MODELLING STUDIES OF
FISH PRODUCTION IN INTEGRATED
AGRICULTURE-AQUACULTURE SYSTEMS

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Anne A. van Dam

**Modelling studies of
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1995

Stellingen

1. Bij vissen begrenst de zuurstofopnamecapaciteit van de kieuwen de hoeveelheid voedsel die kan worden opgegeten en benut.
   Dit proefschrift

2. Bij watertemperaturen boven 25°C en ongelimiteerde voedselbeschikbaarheid zijn zuurstofconcentraties beneden 5 mg l^{-1} al beperkend voor de voedselconsumptie en groei van tilapia's.
   Dit proefschrift

3. Het heeft geen zin om tilapia's in rijstvelden waar de watertemperatuur boven 30°C blijft bijvoedering te verstrekken.
   Dit proefschrift

4. Voor de ontwikkeling van "low-tech" visproduktiesystemen is het gebruik van "high-tech" onderzoeksmethoden zinvol.

5. Een toename van visteelt op basis van vismeelhoudende voeders draagt niet bij aan groei van de wereldvisproduktie.
   Tacon, G.J. (1993) Feed ingredients for warmwater fish: fish meal and other processed feedstuffs. *FAO Fisheries Circular* **856**. Food and Agriculture Organization, Rome.

6. Bij statistische toetsen wordt te weinig aandacht geschonken aan onbetrouwbaarheid, waardoor gemakkelijk een fout van de tweede soort wordt gemaakt.
   Peterman, R.M. (1990) Statistical power analysis can improve fisheries research and management. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 2-15.

7. V.W.O.-examenresultaten zijn geen goed criterium voor "selectie aan de poort".
   Drenth, P.J.D. (1995) *In Nederland is selectie onmogelijk*. 15^e Duijkerlezing, 30 maart 1995, Amsterdam.
   Deze promovendus

8. Levensmiddelenproducenten moeten bij de etikettering mededelingen over wat er *niet* in hun produkten zit weglaten.

9. Zonder rechtvaardigheid geen duurzaamheid.

Stellingen behorend bij het proefschrift "Modelling studies of fish production in integrated agriculture-aquaculture systems" van A.A. van Dam, Wageningen, 10 mei 1995.

'Anyway, I started bitching one night before the broadcast. Seymour'd told me to shine my shoes just as I was going out the door with Walker. I was furious. The studio audience were all morons, the announcer was a moron, the sponsors were morons, and I just damn well wasn't going to shine my shoes for them, I told Seymour. I said they couldn't see them *any*way, where we sat. He said to shine them anyway. He said to shine them for the Fat Lady. I didn't know what the hell he was talking about, but he had a very Seymour look on his face, and so I did it. He never did tell me who the Fat Lady was, but I shined my shoes for the Fat Lady every time I ever went on the air again - all these years you and I were on the program together, if you remember.'

(from: J.D. Salinger, "Franny and Zooey")

Abstract

MODELLING STUDIES OF FISH PRODUCTION IN INTEGRATED AGRICULTURE-AQUACULTURE SYSTEMS

Thesis by Anne A. van Dam, Department of Fish Culture and Fisheries, Wageningen Agricultural University, Wageningen, The Netherlands

The general objective of this thesis is to formulate a general model for fish production in integrated ponds and ricefields as a means of obtaining a better understanding of these production systems. Integrated culture systems produce fish without large industrial energy inputs and have positive effects on the whole farm system. A main characteristic is their environmental variability, notably dissolved oxygen concentration and temperature. A systems approach using mathematical models is advocated because it can lead to insights that have universal applicability while avoiding the pitfalls of site- and species-specific, expensive experimental work. Two modelling approaches are distinguished: descriptive models, generally the result of statistical analysis of datasets; and explanatory models, based on knowledge of the biological processes underlying fish production.

Multiple regression analysis (a descriptive modelling technique) was used for the analysis of data from 15 integrated rice-fish production experiments with the Nile tilapia (*Oreochromis niloticus* L.) in the Philippines. Results showed that this technique led to insights that had not been obtained through separate analysis of the experiments. Main drawback of this method was that the models were not applicable to other production environments.

An explanatory model (called Fish Growth Simulator, or FGS) for growth of *O. niloticus* was developed on the basis of an existing simulation model for the African catfish *Clarias gariepinus* Burchell (1822). After parameterization and calibration, the model gave good predictions of fish growth in independent datasets. Parameterization and calibration of the same model for the rainbow trout *Onchorhynchus mykiss* (Walbaum) demonstrated the generality of the model and it was concluded that, provided that enough data are available, the model may be used to predict growth in a wide range of fish species. Food amount and composition, and temperature were the environmental variables upon which the model based its predictions.

FGS was expanded with a dissolved oxygen module to accomodate oxygen as an environmental variable. The module was based on the hypothesis that oxygen is needed in sufficient amounts for aerobic metabolism, and that gill surface area limits the supply of oxygen to fish. The resulting model allowed the simulation of fish growth under low dissolved oxygen concentration and also provided an explanation for differences in the final weight of fishes, both within and between species.

FGS was used for simulation of food and oxygen limitations in waste-fed fish ponds in Honduras, Thailand and Rwanda. The model simulated fish growth for various combinations of environmental conditions: temperature, food availability and dissolved oxygen concentration. Validation, using data from Indonesia and Panama, was not successful because estimates of the food consumption rate in these countries were not reliable.

In the last chapter methodology, the role of oxygen in fish metabolism and growth, model implications for the management of integrated agriculture-aquaculture systems and implications for further work are discussed.

Contents

Chapter 1

FISH PRODUCTION IN INTEGRATED AGRICULTURE-AQUACULUTRE SYSTEMS: GENERAL INTRODUCTION

Background

Fish is an important source of animal protein for human consumption, especially in the developing countries where it provides some 25% of the total animal protein consumption (Huisman, Born and Verdegem 1993). Total world fish production (including finfish, shellfish and seaweeds) has grown since the 1950s to about 104 million tonnes per year in 1990. Capture fisheries contributed about 90 million tonnes and aquaculture 14 million tonnes (13.5%) to total fish production (FAO 1991 in Huisman et al. 1993). Capture fisheries yields are stagnating because of overfishing and environmental degradation. Maintaining or possibly increasing production from fishing may be achieved through improved fish resources management and reduction of postharvest losses. The prospects for aquaculture are more promising and aquaculture is likely to further increase its share in total fish production (ICLARM 1992; Huisman et al. 1993).

Fish can be cultured in a variety of systems, ranging from extensive ponds without feeding or fertilization to intensive recirculating tank systems with complete high-protein feeds, water treatment and oxygenation. Earthen ponds can produce fish solely on the basis of solar and biological energy inputs and need less industrial energy per kg of fish produced than more intensive systems like concrete raceways and recirculating systems (Pitcher and Hart 1982; Olah and Sinha 1986; Li 1987). Fishponds can be fed with agricultural wastes and by-products. Organic crop or livestock wastes of low nutritional quality (i.e., high in cellulose and low in protein) can be mineralized by the microbial community at the pond-sediment interface. The resulting microbial biomass can be utilized by fish and the inorganic nutrients either accumulate in the pond sediment or are utilized by primary producers (phytoplankton) that can also serve as fish feed. With appropriate management, atmospheric nitrogen can be absorbed by nitrogen-fixing forms of phytoplankton. For these reasons, fishponds have been promoted as a means of increasing inland fish production in developing countries. Submerged ricefields are very similar to fishponds and may also serve as fish husbandry systems (dela Cruz et al. 1992).
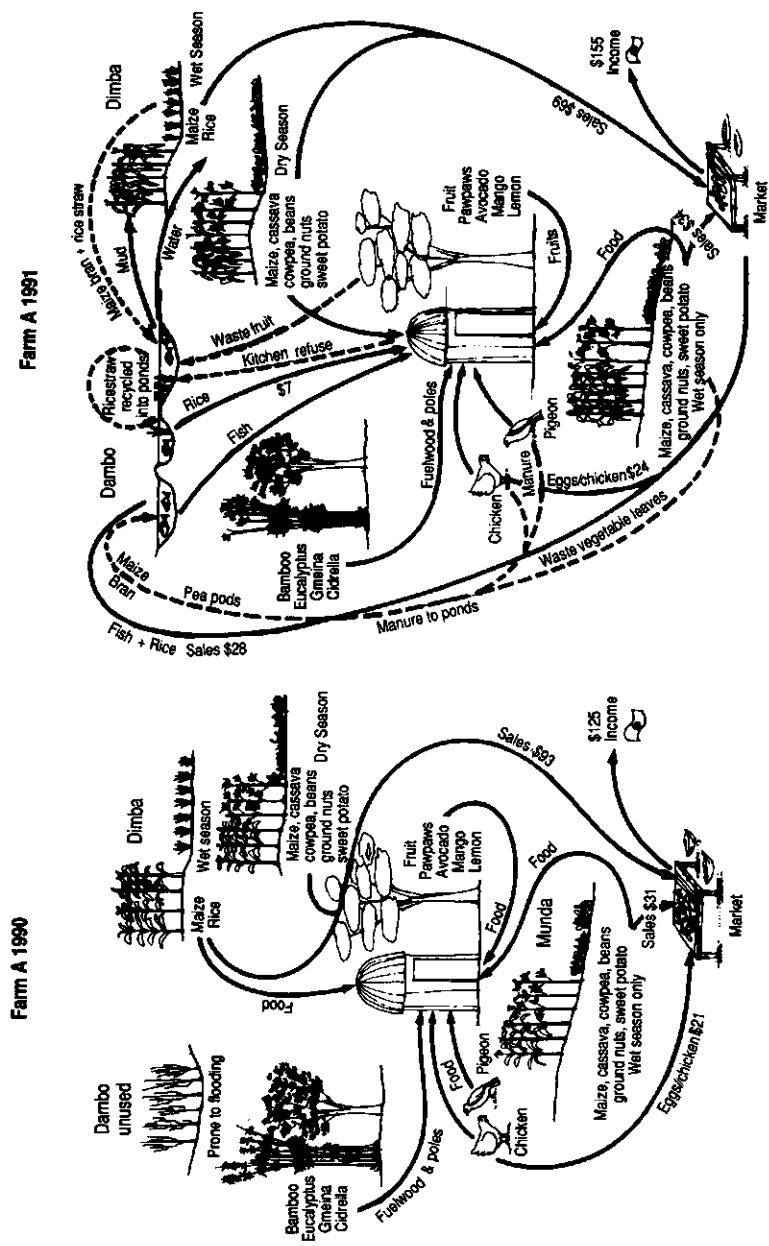
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Figure 1.1. Farming system in southern Malawi before and after adoption of aquaculture. From: ICLARM (1993).

Apart from bringing nutritional benefits, fishponds can be valuable elements of integrated tropical farming systems. Integrating fishponds with other agricultural enterprises may stimulate synergistic effects within the whole farm. Fishponds can enhance the cycling of nutrients, converting crop and livestock wastes into high-quality fish protein and fertile pond mud. Fishponds can play a role in water management and increase the productivity of lowlands (Edwards, Pullin and Gartner 1988; Lightfoot 1990; Christensen 1985). In this way, fishponds increase the diversity of species, the number of resource flows, the total farm output and the net farm income; in other words, they improve the productivity and efficiency of farming systems, possibly leading to more sustainability (Lightfoot, Bimbao, Dalsgaard and Pullin 1993; Figure 1.1). A typical example of the synergism between fish and crops is the positive effect (on average 15%) of fish on rice yields in integrated rice-fish systems (Lightfoot, van Dam and Costa-Pierce 1992). More examples of improvements in income and production after introduction of aquaculture on farms have been reported (Ahmed, 1992; Ahmed, Bimbao and Sevilleja 1992; Lightfoot and Noble 1993).

