygen is just enough for routine metabolism and no feed can be processed. When O2FCP is negative, even routine metabolism cannot be satisfied and must be reduced to maintain aerobic metabolism. In some species, anaerobic metabolism will become important under such conditions.

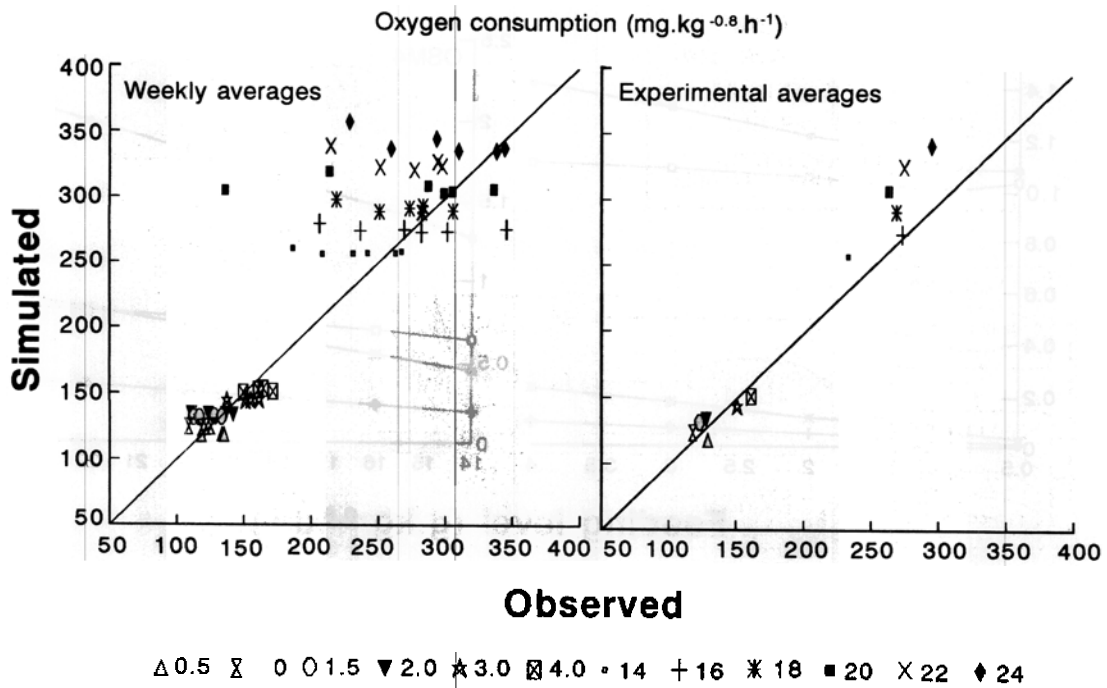
The main effect of a low PAMB is a drop in the gill oxygen pressure gradient DP. Little information about the shape of the relationship between PAMB and DP for various species is available; it is probably the resultant of all variables regulating respiration: ventilation rate, surface area for diffusion, blood oxygen transport characteristics, and oxygen demand. For the time being, we summarize equations 2, 3 and 4:

$$O2MAX = OLEF \times W^{GSEX} \quad (13)$$

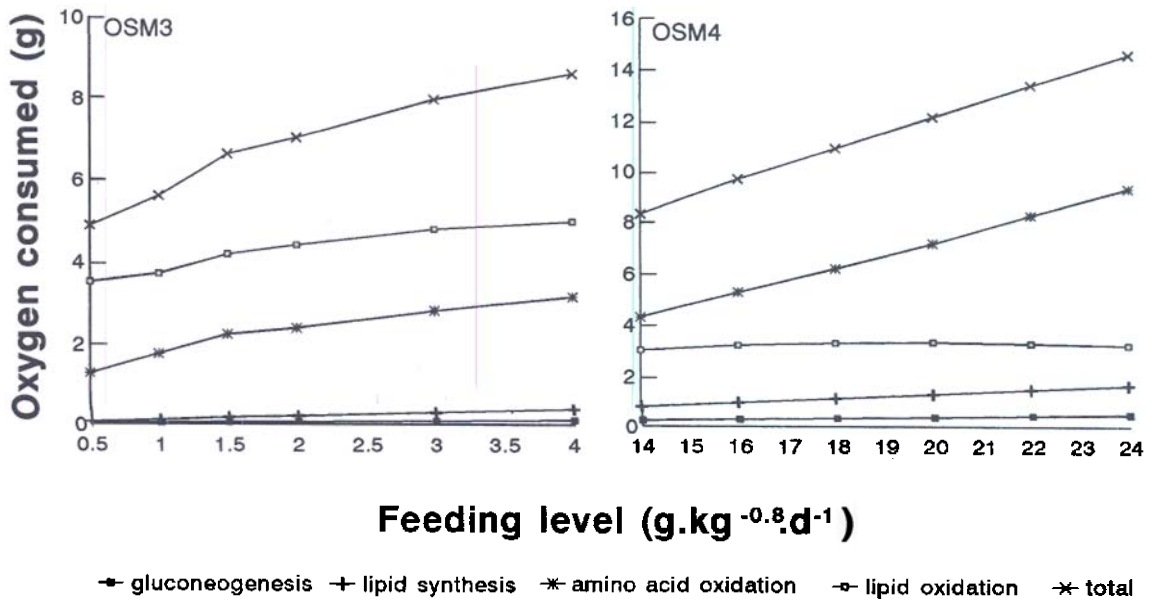
in which the oxygen limitation empirical factor, OLEF, combines the effects of oxygen pressure and fish gill characteristics:



**Figure 1** Relational diagram of FGS3. TEMP, temperature; PAMB, ambient oxygen pressure; O2MAX, maximum potential oxygen supply; AALIRAT, auxiliary variable determining the ratio of protein to fat oxidation; AAFDGL, parameter determining the proportion of amino acids that is converted to glucose; PROLEV, protein feeding level (in g protein kg<sup>-0.8</sup> day<sup>-1</sup>). Shaded boxes are used to group variables in the figure but are not variables in the model. Rate variables that contribute to the oxygen demand (gluconeogenesis, lipid synthesis from glucose, amino acid oxidation and lipid oxidation) are printed bold. For further explanation, see text and van Dam & Penning de Vries (1995).



**Figure 2** Comparison of simulated and observed oxygen consumption (in  $\text{mg kg}^{-0.8} \text{h}^{-1}$ ) at feeding levels ranging from 0.5 to 4.0 (experiment OSM3) and 14 to 24 (experiment OSM4)  $\text{g kg}^{-0.8} \text{day}^{-1}$ . Both experiments lasted 6 weeks; in OSM3 (lower feeding levels) oxygen consumption was measured for 3-4 weeks. The graphs show weekly values (left) and the average of the weekly values (right). Observed weekly values (left) increased with time.



**Figure 3** Total simulated oxygen consumption (g) and its breakdown into gluconeogenesis, lipid synthesis, amino acid oxidation and lipid oxidation in relation to feeding level for experiments OSM3 and OSM4. Amino acid and lipid oxidation together always account for at least 90% of total oxygen demand.