Systems approach and modelling of aquaculture systems

Under well-controlled conditions on experimental research-stations, integrated agriculture-aquaculture (IAA) systems can produce high fish yields solely on the basis of farm by-products and wastes (Edwards 1980; Hopkins and Cruz 1982). It has been difficult, however, to realize such integrated systems under practical farm conditions. Despite the potential of IAA systems, socioeconomic and biotechnical constraints have limited their adoption by large groups of farmers. Even in Asian countries with long aquaculture traditions, less than 1% of the total farming population is involved in IAA farming systems (ICLARM 1992).

Several reasons have been given to explain this situation. Socioeconomic constraints, encountered during and after the "transfer" of the technology to farmers lie at the root of a large part of the failures. Consideration for the context of aquaculture development (i.e., national development policies, relationships to other sources of protein,

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organic
fertilization

▪

↓

excretion/	organic matter	
natural mortality/	(dissolved, particulate)	breakdown/
respiration	dissolved oxygen	consumption

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AUTOTROPHIC                          HETEROTROPHIC
PATHWAY                              PATHWAY

                    breakdown            fish
                                      small nekton
phytoplankton       consumption       zoobenthos
macrophytes                           zooplankton
periphyton                            bacteria
                                      protozoa
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photosynthesis	inorganic matter	mineralization
	(carbon dioxide, nitrogen and	
	phosphorous forms, etc.)	

▲
▪

▪
inorganic
fertilization

Figure 1.2. General structure of the pond ecosystem

biophysical and socioeconomic environment), and new approaches to agricultural and aquacultural research and extension should overcome some of these constraints (Chambers, Pacey and Thrupp 1989; ICLARM and GTZ 1991; Lightfoot, Bimbao, Dalsgaard and Pullin 1993; Middendorp 1994). On the biotechnical side, the complexity of integrated systems and the large variability in species, farm systems and environments are major hurdles in research for improved productivity.

Conventional agricultural research addresses productivity problems with dose-response experiments and statistical analysis. Such experiments can yield important information about how the whole system functions under specific conditions, but it is difficult to extrapolate research results to other areas. Moreover, the number of potential

aquaculture species is vast, especially when compared to livestock production. Also large is the number of potential feeds and fertilizers. Superimposed on these are the effects of soil type, water characteristics and climate. In addition, the variability in farming systems is large (rice-based/maize-based, irrigated/rainfed, lowland/highland, etc.). The amount of experimental work needed to cover all environments would be enormous.

Despite the large variability in factors affecting fish production in ponds, the underlying physical and biological processes are similar. The same species of zooplankton and algae appear in fishponds around the world. The relative importance of the various groups in the pond may vary, and the rates at which processes run may be different; the main relationships between groups are identical (Pullin 1987; Figure 1.2). At the farm system level, similar parallels can be found in nutrient and energy cycles among the different farm enterprises.

The basic physiological and ecological processes in ponds and on farms offer possibilities for a production ecology approach using systems analysis. General pond and farm models may help to gain insight in how pond and farm systems function. General models will allow comparison of systems, whose behaviours appear to be different but are in fact manifestations of the same basic processes under different conditions. Such models will allow theoretical evaluations of proposed management strategies and extrapolation of research results to other climatic zones. In this way, they can help accelerate research output and thereby save time and money.

This thesis aims at general insight into fish growth and fish production in tropical pond systems (including ricefields) using a model as an integrative tool. The main objective of constructing such a model is to obtain a better insight and understanding of the way various variables affect fish productivity in ponds, and to find ways to improve it. Model construction is thus primarily a means towards obtaining a better understanding of fish production. If it is possible to validate the model, it may be used for predictive purposes. Although the ultimate goal is a model that simulates a whole pond system (including natural fish food organisms as affected by climate and pond inputs), fish growth and yield are the central topics in this thesis.

Overview of the chapters

Chapter 2 is a review of earlier studies using models of aquaculture pond systems. An important element of a systems approach is quantification of the system. Descriptive (also called empirical) models do this by relating system variables in a mathematical equation using statistical techniques to estimate the equation parameters and their confidence limits. Such models do not explain the mechanisms underlying the observations and cannot be used outside the range of conditions they were estimated in. Their strength is in summarizing and analyzing large datasets, giving insight in the relationships between the system variables. By contrast, explanatory (also called theoretical or mechanistic) models quantify the system on the basis of knowledge about the processes that occur in the system, their relationships with each other and with external factors. If formulated and parameterized correctly, an explanatory model explains systems behaviour over a wide range of conditions and, if well validated, may be used for predictions.

In *Chapter 3*, descriptive models are used to analyze the interactions between fish and rice in an experimental rice-fish system. This work was done as part of a research project for the development of integrated rice-fish farming systems at the Freshwater Aquaculture Center of Central Luzon State University, Philippines. Research at this Center had been going on for more than 10 years and all experiments were described in semi-annual technical reports. Many individual experiments, comprising triplicated randomized treatments analyzed with analysis of variance, did not yield statistically significant results. Drawing on the work of Pauly and Hopkins (1983) and Prein (1985), multiple linear regression was used to analyze the combined data which resulted in insights that were not obtained from the separate analyses of experiments. Although the statistical models in this chapter explain a large part of the variation in tilapia growth and yield, they do not give a causal explanation. To understand fish production under a wide range of culture conditions, an explanatory model is needed.
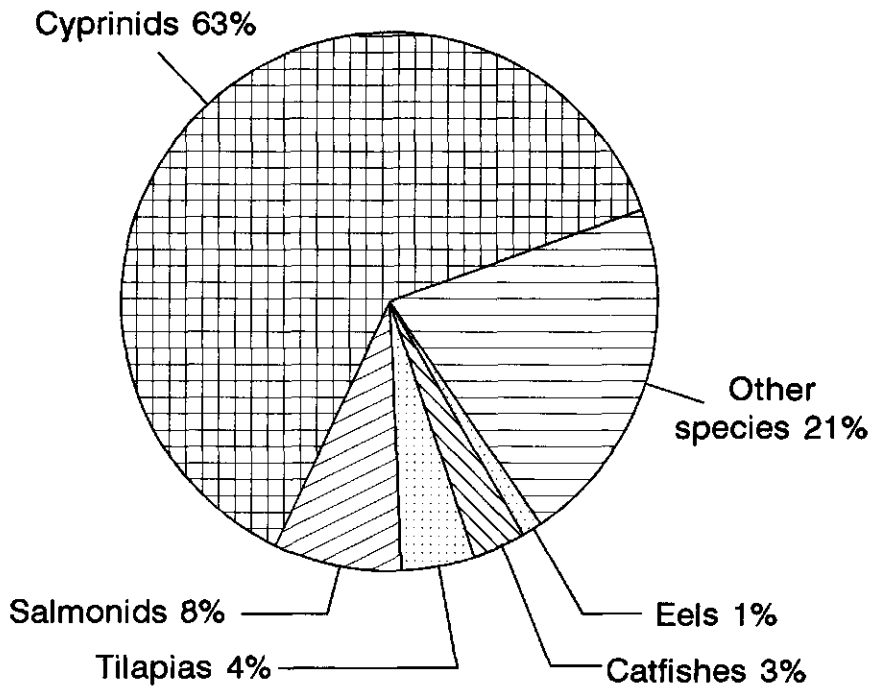
Figure 1.3. Species composition of finfish production from aquaculture. Global annual tilapia production was about 350,000 tonnes in 1990, representing 4% of total aquaculture finfish production (based on Pullin 1991 and Huisman et al. 1993).

In *Chapter 4*, the parameterization and calibration of an explanatory fish growth model is given. Such a model should incorporate the most important variables affecting fish growth: food quantity and composition; water temperature; and dissolved oxygen. For incorporation into a pond model, the fish growth model should also quantify the effects of the fish on its environment: oxygen consumption, and waste production. Such a model should be applicable to the variety of fish species used in tropical aquaculture systems.

A general model that meets the majority of these requirements was developed by Machiels at the Department of Fish Culture and Fisheries, Wageningen Agricultural University (Machiels and Henken 1986, 1987; Machiels and van Dam 1987; Machiels 1987). Machiels parameterized and calibrated his model for the African catfish *Clarias*

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gariepinus (Burchell), using the experimental data from the Department's fish laboratory. Main variables in this controlled environment were water temperature, and food amount and composition. The general physiological and biochemical principles of fish growth were incorporated and the model should therefore be applicable to other fish species. The model predicts growth on the basis of food quantity and composition and also computes the amount of oxygen needed for metabolism. In addition, the model allows computation of faecal wastes and ammonia excretion.

In this chapter, Machiels' model was calibrated for two other fish species: the Nile tilapia *Oreochromis niloticus* (L.), a herbivore, feeding mainly on phytoplankton and detritus; and the rainbow trout *Oncorhynchus mykiss* (Walbaum), a carnivore used primarily in intensive feedlot systems. Tilapias are important pond culture species in the tropics with a global production of around 350,000 tonnes (Pullin 1991; Huisman et al. 1993) (Figure 1.3). At present, *O. niloticus* is the most important tilapia species in aquaculture (around 170,000 tonnes in 1989; Huisman et al. 1993). The data used to calibrate and test the models were taken from experimental systems similar to those used by Machiels, in which effects on fish growth other than from food and temperature were eliminated.

In fishponds with high levels of organic inputs, microbial respiration can lead to low dissolved oxygen concentrations. Oxygen is needed by all aerobic heterotrophic organisms for the generation of energy. Machiels' model had ignored the oxygen concentration of the water. Since oxygen is particularly important in pond fish production, in *Chapter 5* the model was extended with an oxygen limitation module. The new model was called Fish Growth Simulator (FGS).

In most fish species, the main barrier to oxygen are the gills. Pauly (1981) recognized this and related the growth performance of fishes to the size of their gill surface area. His work resulted in a generalized Von Bertalanffy Growth Function that could be used to describe and explain the growth of fish populations under different environmental conditions. The Von Bertalanffy equation cannot be used, however, to

evaluate the effects of differences in food composition on fish growth. In FGS, Machiels' model and Pauly's oxygen limitation theory were combined.

In chapters 4 and 5, FGS was developed with data from highly controlled tank environments. In *Chapter 6*, the model was used to simulate fish growth in waste-fed fish ponds to analyze the effects of food and oxygen limitation on fish growth. The data used for this study were from the Pond Dynamics/Aquaculture Collaborative Research Support Program (PD/A CRSP), a program supported by the U.S. Agency for International Development in which a number of American universities and developing country aquaculture institutions participate. Part of the PD/A CRSP was a "global experiment" from 1982 to 1987, in which standardized experiments were conducted in a number of sites around the tropics. The rationale for standardization was that it would allow comparison of data from different geographic locations. Field data were collected in a central data base, analyzed centrally and used for various modelling exercises by the CRSP Data Analysis and Synthesis team (Egna, Brown and Leslie 1987). The data used in chapter 6 are from this CRSP database.

The main feature of FGS is its ability to evaluate through simulation the effects of food composition and quantity, temperature and dissolved oxygen concentration. In the controlled experiments, food intake was usually known. Under pond conditions, fish consume natural food which makes it necessary to estimate their food consumption rate. In addition, the total biomass in some ponds exceeded the carrying capacity towards the end of the culture period, resulting in food limitation. Therefore, a mechanism for food limitation was built into the model. The new model was calibrated using data from Thailand, Honduras and Rwanda (total dataset of 102 ponds) and was validated using independent data from Indonesia and Panama (33 ponds).

Chapter 7 concludes the thesis with an overall discussion of assumptions and results in the light of the initial objectives. A number of implications for fishpond management and for further research are considered.

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Chapter 2

MODELLING OF AQUACULTURE POND DYNAMICS[*]

Abstract

Aquaculture pond models are reviewed. Empirical pond models can be used for the analysis of large pond datasets, while theoretical models are based on knowledge of the processes underlying the system. Existing models deal with fish production in ponds, the foodweb and pond water quality. Most succesful models in terms of predictive ability and applicability in day-to-day management are models for dissolved oxygen and temperature. Fish growth models are constrained by difficulties in modelling food consumption and natural food quality. Pond models generally lack elements of the heterotrophic foodchain and of hydromechanical aspects of pond production. Modelling will become more important as a tool in pond research, but the use of pond models in actual management will depend on how well research results can improve the current models.

Introduction

Developing conceptual models of the systems they are studying is something all researchers do. These models can consist of a picture, a description in words, a miniature replicate or simply some ideas in the mind of the researcher. The word "modelling" however is used primarily to indicate the technique of using mathematical equations to describe a system. By changing the input variables of the equations, the system can be simulated under various conditions. Modelling techniques and model classifications are described elsewhere (e.g. Cuenco 1989).

An important distinction is that between empirical and theoretical models. Empirical models describe data without explaining the mechnanisms causing the relationships between the data. The model equations show relationships between variables or can be used to predict certain variables from other variables.

Theoretical or mechanistic models consist of a number of balance equations describing the flow rates in the system. Various "currencies" can be used, such as energy, mass, nitrogen etc. The rate variables are integrated over time to give the state variables. The modeller incorporates his/her knowledge about the system processes in the model and can simulate system behaviour in time with different inputs or environments.

Models can be applied in research, in management and in training/teaching. In research, models are useful for the analysis of large datasets, identification of knowledge gaps and testing hypotheses without doing expensive experiments. In management, models are used to predict system behaviour for different management strategies. As a teaching aid, models can increase understanding of the dynamics of complex systems without having to work with the real system.

Although numerous models of other aquatic systems (e.g. fish growth models, lake water quality models) are of interest to pond modellers, this review will concentrate on models of stillwater ponds (Table 2.1). More details of aquaculture systems modelling are discussed in reviews by Bernard (1986), Fridley (1986), Piedrahita (1988) and Cuenco (1989).

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Table 2.1. Summary of empirical and theoretical models of pond ecosystems

Model	Type and Focus	Remarks
Boyd et al. 1978	empirical, dissolved oxygen	channel catfish ponds
Busch et al. 1977	empirical, dissolved oxygen	channel catfish ponds
Cuenco et al. 1985a,b,c	theoretical, fish growth in ponds	general model, validated with channel catfish
van Dam 1990	empirical, fish growth in rice-fish culture	multiple regression analysis
Diana et al. 1988a	empirical, whole pond	data from Thailand
Diana et al. 1988b	theoretical, fish growth in ponds and tanks	for *Clarias batrachus*
Klemetson and Rogers 1985	theoretical, water temperature	
Krant et al. 1982	theoretical, water temperature	
Madenjian et al. 1987	empirical/theoretical, dissolved oxygen	
Meyer and Brune 1982	theoretical, dissolved oxygen	
Meyer et al. 1983	theoretical, dissolved oxygen	
Milstein et al. 1985a,b	empirical, plankton	principal component analysis
Milstein et al. 1988	empirical, pond	canonical correlation analysis
Piedrahita 1989	theoretical, dissolved oxygen	
Piedrahita et al. 1983	theoretical, pond	
Piedrahita et al. 1984	theoretical, pond	
Prein 1985	empirical, fish growth in ponds	multiple regression analysis
Romaire and Boyd 1979	empirical, dissolved oxygen	channel catfish ponds
Romaire et al. 1978	empirical, dissolved oxygen	tilapia ponds
Ross and McKinney 1989	theoretical, fish growth	tilapia
Svirezhev et al. 1984	theoretical, pond	polyculture
Tysso 1986	theoretical, fish growth	with population model for cultured fish
Wolfe et al. 1986	theoretical, pond	artificial solar algae pond with *Oreochromis aureus*

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Fish production

A host of fish growth models exist, but only a few with direct importance for pond culture are discussed here. Most fish growth models, including the fish components in comprehensive pond models, are based on the balanced energy equation: fish growth equals energy consumed minus respiration and excretion losses (Piedrahita, Brune, Tchobanoglous and Orlob 1984; Svirezhev, Krysanova and Voinov 1984; Cuenco, Stickney and Grant 1985a,b,c; Ross and McKinney 1989). Estimating the terms of the balanced energy equation requires experiments in closed-circuit respirometers with monitoring of gaseous exchange and collection of faeces. Linking experimental results to fish in a pond situation creates various problems.

Fish respiration is related to weight according to an empirical relationship. The effect of food composition on respiration (Ross and McKinney 1989) is usually not modeled. An exception is the biochemical growth model of Machiels and Henken (1986); this however, was not based on a pond situation. More problems arise in estimating the amount of food fish consume, both at satiation and below (Diana, Kohler and Ottey 1988).

Mechanisms for the regulation of food intake are not sufficiently clarified to formulate a good model. Most modellers assume negative effects of low DO-levels and high unionized ammonia concentrations (Piedrahita et al. 1984; Cuenco et al. 1985a; Wolfe, Zweig and Engstrom 1986), although no consensus about the mechanism exists. Most toxicity studies are done with fixed levels of toxic substances, results of which are difficult to link to ponds with diurnally fluctuating concentrations (Cuenco et al. 1985c).

Food web

In empirical pond models, a statistical technique is used to structure large amounts of multivariate data. Milstein, Hepher and Teltsch (1985a,b) used principal components analysis to examine interactions between fish species in polyculture and their effects on phyto- and zooplankton populations. Input-output relationships and the effects of water quality parameters were studied using multiple regression (Prein 1985; van Dam 1990,

Chapter 3) and canonical correlation analysis (Milstein, Hulata and Wohlfarth 1988).

Theoretical pond models are based on the generally accepted concepts of fish production in ponds: photosynthetic binding of inorganic nutrients into phytoplankton and macrophytes (the autotrophic pathway) and breakdown of this plant material by a range of heterotrophs, including fish (heterotrophic pathway). By managing pond inputs and harvesting techniques, fish production is optimized.

The autotrophic pathway is represented in most models with a phytoplankton equation describing photosynthetic production depending on solar radiation and nutrient concentrations. The amount of light penetrating into the water column depends on turbidity, for which different measures are used (Secchi disk reading, phytoplankton density, etc.). Nutrient limitations are modeled with a Michaelis-Menten model (Piedrahita et al. 1984; Svirezhev et al. 1984). These phytoplankton models are all rather descriptive. Only Wolfe et al. (1986) model algal growth as the incorporation of nitrogen into algal biomass and so attempt a more theoretical approach. Except in Piedrahita et al. (1984), no distinction is made between different species of phytoplankton.

Heterotrophic productivity at the level of primary and secondary consumers is given much less attention in most pond models. Some models contain zooplankton (Piedrahita et al. 1984, Svirezhev et al. 1984), but bacterial production is usually modeled without reference to taxa, as a form of oxygen consumption by organic material. Wolfe et al. (1986) actually model bacterial biomass and its role in the fish diet. The general recognition of the importance of bacteria and detritus in the foodweb of fishponds is, however, generally not reflected in pond models (Pullin 1987).

Water quality
Water quality is coupled to all life processes in the pond water. In their water quality aspects, pond models resemble lake models very much. Given the intentional eutrophication of pond water and the importance of sediments (compared to deeper lakes), pond water quality modelling might need a more specific approach. Most of the work on pond water quality modelling has been done on dissolved oxygen (DO).

Empirical models for the prediction of oxygen levels in catfish and tilapia ponds in Alabama were developed by Boyd, Romaire and Johnston (1978), Romaire, Boyd and Collis (1978) and Romaire and Boyd (1979). Objective of these models was to help fish farmers decide on the necessity of emergency aeration to prevent early morning DO-depletion (and resulting fish mortality). Multiple regression models using dusk DO-concentration and respiration of fish, benthos and plankton to predict dawn DO-levels for the next day gave very good results ($R^2 = 0.80$-0.97). Plankton respiration turned out to be the most important contributor to DO-loss and could be measured easily because of its strong correlation with Secchi-disk depth. Measuring water temperature, DO-level and Secchi depth at dusk was enough to get an accurate prediction of DO-levels at dawn.

Madenjian, Rogers and Fast (1987a) evaluated the statistical models of Boyd and Romaire for application in Hawaiian prawn culture. They found a much weaker relationship between Secchi disk depth or chlorophyll a concentration and plankton respiration, while benthic respiration contributed more to overnight DO-loss. They developed a theoretical model (Madenjian, Rogers and Fast 1987b), using DO at dusk and three hours after dusk, as well as the expected average wind speed for the night as inputs. The model related oxygen loss to whole-pond respiration (depending on temperature) and to oxygen diffusion from the air (depending on wind speed and pond DO-levels). This simple dynamic model with easy-to-measure input requirements predicted dawn DO-concentrations on average within 0.5 mg l^{-1} from the actual values.

Theoretical models of pond oxygen were reported by Meyer and Brune (1982), Meyer, Brune and Haight (1983) and Piedrahita (1989). In these models, short-term (diurnal) oxygen fluctuations are modeled based on oxygen input through reaeration and photosynthesis and oxygen consumption through respiration of various organisms. These models are primarily research-oriented. Inclusion of a component for the simulation of pond mixing and its effects on sediment stirring and BOD would be a major improvement of the model (Meyer and Brune 1982).

The temperature models of Krant, Motzkin and Gordin (1982) and Klemetson and Rogers (1985) are both based on energy budgets that balance heat inputs from sun and hot water sources to losses through evaporation, convection, radiation and outflow. Klemetson

and Rogers used their model to evaluate site potential for warmwater aquaculture. Both models assumed complete mixing of pond water and predicted temperatures accurately. These models demonstrate that it is easier to model physical processes than biological processes.

All pond models are point models, i.e. they assume that the concentrations of nutrients in the water are the same, and that the pond water is fully mixed everywhere. The role of stratification on water quality and nutrient cycling in ponds (Chang and Hai 1988; Costa-Pierce and Pullin 1989; Wei and Laws 1989) has been ignored completely so far. Stratification models for lakes and reservoirs do exist and can be applied to aquaculture (Marjanovic and Orlob 1986; Losordo and Piedrahita 1988).

Conclusions

Empirical pond models employ multivariate statistical techniques like multiple regression analysis, principal component or canonical correlation analysis to analyze large datasets. Apart from pond data (e.g. harvesting and stocking data, water quality, plankton composition), secondary data such as climate and soil data can be incorporated so that data from different locations can be analyzed simultaneously (Pauly and Hopkins 1983). As data are collated from many different experiments, errors can be large and coefficients of determination (R^2) low, making the models unsuitable for predictive purposes. The power of these methods is their ability to detect effects of variables in huge data sets. More traditional methods like analysis of variance based on single experiments often fail to demonstrate effects with statistical significance due to large within-treatment variation in pond experiments (Cuenco 1989; van Dam 1990).