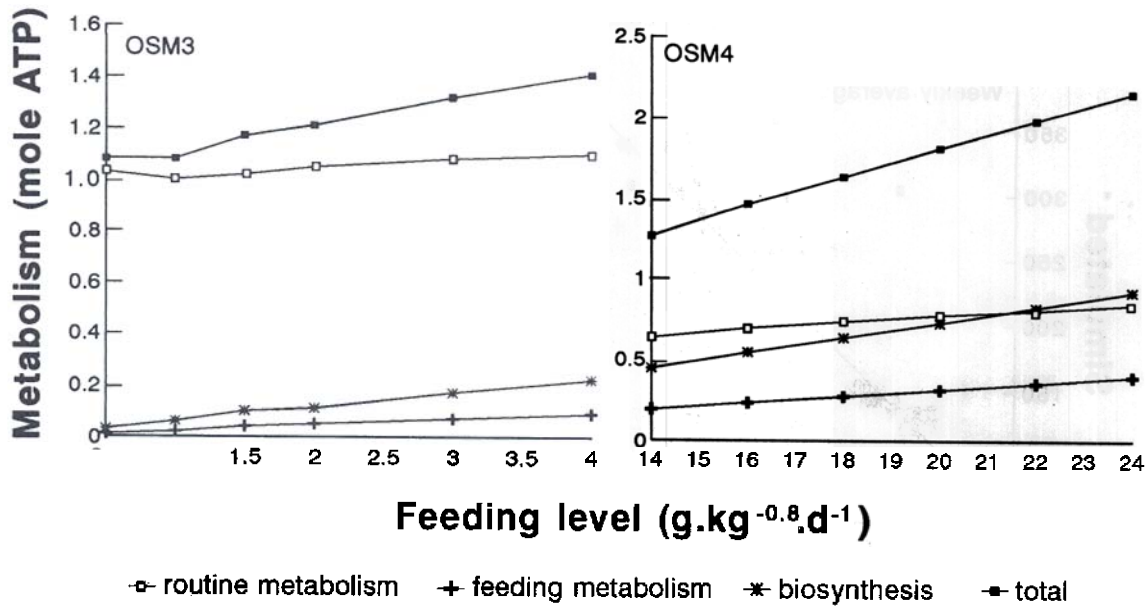


Figure 4 Total simulated energy metabolism (mole ATP) and its breakdown into routine metabolism, feeding metabolism and biosynthesis in relation to feeding level for experiments OSM3 and OSM4.

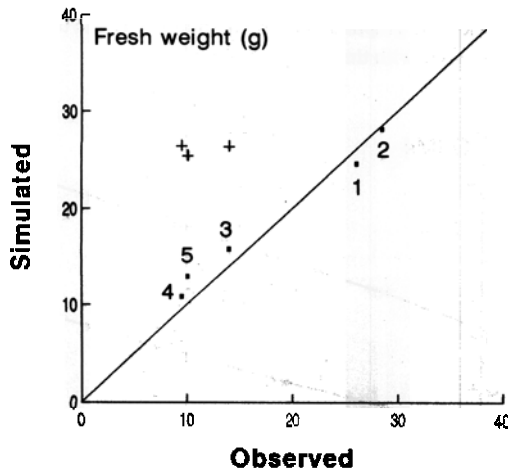


Figure 5 Comparison of simulated and observed fresh weight in the experiment of Tsadik & Kutty (1987). Numbers indicate the five tanks. Crosses show the simulated final weights of TSAD3-5 without oxygen limitation module.

$$OLEF = \frac{DP \times GARF \times K \times GSCF}{WBD} \quad (14)$$

For a given a fish species, the value of OLEF depends primarily on DP, and thus on PAMB.

**Parameterization for *O. niloticus***

The O<sub>2</sub>-diffusion constant K was estimated at 5 × 10<sup>-6</sup>, between its value in water (about 1 × 10<sup>-5</sup>; Hughes 1966; Randall & Daxboeck 1984) and the values for eel skin (1.199 × 10<sup>-6</sup>; Randall & Daxboeck 1984) and connective tissue (2.980 × 10<sup>-6</sup>; Hughes 1966) (all in g day<sup>-1</sup> m<sup>-1</sup> (mm Hg)<sup>-1</sup> converted from units in source, 20°C). K increases with temperature (1% per °C; Randall 1970).