A few studies compare the use of empirical and theoretical models when applied to the same problem. Smith (1987, chapter 2; also Smith and Piedrahita 1988) applied the empirical oxygen model of Boyd and Romaire and a theoretical model to a channel catfish pond. Main differences between the models were the equations for oxygen generation and respiration by the plankton. While the empirical model gave a good prediction, the theoretical model had to be adjusted with elements of non-algal turbidity, plankton

respiration and nutrient limitation. Keller (1989) similarly modeled data from a coastal eutrophication experiment using principal components regression and a mechanistic model. Both models fitted the data very well, but there was also a significant difference between predictive ability, the mechanistic model giving more accurate predictions (F-test).

Empirical methods are generally considered to have less predictive value and a narrower applicability than theoretical models (Piedrahita 1988) and also to be less elegant (Cuenco 1989). The main advantage of theoretical models is the possibility to build in dynamic processes and feedback loops that are the key to understanding a system. Most theoretical pond models however contain empirical elements and are still far from being widely applicable while empirical models can compete quite well in terms of predictive ability. The choice of modelling technique should be based on a proper evaluation of modelling objectives and available resources.

All theoretical modelling involves some degree of simplification, but some aspects of pond dynamics have been unjustifiably ignored in pond models so far. Especially physical aspects (stratification, effects of wind on mixing), the sediment-water interface and bacterial production should be given more attention. There is as yet no concensus about the relative importance of the autotrophic and heterotrophic pathways in fish production in ponds. Some research results suggest that heterotrophs contribute much more to aquatic productivity in ponds than autotrophs (Costa-Pierce and Craven 1987); pond models have failed to address these issues so far.

Many elements of theoretical pond models are descriptive and empirical, not being based on knowledge of the underlying processes. Models can help identify knowledge gaps, but research results will have to fill these gaps. Only then can models be improved.

Pond models will become more important as tools for studying pond dynamics and improving pond management. In earlier days, the need for large and expensive computers made modelling an option only for a "happy few" scientists with strong institutional support. Now that many researchers and managers have access to relatively cheap personal computers, modelling can and should become a more widespread technique. Data acquisition systems (Losordo, Piedrahita and Ebeling 1988) can help in gathering the vast amounts of data needed for calibration and validation. Both statistical software (e.g.,

Microstat, SAS, SPSS, Statgraphics, Systat) and packages for dynamic simulation (e.g., PCSMP, Dynamo, Stella) are now readily available for use on personal computers.

The impact of pond modelling on actual fish production from ponds will depend on the type of system. High-input, intensive systems where fish production depends entirely on artificial, high-quality feeds are constrained by water quality, and models that address water quality are reasonably successful (e.g. temperature and DO-models). Fish growth in such systems can be modelled quite well. These models, both empirical and theoretical, are the most likely to find application in management of commercial pond operations. Low-input ponds integrated with other agricultural activities, as found in many third-world farming systems, are more constrained by lack and variability of inputs and lack of knowledge about management. For such ponds, models that focus on the conversion of waste materials into fish biomass through algal and detrital pathways are needed. Due to the complexity of the foodwebs and a narrow scientific base, such models are difficult to formulate and a lot of research is needed to develop them. Management applications will emerge only in the long term.

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Chapter 3

MULTIPLE REGRESSION ANALYSIS OF ACCUMULATED DATA FROM AQUACULTURE EXPERIMENTS: A RICE-FISH CULTURE EXAMPLE[*]

Abstract

Data from 15 rice-fish experiments, conducted at the Freshwater Aquaculture Center of Central Luzon State University, Philippines during the years 1976-1983, were analyzed using the multiple linear regression technique with the objective to explain the variation in fish production from input and climate data. The experiments dealt with the effects of various management practices on the production of Nile tilapia, Oreochromis niloticus *(L.) in concurrent culture with several varieties of lowland irrigated rice,* Oryza sativa *(L.). Climate data were obtained from the nearest weather station.*

Significant models (P< 0.001) were derived for gross fish yield (kg ha⁻¹), net fish yield (kg ha⁻¹), fish recovery (%), fish growth rate (g day⁻¹) and rice yield (kg ha⁻¹). For gross fish yield, 66% of the variation could be explained by seven independent variables: length of the culture period, fish stocking weight and density, nitrogen and phosphorous application rates, insecticide application and air temperature.

The interpretation of the regression results is discussed. Despite the problems with linking regression coefficients to "real life" processes, this kind of exploratory data analysis, applying modern statistical techniques, can be a useful tool in summarizing the results of previous research and obtaining more information from existing data.

Introduction

Aquaculture experiments often consist of a small number of treatments, that are expected to influence a dependent variable. The treatments differ in one important factor while other factors are kept the same for all treatments. Ideally, every treatment is replicated at least three times. Statistical analysis usually consists of analysis of variance (ANOVA).

There are some disadvantages to this method. As experimental units (e.g. ponds) are expensive, the researcher has to decide between testing a few treatments with the required number of replications and testing more treatments with fewer replications. Furthermore, the effect of only one or a few factors can be measured in every experiment. Finally, the number of experimental units is small which makes it difficult to prove anything with statistical significance. All this makes it worthwhile to look for more effective ways of analyzing aquaculture experiments.

Pauly and Hopkins (1983) described a method for analyzing pond growth experiments using the multiple linear regression technique. Prein (1985) used this technique to analyze accumulated data on animal-fish farming from several experiments. The basic idea behind the method is that differences between experiments can be quantified, and used to explain variation in a dependent variable.

For instance, by making climate variables a part of the model, experiments that were conducted in different seasons can be compared. Likewise, experiments of different duration or with different inputs can be compared when the length of the culture period or the input variables are included in the model.

The model equation is:

$$Y = a + b_1X_1 + b_2X_2 + ... + b_kX_k + \epsilon \qquad (3.1)$$

with

Y	:	dependent variable
$X_{1..k}$	:	independent or explaining variables
$b_{1..k}$	:	partial regression coefficients
a	:	constant (intercept)
ϵ	:	residual

The regression coefficients are estimated by the method of least squares, using a computer and a suitable statistical software package. By comparing the partial regression coefficients (sign, value) inferences can be made about the effects of various independent variables on the dependent variable. A discussion of the backgrounds of multiple linear regression can be found in most textbooks on statistics (Blalock 1972; Yamane 1973; Snedecor and Cochran 1980; Parel, Orense & Tan 1986).

In this paper, the multiple linear regression technique was used to analyze a number of experiments on concurrent rice-fish culture that were conducted at the Freshwater Aquaculture Center (FAC) of Central Luzon State University (CLSU) in the Philippines, from 1974 to 1983. The culture system developed at the FAC was described by Arce and dela Cruz (1979), dela Cruz (1980) and in some extension leaflets (BFAR, undated; NFAC, undated; PCARR 1979).

Material and methods

Fifty experiments on rice-fish culture were described in unpublished Technical Reports of the FAC. Only experiments dealing with concurrent culture of Nile tilapia, *Oreochromis niloticus* (L.) and rice, *Oryza sativa* (L.) were considered. Pesticide toxicity tests (resulting in 100 % fish mortality), trials with other fish species like *Cyprinus carpio* (L.) or *O. aureus* (Steindachner), other crop species like Taro, *Colocasia esculenta* (L.) or with organic fertilizers, and experiments that lacked adequate description were excluded from the analysis.

Although most production data could be included in the analysis without modification, some needed reexpression. For herbicide application, basal insecticide application and feeding, the problem of expressing the variety of chemicals used and feeds given was avoided by indicating the presence or absence of such a treatment (dummy variables, Blalock 1972, Yamane 1973). In the case of insecticide sprayings, the number of spray applications was used as a variable rather than including separate variables for every chemical used. The fertilizer applications were recalculated to give the amounts of nitrogen, phosphorous and potassium in kilograms per hectare applied either basally

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(incorporated in the soil before transplanting the rice seedlings) or as a top dress (broadcasted in the field about one month after transplanting).

Climate data were obtained from the Philippine Agronomical, Geophysical and Astronomical Services Administration (PAGASA)-CLSU Station, which is located approximately one kilometer from the experimental site. There were six variables: daily maximum and minimum air temperature (degrees Celsius), daily rainfall and evaporation (in millimeters), daily sunshine duration (in minutes) and daily wind speed (in knots).

The remaining dataset was checked for obvious errors and loaded into a microcomputer using a statistical software package (Ecosoft, 1981). Some of the independent variables were transformed using a logarithmic (base 10) transformation in order to stabilize the variance (Kendall and Buckland, 1982).

For every dependent variable a simple linear regression was calculated using the independent variable that had the strongest correlation with the dependent variable. Then, independent variables were added to the model one at a time. An independent variable would be retained in the model if its partial regression coefficient (b) was significantly different from zero, as shown by the t-test. The procedure was followed in a flexible way, comparing the performance of independent variables and sometimes discarding variables that had been entered into the model in an earlier step. Pairs of independent variables with high correlation coefficients were not jointly included in a model in order to avoid multicollinearity problems. For every dependent variable two models were constructed. In every second model, logarithmic tranformations (base 10) of independent variables were used to compare their performance in the model with the untransformed variables.

After construction of the models, it was verified whether the assumptions of linear regression (zero mean error, constant error variance, independent errors, see Parel et al. 1986) were satisfied. This was done by examination of residual plots (plots of the residuals against every X and against the estimated Y) for structural patterns, and by calculation of the Durbin-Watson statistic d (Durbin and Watson 1951; Yamane 1973; Parel et al. 1986). The Durbin-Watson statistic is compared with significance points d_L and d_U, as given by Durbin and Watson (1951), to test the null hypothesis that autocorrelation does not exist.

Standardized partial regression coefficients or beta weights were calculated as: beta $= b \times (s.d._x/s.d._y)$, where $s.d._x$ and $s.d._y$ are the standard deviations of the independent and dependent variable, respectively, to compare the effects of variables expressed in different units on a dependent variable (Blalock 1972; Yamane 1973).

Results and discussion

The dataset

The final dataset consisted of 198 cases with 36 variables each from 15 experiments (FAC 1976, 1978, 1979a, 1979b, 1980, 1981a, 1981b, 1982). There were five dependent variables: gross fish yield (fish biomass harvested in kilograms per hectare), net fish yield (fish biomass harvested minus fish biomass stocked in kilograms per hectare), recovery percentage (% of fish stocked that were harvested), fish growth rate (in grams per day), and rice yield (in kilograms per hectare). The 31 independent variables consisted of 18 original variables straight from the technical reports, six climate variables, and seven computed variables. For the most important variables, mean and standard deviation are given in Table 3.1.

Although the average gross yield was 122.9 kg ha^{-1} per culture period, the net yield or real fish production was only 51.4 kg ha^{-1}. In 32 cases (16.2 %) production was negative (i.e., less fish biomass was harvested than stocked). The mean length of the fish culture period was 79 days with an average fish recovery of 55.6% and average *O. niloticus* growth rate of 0.35 g day^{-1}. Average rice yield was 4337 kg ha^{-1}.