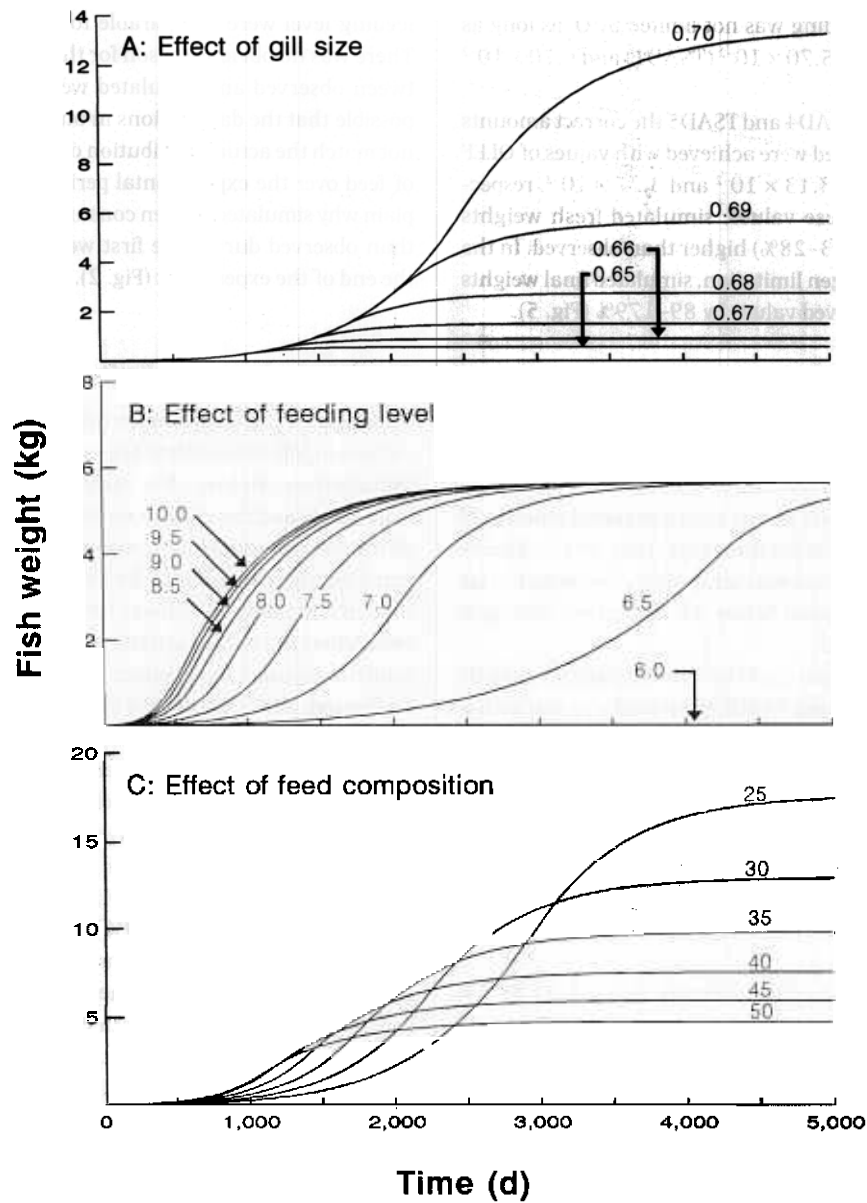
Values for *O. niloticus* of GSCF = 5.76 × 10<sup>-4</sup> m<sup>2</sup> g<sup>-1</sup> and GSEX = 0.75 were reported by Fernandes & Rantin (1986). GARF was estimated at 0.65, as 60–70% of the gill surface is in touch with blood channels (Hughes 1966, 14 species). Measurements of WBD are not available for *O. niloticus*. The mean value for benthic teleosts in Hughes & Morgan (1973) was adopted here (3.6 × 10<sup>-6</sup> m).

**Simulation results**

**Oxygen demand**

The average simulated values for the whole experiment agreed well with experimental results (Fig. 2). The model predicted a constant weekly oxygen consumption at each feeding level while the observed values increased with time.

Lipid and protein oxidation accounted for 90–95%



**Figure 6** Simulation of final fish weight using data from Lake Turkana. (A) Effect of varying the exponent (GSEX) of the allometric relationship between gill area and body weight between 0.65 and 0.70. Simulation conditions: OLEF = 0.068, feeding level = 7 g kg<sup>-0.8</sup> day<sup>-1</sup>. (B) effect feeding levels 6.0–10.0 g kg<sup>-0.8</sup> day<sup>-1</sup>. Simulation conditions: GSEX = 0.69, OLEF = 0.068. (C) Effect of feed composition: protein content varied from 25% to 50% dm. Simulation conditions: feeding level = 8 g kg<sup>-0.8</sup> day<sup>-1</sup>, GSEX = 0.69, OLEF = 0.068.

of total oxygen use. Amino acid oxidation replaced lipid oxidation as the feeding level increased (Fig. 3).

At maintenance feeding levels, routine metabolism accounted for about 80% of the energy requirement. At maximum feeding levels, routine metabolism absorbed about 40% of total energy, while feeding metabolism and energy for biosynthesis accounted

for about 15% and 45%, respectively (Fig. 4).