Regression analysis

Regression results are shown in Tables 3.2-3.6. All models were significant ($P < 0.001$). Examination of residual plots indicated no systematic patterns that could suggest violation of the zero mean error or the constant error variance assumptions. Not all variables were independent of each other, indicating the possibility of multicollinearity problems (Yamane 1973). The highest correlation between independent variables was 0.444

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Table 3.1. Descriptive statistics of the most important variables in this study. Number of cases (n) = 198

Name	Mean	SD	Min.	Max.
Dependent variables				
Gross fish yield (kg ha^{-1})	122.86	77.66	2.5	390.0
Net fish yield (kg ha^{-1})	51.35	68.62	-105.0	300.0
Fish recovery percentage (%)	55.62	25.49	1	100
Fish growth rate (g d^{-1})	0.347	0.123	0.14	0.84
Rice yield (kg ha^{-1})	4337.46	1689.08	600	8250
Independent variables				
Plot size (m^2)	201.52	27.55	100	400
Period (d)	78.97	17.73	50	114
Log period (d)	1.89	0.0995	1.70	2.06
Stocking density (no. ha^{-1})	5878.79	1883.80	2000	10000
Log stocking density (no. ha^{-1})	3.75	0.128	3.30	4.00
Stocking size (g)	12.80	9.41	1	44
Log stocking size (g)	0.958	0.404	0	1.64
Basal N application (kg ha^{-1})	63.11	13.18	40.2	79.5
Log basal N applic. (kg ha^{-1})	1.79	0.0961	1.60	1.90
Top dress N applic. (kg ha^{-1})	23.18	31.40	0	89.3
Basal P application (kg ha^{-1})	30.84	13.66	10.5	55.2
Log basal P applic. (kg ha^{-1})	1.44	0.205	1.02	1.74
Top dress P applic. (kg ha^{-1})	3.23	8.02	0	28
Herbicide application (dummy)	0.136	0.344	0	1
Basal insect. applic. (dummy)	0.707	0.456	0	1
No. of insecticide sprayings	1.19	0.879	0	3
Feed (dummy)	0.222	0.417	0	1
Avg. max. air temperature ($^\circ$C)	32.29	1.30	30.2	34.7
Avg. min. air temperature ($^\circ$C)	22.84	0.690	21.2	24.0
Avg. daily wind speed (knots)	4.97	1.04	3.2	7.0
Avg. daily evaporation (mm)	5.50	1.39	3.5	7.4
Avg. daily rainfall (mm)	3.68	2.81	0.1	8.8
Avg. daily sunshine (min)	476.85	85.51	350	611

(between stocking size and basal phosphorous application). With 198 cases, this was significant (P<0.05) but considered not to be a cause for concern, because at the most only $(0.444)^2$ x 100 = 19.7% of the variance in one variable is explained by the other.

The Durbin-Watson statistic d (see Tables 3.2-3.6) was calculated but the testing tables provided by Durbin and Watson (1951) do not go beyond 100 cases and five independent variables. Using the d_L and d_U-values for N=100 and k=5 ($d_L=1.57$ and $d_U=1.78$, $\alpha=5\%$), the test (H_0: autocorrelation r=0 against H_1: r$\neq$0) suggested that in models 1, 7, 8, 9 and 10 autocorrelation of the residuals occured ($d<d_L$), while for models 2, 3, 4, 5 and 6 the test seemed inconclusive ($d_L<d<d_U$). The effect of the autocorrelation may be that in some cases the variance of the partial regression coefficients is underestimated which can lead to acceptance of the hypothesis that b is unequal to zero when in fact it is not significantly different from zero. Because most b-values in this study were significant at the 0.1% level, no attempt was made to remove the autocorrelation (see also Draper and Smith 1981).

Four groups of independent variables can be recognized: fish variables (stocking size and density), fertilizer variables, pesticide variables and climate variables, leaving length of the culture period as a separate variable.

For the yield models (gross yield: models 1 and 2; net yield: models 3 and 4), the fish and fertilizer variables, together with temperature and length of the culture period were the most important explanatory variables. Pesticides did have negative effects in models 1 and 3, but their beta weights ranked low, their level of significance was lower and they disappeared from models 2 and 4 (see Figure 3.1). The negative effect of phosphorous fertilization was remarkably strong, ranking third in beta weight in models 1, 2 and 3 and even first in model 4 (see also Figure 3.1).

In the fish recovery models (models 5 and 6) the patterns were the same, although stocking density had a negative effect which was quite strong in model 6 (second ranking beta weight).

Stocking size and the number of insecticide sprayings were the most important variables explaining fish growth rate (models 7 and 8), with the fertilizer applications ranking second. Again, phosphorous application had a negative effect. In model 8, length

Table 3.2. Multiple regression models for gross fish yield (kg ha⁻¹). All partial regression coefficients (*bs*) were significant at the 0.1% level, except when marked ' (5%) or '' (1%). Also given are the standard errors (SE) of the *bs* and the standardized *bs* or beta weights (rankings between brackets). Number of cases = 198

Independent variables	Model 1			Model 2		
	b	SE	beta	b	SE	beta
Period (d)	1.57	0.225	0.359(4)			
Log period (d)				230.26	42.23	0.295(5)
Stocking density (no. ha⁻¹)	0.012	0.002	0.279(6)			
Log stocking density (no. ha⁻¹)				136.31	27.31	0.225(6)
Stocking size (g)	3.78	0.432	0.458(1)	3.82	0.423	0.463(2)
Basal N application (kg ha⁻¹)	1.74	0.283	0.296(5)			
Log basal N application (kg ha⁻¹)				276.07	36.36	0.342(4)
Basal P application (kg ha⁻¹)	-2.05	0.318	-0.361(3)			
Log basal P application (kg ha⁻¹)				-166.37	21.16	-0.439(3)
No. of insecticide sprayings	-10.03'	4.15	-0.114(7)			
Maximum air temperature (°C)	26.97	3.21	0.452(2)	28.67	3.17	0.481(1)
Constant (a)	-1022.83			-2051.25		
Coeff. of determination (R²)	0.6571			0.6676		
F-value	52.013			63.946		
Probability	<0.001			<0.001		
Durbin-Watson statistic	1.5120			1.5738		

Table 3.3. Multiple regression models for net fish yield (kg ha⁻¹). All partial regression coefficients (*b*s) were significant at the 0.1% level, except when marked ˙ (5%) or ˙˙ (1%). Also given are the standard errors (SE) of the *b*s and the standardized *b*s or beta weights (rankings between brackets). Number of cases = 198

	Model 3			Model 4		
	b	SE	beta	b	SE	beta
Independent variables						
Period (d)	1.86	0.279	0.481(1)			
Log period (d)				178.50	39.41	0.259(4)
Stocking density (no. ha⁻¹)	0.0064**	0.0022	0.176(6)			
Basal N application (kg ha⁻¹)	2.09	0.297	0.402(4)			
Log basal N application (kg ha⁻¹)				272.96	37.00	0.382(3)
Basal P application (kg ha⁻¹)	-2.25	0.292	-0.448(3)			
Log basal P application (kg ha⁻¹)				-180.65	19.68	-0.539(1)
Herbicide application (dummy)	-36.90˙˙	13.20	-0.185(5)			
No. of insecticide sprayings	-12.09˙˙	4.27	-0.155(7)			
Maximum air temperature (°C)	23.82	3.31	0.452(2)	27.74	3.24	0.527(2)
Constant (a)	-945.78			-1409.14		
Coeff. of determination (R²)	0.5536			0.5432		
F-value	33.659			57.387		
Probability	<0.001			<0.001		
Durbin-Watson statistic	1.5702			1.5827		

Table 3.4. Multiple regression models for fish recovery percentage. All partial regression coefficients (*bs*) were significant at the 0.1% level, except when marked * (5%) or ** (1%). Also given are the standard errors (SE) of the *bs* and the standardized *bs* or beta weights (rankings between brackets). Number of cases = 198

Independent variables	Model 5			Model 6		
	b	SE	beta	b	SE	beta
Period (d)	0.393	0.112	0.273(6)			
Stocking density (no. ha^{-1})	-0.0043	0.000821	-0.309(4)			
Log stocking density (no. ha^{-1})				-79.91	11.22	-0.401(2)
Stocking size (g)	0.894	0.202	0.330(2)	0.701	0.176	0.259(4)
Basal N application (kg ha^{-1})	0.749	0.130	0.387(1)			
Log basal N application (kg ha^{-1})				64.15	15.74	0.242(5)
Basal P application (kg ha^{-1})	-0.586	0.133	-0.314(3)			
Log basal P application (kg ha^{-1})				-41.63	7.98	-0.334(3)
Herbicide application (dummy)	-19.68**	5.98	-0.266(7)			
Maximum air temperature (°C)	5.79	1.39	0.296(5)	7.90	1.29	0.404(1)
Constant (a)	-174.75			36.47		
Coeff. of determination (R^2)	0.4469			0.4147		
F-value	21.935			27.206		
Probability	<0.001			<0.001		
Durbin-Watson statistic	0.6386			1.5949		

Table 3.5. Multiple regression models for fish growth rate. All partial regression coefficients (*b*s) were significant at the 0.1% level, except when marked * (5%) or ** (1%). Also given are the standard errors (SE) of the *b*s and the standardized *b*s or beta weights (rankings between brackets). Number of cases = 198

	Model 7			Model 8		
	b	SE	beta	b	SE	beta
Independent variables						
Log period (d)				-0.250**	0.0753	-0.202(3)
Stocking size (g)	-0.0037	0.0010	-0.283(2)			
Log stocking size (g)				-0.123	0.0201	-0.405(1)
Basal N application (kg ha^{-1})	0.0019**	0.00062	0.204(4)			
Basal P application (kg ha^{-1})	-0.0020**	0.00065	-0.222(3)			
Log basal P application (kg ha^{-1})				-0.118**	0.0395	-0.196(4)
Herbicide application (dummy)	-0.0535	0.0251	-0.150(5)			
No. of insecticide sprayings	-0.0413	0.0082	-0.292(1)	-0.0309	0.0078	-0.221(2)
Constant (a)		0.3886			1.1419	
Coeff. of determination (R^2)		0.3549			0.4097	
F-value		21.129			33.495	
Probability		<0.001			<0.001	
Durbin-Watson statistic		1.3130			1.4420	

Table 3.6. Multiple regression models for rice yield (kg ha^{-1}). All partial regression coefficients (*bs*) were significant at the 0.1% level, except when marked * (5%) or ** (1%). Also given are the standard errors (SE) of the *bs* and the standardized *bs* or beta weights (rankings between brackets). Number of cases = 198

| Independent variables	Model 9			Model 10		
	b	SE	beta	b	SE	beta
Independent variables						
Period (d)	18.29	5.06	0.192(4)			
Log period (d)				4787.84	931.77	0.282(4)
Stocking density (no. ha^{-1})	-0.503	0.0478	-0.561(2)			
Log stocking density (no. ha^{-1})				-5118.57	626.78	-0.388(2)
Basal N application (kg ha^{-1})	79.58	5.91	0.621(1)			
Log basal N application (kg ha^{-1})				10083.71	815.39	0.574(1)
Basal P application (kg ha^{-1})	18.44**	6.06	0.149(5)			
Log basal P application (kg ha^{-1})				2172.05	384.04	0.263(5)
Herbicide application (dummy)	672.48*	264.99	0.137(6)	539.14*	270.07	0.110(6)
Basal insecticide appl. (dummy)	1579.52	194.48	0.427(3)	1418.28	180.70	0.383(3)
No. of insecticide sprayings	250.45**	88.32	0.125(7)			
Constant (a)	-1237.20			-7761.74		
Coeff. of determination (R^2)	0.7088			0.7064		
F-value	66.080			76.574		
Probability	<0.001			<0.001		
Durbin-Watson statistic	0.9037			0.8985		
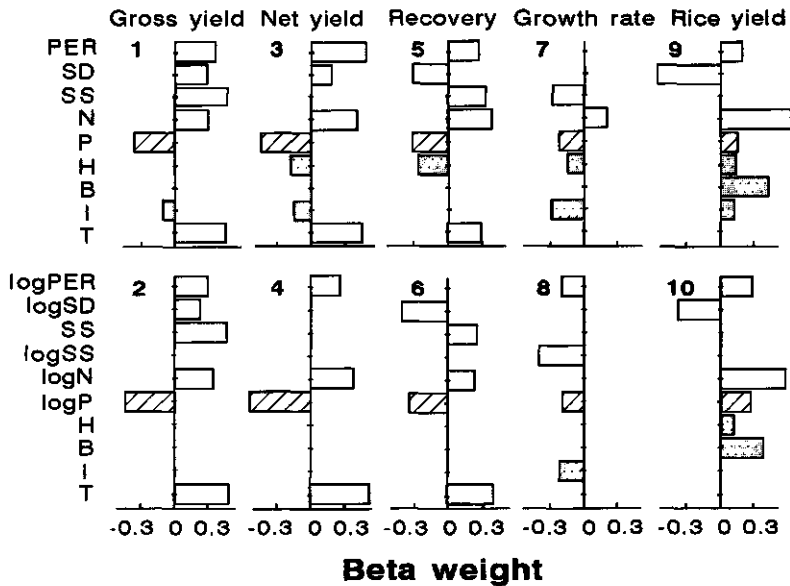
Figure 3.1. Beta-weights of variables in models 1-10. Pesticides (dotted bars) were of minor importance in models 1-6, had a strong negative effect on fish growth rate (models 7 and 8) and positive effects on rice yields (models 9 and 10). Phosphorous fertilization (striped bars) showed a negative effect on all fish variables (PER=length of the culture period, SD=stocking density, SS=stocking size, N=basal nitrogen application, P=basal phosphorous application, H=herbicide application, B=basal insecticide application, I=number of insecticide sprayings, T=maximum air temperature).

of the culture period had a negative effect, which may be an indication of food limitation towards the end of the culture period.

High fish stocking densities negatively affected rice yield (models 9 and 10). This seems to be a real effect of the fish, as field design and the number of rice plants were the same for all stocking densities. Of the pesticides, basal insecticide application most strongly influenced rice yield. Herbicide application and insecticide spraying were less important. This strengthens the FAC recommendation of using basal insecticides: it improves rice yield and does not appear to affect fish yield.

In general, the output of this culture system was strongly dependent on the fish input. Stocking bigger fish resulted in better recovery and bigger harvests, but the net

yield, which is the amount of fish biomass generated within the rice field during the culture period, was not influenced by increased stocking size.

Where nitrogen application increased all dependent fish variables, most likely by stimulating the food chain, phosphorous application had a negative effect. The effect was quite strong. Model 1 suggests that for every kg of P applied basally, gross fish yield will decrease by about 2 kg (all other variables remaining constant). This means a 60 kg fish yield decrease at an average of 30 kg P ha^{-1} per crop. A possible biological explanation is that phosphorous induces the growth of certain types of phytoplankton that are not readily consumed or digested by the fish (Colman and Edwards, 1987).

The expression of pesticide applications using dummy variables causes a loss of information as the toxicity of different chemicals varies considerably. The roughness of the dummy variables was mirrored in the relatively high standard errors of most pesticide coefficients, causing reduced significance levels. Pesticide applications were most important in the fish growth rate and rice yield models. In the fish yield and recovery models, beta weights of pesticide variables ranked relatively low (see Tables 3.2, 3.3 and 3.4 and Figure 3.1) whereas especially the number of insecticide sprayings was one of the most important variables explaining fish growth rate. This indicates that pesticides have an indirect effect on fish yields, working through the food chain. They may still cause fish mortality if their action depletes the food source of the fish. Moody (1992) reviewed several papers reporting on herbicide toxicity to crustaceans, notably *Daphnia* spp. Pesticide toxicity research should focus more on the effects of pesticides on the foodchain in rice-fish systems (Litsinger 1992).

It is difficult to interpret the recovery models. Recovery percentage in this study is a combined effect of fish mortality/survival, fish escape, predation by birds and poaching by humans. The importance of improving *O. niloticus* recovery can be illustrated by plotting either gross or net yield against recovery percentage. The regression equation for net yield ($R^2=0.458$, $P<0.001$) shows that improving recovery by 10% will raise net
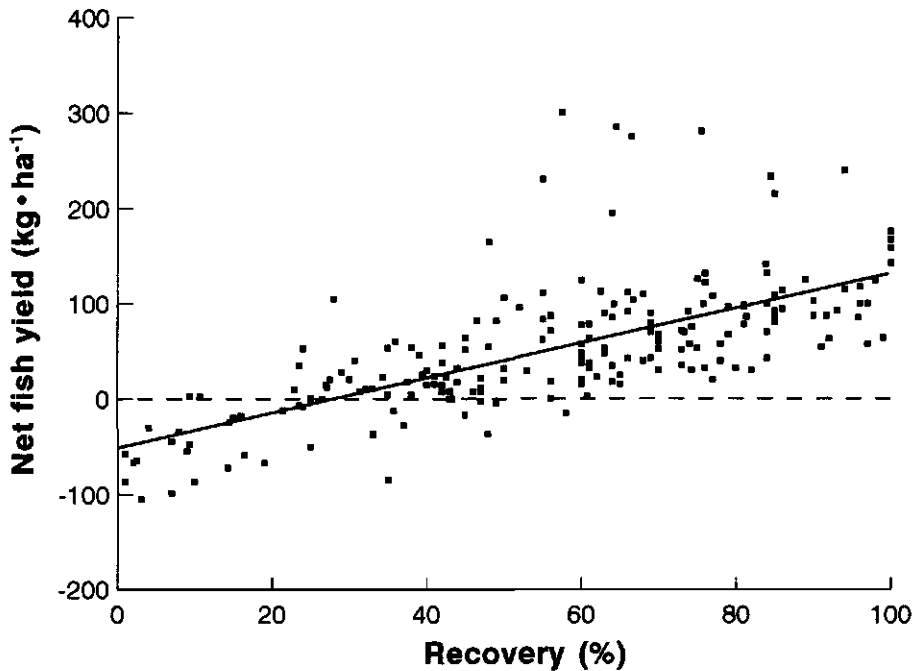
Figure 3.2. Relationship between recovery percentage (percentage of fish stocked that were harvested, horizontal axis) and net fish yield in kg•ha^{-1} (fish biomass harvested minus fish biomass stocked, vertical axis) in 198 rice-fish plots from 15 experiments. Regression equation:
$Y = -49.99 + 1.82 \cdot X$, $R^2 = 0.458$, $n = 198$, $P < 0.001$.

yield by 18 kg ha^{-1} (see Figure 3.2). The correlation between net yield and growth rate was much weaker.

It is questionable whether the rice paddy is a good environment for *O. niloticus*. Although varying with the environment, its food preference is generally phytoplankton and detritus which it can utilize efficiently by filtering the water (Bowen 1982; Colman and Edwards 1987). In rice paddies, with a bigger surface to volume ratio than ponds, the bottom is probably a more important food source than the water column. Phytoplankton disappears from the paddy water towards the end of the rice culture period as the rice canopy closes and shuts off the sunlight. This also implies that less carbon (in the form of CO_2) is trapped in the aquatic part of the system to feed the heterotrophic foodchain.

Common carp (*Cyprinus carpio*), which is a benthos feeder, performs much better in rice fields. Thirty-nine cases from five experiments at the FAC (FAC 1975, 1977a, 1977b) showed an average carp recovery of 80.2%. Carps in rice fields in Czechoslovakia fed mostly on bottom macrofauna (Onderiková 1957). The successful recent development of Indonesian rice-fish culture is based almost entirely on carp species and milkfish, *Chanos chanos* (Forskal) (Koesoemadinata and Costa-Pierce 1992).

An option for improving *O. niloticus* performance would be to enhance the detrital foodchain by applying organic fertilizers. Yields can be further improved if the culture period is extended, either by planting rice varieties that need more time to mature or by changing the culture system. A small pond could be connected to the rice field so that tilapia can be stocked before transplanting or kept after the rice harvest. This would also facilitate phytoplankton production. The technical and economic feasibility of any alternative would have to be studied though.

This study shows that exploratory data analysis using the multiple linear regression technique can be a useful tool in summarizing and analyzing large datasets. Existing sets of data that had never been analyzed as a whole before can thus yield more information than had originally been extracted. The potential for analysis of data collected with the aim of analyzing them with the multiple linear regression techniqe is even greater because such data are more complete and contain less errors.

The models presented here were not verified with independent data. Indeed, they are not meant to be used as predictive models and the ecological inferences made are hypotheses. Nonetheless, the models stimulate thinking about the rice-fish system under study and suggest relationships between variables that might otherwise not have been disclosed. The next steps in the study are to design and implement experiments to examine the hypotheses presented.

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Chapter 4

PARAMETERIZATION AND CALIBRATION OF A MODEL TO SIMULATE EFFECTS OF FEEDING LEVEL AND FEED COMPOSITION ON GROWTH OF *OREOCHROMIS NILOTICUS* (L.) AND *ONCORHYNCHUS MYKISS* (WALBAUM)[*]

Abstract

A dynamic model to simulate growth of the African catfish Clarias gariepinus *(Burchell) was parameterized and calibrated for Nile tilapia* Oreochromis niloticus *(L.) and rainbow trout* Oncorhynchus mykiss *(Walbaum). The model predicts fish weight and fat percentage from the amount and composition of the feed and water temperature. The major factor determining the efficiency of feed conversion is the proportion of energy provided by protein oxidation, which is positively related to the protein feeding level and the protein/energy ratio of the feed.*

The model predicted fresh weight of the herbivorous Oreochromis niloticus *in independent experimental data with a mean deviation of -2.1% (range -23% to +37%) of observed values (fish weights 10-40 g). For the carnivorous* Oncorhynchus mykiss, *this value was 4.8% (range -21% to +24%, 50-800 g). Options for further improvement of the model are discussed. We conclude that the structure of the model applies to a broad range of fish species and feeding schedules, provided that both feed and fish are characterized by a set of specific parameters.*

Introduction

Machiels and co-workers developed a model to simulate growth of the African catfish *Clarias gariepinus* (Burchell), which accounts for the effect of temperature and the amount and composition of the feed (Machiels and Henken 1986, 1987; Machiels and Van Dam 1987; Machiels 1987). This model (referred to here as the Fish Growth Simulator 1: FGS1) was developed on the basis of physiological and biochemical principles, expected to be common to all fish species.

Our objective is to assess whether the structure of FGS1 is valid for other fish species. We parameterized and calibrated FGS1 for two species: the herbivorous Nile tilapia *Oreochromis niloticus* (L.), one of the most important species in integrated pond aquaculture; and the carnivorous rainbow trout, *Oncorhynchus mykiss* (Walbaum), a species widely used in intensive systems. We also validated the model with independent datasets.

Material and methods

General

FGS1 was modified with regard to the definition of protein and fat oxidation rates (see model description). We refer to the new model as FGS2. Parameter values for *O. niloticus* and *O. mykiss*, and datasets on their growth as affected by feeding level, feed composition and temperature were obtained from published reports. For each experiment, the model was initialized with the observed starting weight and fat percentage. The amount of feed and its composition, and temperature were specified. Simulated final weight and fat percentage were compared with observed values.

The model was calibrated by adjusting the values of key parameters until the best agreement between observed and simulated values was reached without changing the structure of FGS1. We assume that changes in parameter values reflect biological differences between species. The model and parameter sets were validated with an independent dataset.