#### Low ambient oxygen

For data sets (tanks) TSAD1 and TSAD2, simulation resulted in good estimates of final weight. In these

treatments, feeding was not limited by  $O_2$  as long as OLEF exceeded  $5.70 \times 10^{-2}$  (TSAD1) and  $6.70 \times 10^{-2}$  (TSAD2).

In TSAD3, TSAD4 and TSAD5 the correct amounts of feed consumed were achieved with values of OLEF of  $3.72 \times 10^{-2}$ ,  $3.13 \times 10^{-2}$  and  $3.27 \times 10^{-2}$ , respectively. With these values, simulated fresh weights were slightly (13–28%) higher than observed. In the absence of oxygen limitation, simulated final weights exceeded observed values by 89–179% (Fig. 5).

### Final fish size

In long-term simulations with FGS3, fish fat percentage decreased to zero after some time. This was considered unrealistic as fish need a minimal amount of lipids for essential life functions (Love 1980). Therefore, lipid oxidation was set to zero as soon as the fat percentage dropped below 3%, effectively setting a lower threshold.

To see if gill area could become limiting for growth under non-limiting PAMB, the model was run with a value of OLEF =  $6.80 \times 10^{-2}$  at a feeding level of  $7 \text{ g kg}^{-0.8} \text{ day}^{-1}$ . With GSEX = 0.75 (Fernandes & Rantin 1986), a ceiling fish weight was not yet reached at 105 kg. Values between 0.65 and 0.70 resulted in final weights of 1–13 kg. The final weight appears to be very sensitive to changes in GSEX, doubling from 2.75 to 5.64 kg when GSEX increased from 0.68 to 0.69 (Fig. 6A).

The effect of feeding level was assessed at GSEX = 0.69 for feeding levels between 6.0 and  $10.0 \text{ g kg}^{-0.8} \text{ day}^{-1}$ . Final weight was independent of feeding level, as expected, and was reached in a shorter time at higher feeding levels (Fig. 6B).

The effect of feed composition was assessed at GSEX = 0.69 and feeding level =  $8 \text{ g kg}^{-0.8} \text{ day}^{-1}$ . As a starting point, a theoretical feed with 50% protein, 20% carbohydrates and 12.5% lipids (all in dry matter) and 7% dry matter was taken. Other feed compositions were created by simultaneously lowering the protein content and raising carbohydrate content in steps of 5%. Fish eating high-protein feeds grew faster initially but reached a lower final weight than fish eating low-protein feeds (Fig. 6C).

## Discussion

### Oxygen demand

Simulated oxygen demand and its relationship with

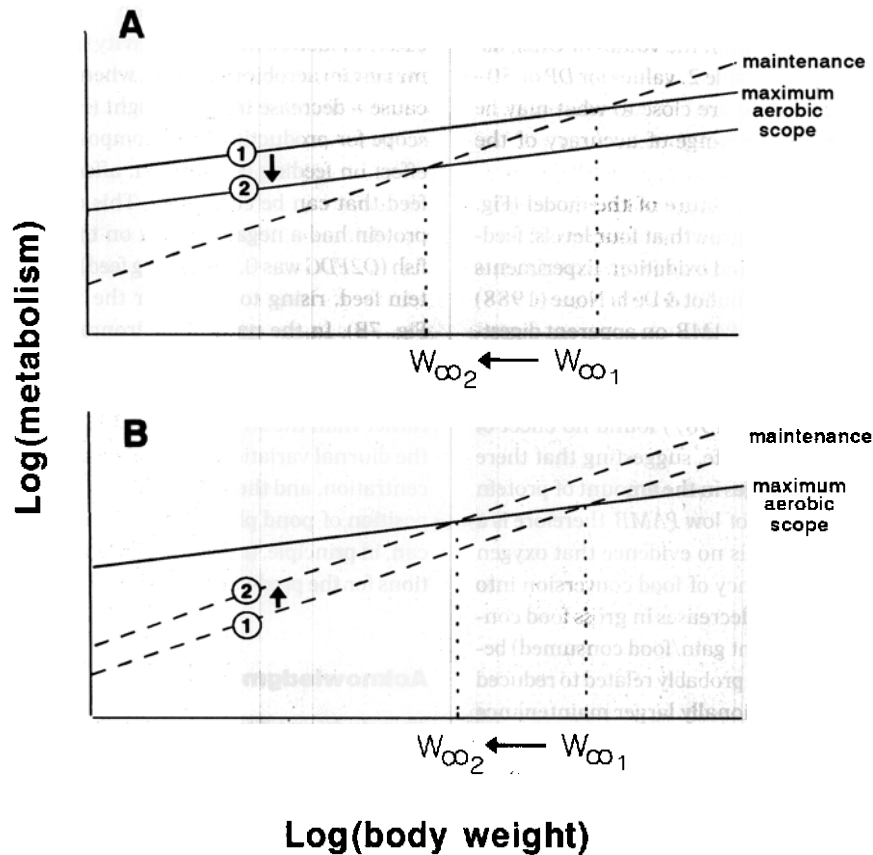
feeding level were comparable to observed values. There was no obvious reason for the discrepancy between observed and simulated weekly values. It is possible that the daily rations in our simulations did not match the actual distribution of the total amount of feed over the experimental period. This could explain why simulated oxygen consumption was higher than observed during the first weeks, and lower at the end of the experiment (Fig. 2).

### Oxygen supply and the limitation model

This model is primarily concerned with the maximum oxygen supply to the fish as the upper limit of aerobic metabolism. Below this maximum, fishes use ventilatory and circulatory mechanisms to facilitate diffusion. The model does not account for possible extra energy expenditure for breathing under low oxygen conditions. Estimates for the oxygen costs of ventilation at routine activity levels are 5–15% of total (i.e. routine) metabolism (Jones 1971; Farrell & Steffenson 1987). Sustained swimming does not increase the oxygen costs of breathing because efficiency of heart activity increases and the fish uses ram-jet ventilation (Farrell & Steffenson 1987). When PAMB decreases, most fishes keep their aerobic metabolism at the same level until the critical PAMB is reached; below the critical PAMB, metabolism decreases. Around the critical PAMB the oxygen costs of breathing must constitute a larger proportion of total metabolism than at higher PAMB, probably at the expense of other elements of routine metabolism.

To quantify oxygen diffusion more precisely, better measurements of K, WBD and GARF in relation to activity level are needed. Apart from the anatomical WBD, water and mucus on the gill surface, blood plasma and the erythrocyte membrane contribute to the diffusion barrier; there is no agreement on their relative importance (Hughes 1984; Piiper & Scheid 1984; Randall & Daxboeck 1984). The value of O2MAX can be verified, however, when it is assumed that oxygen consumption in fishes during maximum sustained swimming equals O2MAX. Nile tilapia of 70.44 g swimming at about 4.4 body lengths per second consumed  $0.879 \text{ g O}_2 \text{ day}$  (Farmer & Beamish 1969). Using the parameters for *O. niloticus* and equations 2 and 4, O2MAX equals  $0.0126 DP$ , which equals 0.879 at  $DP = 69.8 \text{ mm Hg}$ , a reasonable value for DP compared to measurements in other fish (Hughes 1972).

The analysis in Fig. 3 stresses the importance of



**Figure 7** Effect of changes in maintenance metabolism and maximum aerobic scope on the final weight of a fish. (A) A decrease in maximum aerobic scope (e.g. caused by a reduction in ambient oxygen pressure) causes a decrease in final weight. (B) An increase in maintenance metabolism (e.g. caused by an increase in temperature) causes a decrease in final weight.

feeding and biosynthesis in the energy expenditure of the fish. Together they account for about 60% of the total energy expenditure at the highest feeding levels. A reduction in feed intake with subsequent reduction of biosynthesis is thus the obvious way to reduce oxygen need. The reduction in feeding observed in most species under low PAMB confirms this (Stewart, Shumway & Doudoroff 1967; Adelman & Smith 1970; Doudoroff & Shumway 1970; Brett & Blackburn 1981; Pedersen 1987; Tsadik & Kutty 1987; Poullot & De la Noue 1988).