Agreement between simulated (Y) and observed (X) values was quantified using functional linear regression (Jensen 1986). Perfect agreement results in a line with intercept (a) = 0, slope (b) = 1 and a coefficient of determination (R^2) = 1. The deviation (D) of Y

Table 4.1. Input variables of the model. For explanation, see text and Figure 4.1. Types: e, characterizes experiment; s, characterizes species; u, assumed universal to fish. Digestibilities are determined by a combination of fish and feed properties.

Variable (dimension)	Name	Type
initial fish weight (g)	IWF	e
initial fish lipids (% fw)	ILIPER	e
fish protein content (% fw)	PRPERC	s
feed protein digestibility (%)	DIGPR	s,e
carbohydrate digestibility (%)	DIGCA	s,e
feed lipid digestibility (%)	DIGLI	s,e
proportion of digested lipid used for gluconeogenesis (-)	AAFDGL	s
proportion of energy supplied by fat (-)	AALIRAT	s
routine metabolism exponent (-)	RMEX	s
routine metabolism rate constant (mole ATP $g^{-0.8}$ d^{-1})	RMCF	s
cost of protein synthesis (mole ATP g^{-1})	PRATCO	u
cost of lipid synthesis (mole ATP g^{-1})	LIATCO	u
feed dry matter (% of fresh weight)	FEEDDM	e
feed protein (% in dry matter)	FEEDPR	e
feed carbohydrate (% in dry matter)	FEEDCA	e
feed lipids (% in dry matter)	FEEDLI	e
total amount of feed for growth period (g)	TOTFEED	e
water temperature (°C)	TEMP	e

from X was expressed as D = 100 (Y-X)/X (in %). The model was written in Professional Dynamo Plus (Pugh-Roberts 1986) and uses a fixed timestep of 0.125 day. 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: $kg^{0.8}$; 0.8 is the exponent from the relationship between fish weight and routine metabolism) (Winberg 1956; Becker and Fishelson 1990).

Model description and input requirements
An extensive description of FGS1 is given by Machiels and Henken (1986). Its main state variables are the amounts of body protein and body fat (Figure 4.1). These quantities change due to synthesis and oxidation. The rate of synthesis depends on feeding rate, feed composition, digestibilities of the feed components, and on the stoichiometry of the reaction equations of biosynthesis (Machiels and Henken 1986).

Digestion of feed protein, carbohydrates and lipids results in amino acids, glucose, and fatty acids and glycerol respectively. Amino acids are used for glucose or protein synthesis; glucose and fatty acids are used for synthesis of body lipids. Excretion of digested materials is assumed to be negligible.

The energy requirement (or metabolic rate, in mole ATP d^{-1}) is the sum of routine metabolism, feeding metabolism, and energy required for biosynthesis. Feeding metabolism is defined as the energy cost of feeding, digestion and absorption. Energy cost and yield of biosynthesis follow from the stoichiometry of the reaction equations. Energy (ATP) is provided by oxidation of body protein and lipids.

In FGS1, the fraction of the total energy requirement supplied by oxidation of fat depends on the ratio of body fat to body protein. For FGS2, we assumed that this fraction depends on the protein feeding level (in g feed protein (kg fresh body weight)$^{-0.8}$ d^{-1}) because the original formulation gave unsatisfactory results. This was the only major change we made to FGS1. Table 4.1 summarizes the input requirements of the model. A listing of the model is available from the first author on request.
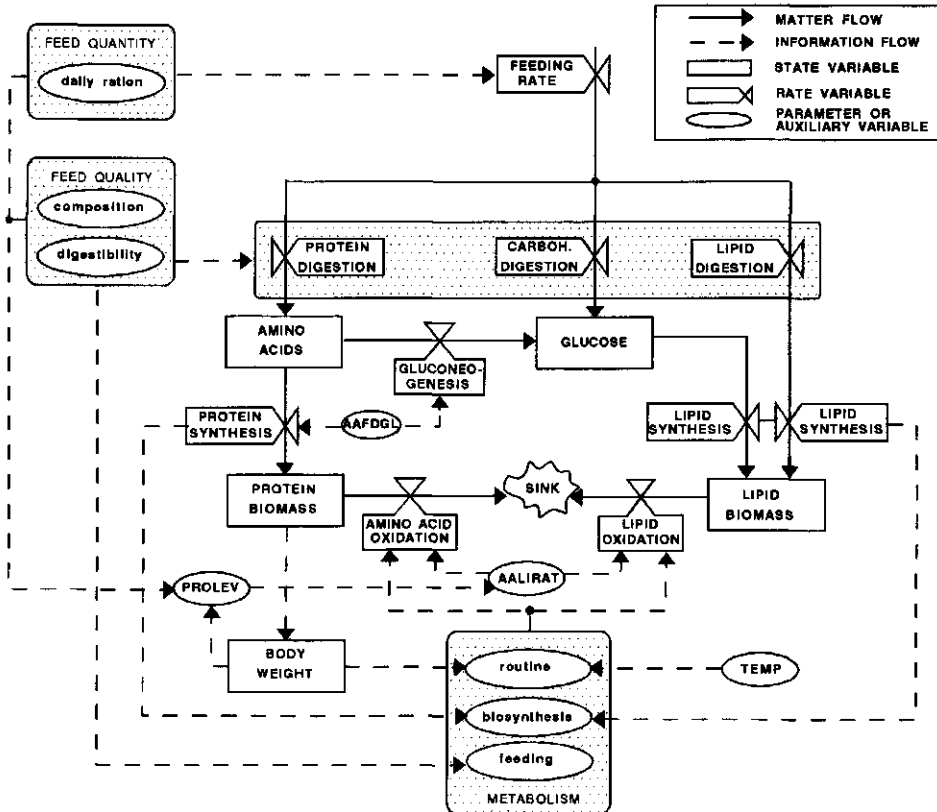
Figure 4.1. Relational diagram of FGS2. TEMP = temperature; AALIRAT = auxiliary variable determining the ratio of protein to fat oxidation; AAFDGL = parameter determining the proportion of amino acids that is converted to glucose; PROLEV = protein feeding level (in g protein$\cdot$kg$^{-0.8}\cdot$d^{-1}). Shaded boxes are used to group variables but are not distinguished individually in the model. For further explanation see text.

Data sources

Oreochromis niloticus

Data from Osman (1988) were used to calibrate the model for feeding level. Experiments involved fasting fish (OSM2), fish around maintenance feeding (OSM3, 0.5-4.0 g $kg^{-0.8}$ d^{-1}), and higher feeding levels (OSM1 and OSM4, 10-24 g $kg^{-0.8}$ d^{-1}). Feed at even higher levels was not consumed fully (Osman 1988) and such trials were omitted. Temperature was 26.5 $^{\circ}$C and feed protein percentage 40% dm.

Data from Magouz (1990; MAG1 and MAG2) and from Wee and Tuan (1988; WEE1) were used to calibrate model parameters for the effect of feed composition. Non-isocaloric feeds with varying protein/gross energy (P/GE)-ratios were fed to fish of about 4.5 g (MAG1) and about 12 g (MAG2) for 70 days and to fish of about 24 g for 50 days (WEE1). Protein content of the feeds ranged from 20-54 %dm. Temperature was 25 $^{\circ}$C for MAG 1 and 2, and 26-29 $^{\circ}$C for WEE1.

For validation, a dataset of nine cases was composed from experiments by Antoine, Wery, Micha and Van Hove (1987), Appler (1985), Appler and Jauncey (1983), De Silva and Gunasekera (1989), Tacon, Jauncey, Falaye, Pantha, MacGowan and Stafford (1983), Wee and Shu (1989) and Wee and Ng (1986).

The datasets are summarized in Table 4.2.

Oncorhynchus mykiss

Data from From and Rasmussen (1984) were used for calibration. They fed fish, varying in size from 2.6-412 g and at temperatures of 5.0-25.6 $^{\circ}$C, at different levels with one type of feed (62.6% dry matter, 52.7% protein). For about 180 experiments, data were complete. In these cases, fat percentage of the fish was computed from the energy content assuming that protein and fat accounted for all energy at 23.62 kJ g^{-1} and at 39.50 kJ g^{-1}, respectively (From and Rasmussen 1984).

There were no data for calibration of the effect of feed composition. For validation, data from Huisman (1976; four feeding levels, initial weight 70 g) and Storebakken and Austreng (1987; six feeding levels, initial weight 400 g) were used.

Table 4.2. Summary of data used for calibration and validation

Dataset		No. of cases	Temp	Initial weight	Feed protein	P/GE ratio	Feeding level[b]
Source[a]	Name		°C	g	% dm	mg J^{-1}	g kg$^{-0.8}$ d^{-1}
Oreochromis niloticus							
1	SIL1	1	26.5	2.9	30	15.2	13
1	SIL2	1	26.5	2.9	25	12.0	14
1	SIL3	1	26.5	2.9	20	9.5	12.5
2	TAC	1	27	5.5	40	18.7	13.5
3	ANT	1	26	5.1	34	16.6	11
4	APP1	1	26	1.0	33	17.6	11
5	APP2	1	26	2.0	33	18.0	13.5
6	WEE1	5	26.5	24	20-50	10-27	12.5
7	WEE2	1	28	4.4	32	15.6	16
7	WEE3	1	28	4.6	32	15.6	16
8	OSM1	16	26.5	1-2	40	19.2	10-20
8	OSM2	6	26.5	20-390	-	-	0
8	OSM3	6	26.5	25	40	20.0	0.5-3.5
8	OSM4	6	26.5	7	40	20.0	12-19
9	MAG1	8	25	4.4	29-54	14-25	14
9	MAG2	9	25	12	33-41	17-20	12.5
Oncorhynchus mykiss							
10	HUI	4	15	70	51	24.2	0-13
11	STO	6	9	400	52	23.0	2.5-10
12	FRO	240	5-26	3-370	63	25.0	0-15

[a]Sources: 1: Sources: 1: De Silva et al. 1988; 2: Tacon et al. 1988; 3: Antoine et al. 1987; 4: Appler 1985; 5: Appler and Jauncey 1983; 6: Wee and Tuan 1988; 7: Wee and Ng 1986; 8: Osman 1988; 9: Magouz 1990; 10: Huisman 1976; 11: Storebakken and Austreng 1987; 12: From and Rasmussen 1984.
[b]As computed with the model

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Parameterization

Oreochromis niloticus

The relationship between protein weight (P in g) and fresh weight (W in g) appeared to be a simple linear relationship (P = -0.513 + 0.163 W; R^2 = 0.996; N = 92, W ranging from 1.7-391 g).

Digestibility for fishmeal protein varies from 80 to 95% (Magouz 1990; De Silva, Keembiyahetty and Gunasekera 1988; Degani and Revach 1991). Protein from plant sources is less digestible: 72% (*Cladophora glomerata*; Appler and Jauncey 1983); 71% (*Hydrodictyon reticulatum*; Appler 1985); 74% (unboiled soybean meal, 87% (boiled soybean meal), 77% (defatted soybean meal; Wee and Shu 1989); 64-72% (bluegreen algae; Getachew 1988). In the model, protein digestibility was set at 80%.