In FGS3, total aerobic metabolic scope is determined by the gill area available for diffusion. The oxygen available after satisfying the requirements for routine metabolism is available for special locomotion and feeding/biosynthesis. This difference between aerobic maximum and routine metabolism is similar to the 'scope for production' defined by Huisman & Valentijn (1981).

In some species, feeding can take up a large part of the scope for production (Jobling 1981). In *Gadus morhua* L., feeding can even use up the entire scope for production, leaving no oxygen for non-routine swimming (Soofiani & Hawkins 1982, 1985). Such species probably rely on anaerobic energy for sudden bursts of activity such as escaping a predator. Other species, notably active pelagic migrating species (Salmonidae, Scombridae), can fit both feeding and swimming into their scope for production. They indeed possess relatively high proportions of dark, aerobic muscle fibres for the utilization of that scope (Boddeke, Slijper & van der Stelt 1959; Blake 1983).

**Effect of low PAMB**

The empirical equation used to simulate the effect of low PAMB is not theoretically satisfactory, but more

data are needed to construct a better model. Calculating back (equation 7) from the values of OLEF using parameter values of Table 2, values for DP of 50–140 mm Hg result. These are close to what may be expected, and within the range of accuracy of the other parameters.

Keeping in mind the structure of the model (Fig. 1), low PAMB can affect growth at four levels: feeding, digestion, synthesis and oxidation. Experiments by Pedersen (1987) and Pouliot & De la Noue (1988) did not show any effect of PAMB on apparent digestibility in rainbow trout. We have not found any reference to work on the effect of PAMB on the efficiency of biosynthesis. Pedersen (1987) found no effect of PAMB on  $\text{NH}_3$  excretion rate, suggesting that there were no significant changes in the amount of protein oxidized. The main effect of low PAMB therefore is a decline in feeding. There is no evidence that oxygen directly affects the efficiency of food conversion into biomass. Often observed decreases in gross food conversion efficiencies (weight gain/food consumed) below the critical PAMB are probably related to reduced feed intake and a proportionally larger maintenance requirement.

#### Final fish size

For *O. niloticus* between 0.5 and 241.0 g a value for GSEX of 0.75 was experimentally determined (Fernandes & Rantin 1986), while a reasonable maximum weight was obtained with values of GSEX between 0.65 and 0.70. In the larval stage, GSEX is generally larger than 1.0; most species show an inflexion point in the relationship between TAGSIZ and *W* at weights between 0.05 and 1 g (Hughes & Al-Kadhomiy 1988). By contrast, little is known about the gills of fish close to their maximum size. We are using the experimental value of GSEX far outside the weight range from which it was experimentally derived. Ageing may decrease the area available for diffusion, e.g. by an increase in connective tissue. Similarly, WBD may be affected by ageing, although variability in WBD is related to differences in species rather than to body size (Hughes & Morgan 1973). The von Bertalanffy parameters computed by Palomares (1991;  $t_0 = 0.787$ ,  $W_\infty = 5700$  g,  $K = 0.176$ ) suggest that 95% of  $W_\infty$  is reached after about 20 years. A feeding level of 6.0–6.5 g  $\text{kg}^{-0.8} \text{day}^{-1}$  results in the right time span and this is in fact the feeding level reported by Harbott (1976).

For a given species, both an increase in mainte-

nance requirements (e.g. when temperature or other external factors increase activity) and a decrease in maximum aerobic scope (e.g. when PAMB is low) can cause a decrease in final weight (Fig. 7). Within the scope for production, feed composition, through its effect on feeding metabolism, affects the amount of feed that can be consumed. This explains why feed protein had a negative effect on the final size of the fish ( $O_2FDG$  was 0.172 g  $\text{O}_2$  (g feed) $^{-1}$  for the 25% protein feed, rising to 0.268 for the 50% protein feed; Fig. 7B). In the natural environment or under culture conditions, factors affecting routine metabolism and aerobic scope may fluctuate, resulting in curves rather than the straight lines of Fig. 7. Examples are the diurnal variations in pond dissolved oxygen concentration, and the seasonal changes in species composition of pond phytoplankton communities. FGS3 can, in principle, utilize information on such fluctuations for the prediction of fish growth.

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