For *C. gariepinus*, carbohydrate and lipid digestibility were estimated to be 40% and 80%, respectively. For *O. niloticus*, reported carbohydrate digestibilities are 80% (corn meal, Degani and Revach 1991), 34-50% (bluegreen algae; Getachew 1988) and 73-92% (wheat starch and cellulose, Magouz 1990). Reported lipid digestibilities range from about 40% (fishmeal) and 35% (poultry meal, Degani and Revach 1991), via 50-62% (bluegreen algae; Getachew 1988) to over 95% (sunflower oil, Magouz 1990). On balance, we assumed that carbohydrate digestibility is a little higher and lipid digestibility is less in tilapia than in *C. gariepinus*, and set both at 50%.

Becker and Fishelson (1990) summarized measurements of routine metabolism which varied from 50 to 82 mg O_2 $kg^{-0.8}$ h^{-1} at 25 °C. We derived from their data (73.8 mg O_2 $kg^{-0.8}$ h^{-1} at 26 °C) a metabolic rate of 1.21 mmole ATP $g^{-0.8}$ d^{-1} (protein and fat oxidation both result in generation of 0.172 mole ATP per g of O_2 consumed). With this value, O_2 consumption rates computed for OSM4 were significantly lower than observed, but when increased by 50% the discrepancy disappeared. Routine metabolism apparently did not account entirely for the activity of the fish. As swimming activity can double or triple routine metabolism (Farmer and Beamish 1969), this was considered a reasonable adjustment.

For lack of better information, we linked feeding metabolism to the composition of the feed by assuming that total heat increment above routine levels is 15% of gross energy

ingested, and subtracting the energy cost of biosynthesis as calculated in the biochemical reaction balance (Machiels and Henken 1986).

Cost of protein and fat synthesis are 70 and 15 mmol ATP g^{-1}, respectively (Jobling 1985).

Oncorhynchus mykiss

The relationship between protein (P, in g) and body weight (W, in g) using the data from From and Rasmussen (1984), appeared to be linear (P $= 0.027 + 0.156$ W; $R^2 = 0.989$; N $= 367$; W ranging from 2.6-412 g).

Protein digestibility is high (85-90%) for fishmeal and purified proteins, and animal proteins are digested much better than proteins from plant origin (Kitamikado, Morishita and Tachino 1964; Mann 1967; Phillips 1969). Lipids are also well digested (80%). Carbohydrates are digested much less, depending on the type of carbohydrate. Sugars (glucose, sucrose) were digested much better (90%) than cooked and raw starch (57 and 38%, respectively) (Phillips 1969). For our simulations protein, carbohydrate and lipid digestibilities were set at 80, 40 and 80% respectively.

Winberg (1956) reported a routine metabolism for salmonid fishes of 0.498 ml O_2 $g^{-0.76}$ h^{-1}, which we converted to 2.88 mmole ATP $g^{-0.8}$ d^{-1}.

The intensity of the feeding metabolism and cost of biosynthesis were assumed to be the same as for *O. niloticus*.

Calibration

Calibration of the model for different fish species is basically a matter of protein partitioning, i.e. choosing parameter values for gluconeogenesis and for the ratio of fat to protein oxidized for energy generation. These parameters are represented by AAFDGL (the fraction of assimilated amino acids converted to glucose, $0 \leq$ AAFDGL ≤ 1) and by AALIRAT (the fraction of total ATP-requirement obtained by oxidation of lipids, $0 \leq$ AALIRAT ≤ 1).

The rate of gluconeogenesis depends on the composition of the diet: high protein-low carbohydrate diets stimulate gluconeogenesis (Cowey, de la Higuera and Adron 1977). Based

on the observation that 4-5% of intraperitoneally injected [^{14}C]-alanine was converted to [^{14}C]-glucose after 1 hour (Hilton and Atkinson 1982), we set AAFDGL at a value of 0.05.

The calibration procedure then focused at an equation for AALIRAT. Simulations with a fixed value of AALIRAT gave acceptable results only for a single feeding level or feed composition. Alternative relationships between AALIRAT and feeding level (g dry matter kg$^{-0.8}$ d^{-1}) or AALIRAT and protein feeding level (g protein kg$^{-0.8}$ d^{-1}) were tested.

Results

Calibration

Best agreement between observed and simulated values for *O. niloticus* was achieved with a relationship between AALIRAT and protein feeding level, AALIRAT decreasing from 0.85 for fasting fish to 0.11-0.36 for higher feeding levels depending on the protein/energy ratio of the feed (mg crude protein (kJ gross energy)$^{-1}$; Figure 4.2). Agreement between simulated (Y) and observed (X) values for fresh weight was: Y = 3.72 + 0.962 X, R^2 = 0.987; mean D = 4.3%, range -23.3 to 47.6%; and for fat percentage: Y = -0.635 + 1.101 X, R^2 = 0.624; mean D = -3.2%, range -53.7 to 72.4% (Figure 4.3).

Good correspondence between simulated (Y) and observed (X) values for *O. mykiss* was achieved with the same relationship between AALIRAT and protein feeding level (Figure 4.2) for fresh weight (Y = -2.02 + 1.03 X, R^2 = 0.996; mean D = -0.5%, range -21.0 to38.2%) and fat percentage (Y = -0.068 + 0.917 X, R^2 = 0.665; mean D = -7.7, range -63.0 to 96.9%) (Figure 4.4). AALIRAT decreased from 0.85 at fasting to 0.15 at high protein feeding levels (P/GE = 25).

Validation

Comparing predictions and observations of fresh weight for *O. niloticus*, we found the following relations: Y = 1.15 + 0.876 X, R^2 = 0.962; mean D = -2.1%, range -22.7 to 37.1% ; and fat percentage: Y = -2.12 + 1.38 X, R^2 = 0.382; mean D = 8.4%, range -59.0 to 62.2% (Figure 4.5).
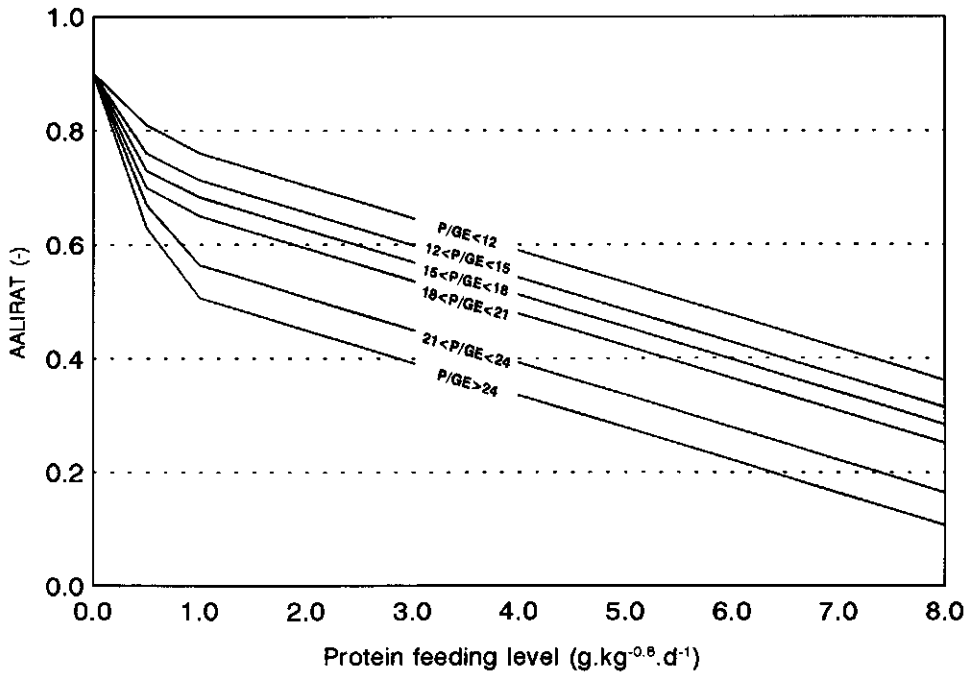
Figure 4.2. Relationship between AALIRAT (proportion of ATP requirement provided by oxidation of body fat) and protein feeding level (g protein•(kg fresh weight)$^{-0.8}$•day^{-1}) for varying protein/gross energy ratios (P/GE in mg crude protein•(kJ gross feed energy)$^{-1}$).

For *O. mykiss* the results for fresh weight were: $Y = 11.9 + 0.989\,X$, $R^2 = 0.929$; mean $D = 4.8\%$, range -20.8 to 24.2% ; and for fat percentage: $Y = -1.17 + 1.13\,X$, $R^2 = 0.535$; mean $D = 0.0\%$, range -26.1 to 23.1% (Figure 4.6).

Discussion

Four groups of rate variables determine the conversion of feed into fish biomass: (1) feeding rate; (2) digestion rates; (3) synthesis rates; and (4) oxidation rates. All rates are affected by a number of factors, notably environment (temperature, oxygen), feed amount and composition, and species-specific factors.
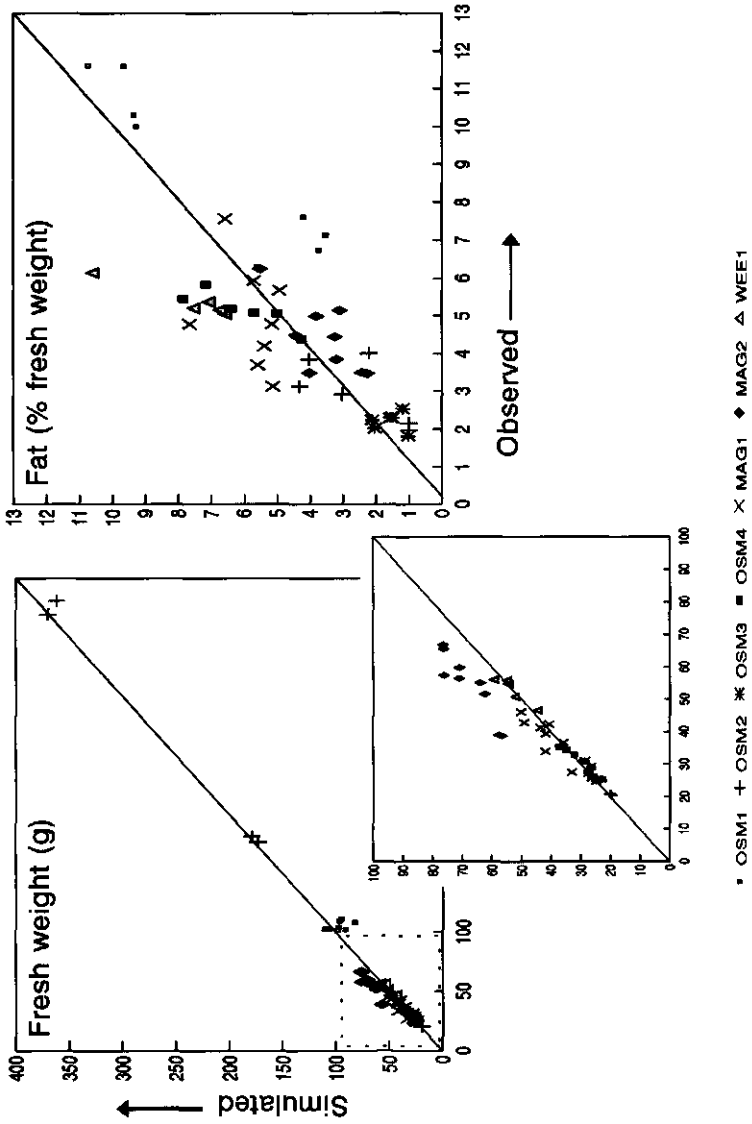
65

Figure 4.3. Calibration results for *Oreochromis niloticus*. The bisectors represent perfect agreement between simulated and observed values. For parameter settings and data sources see text.
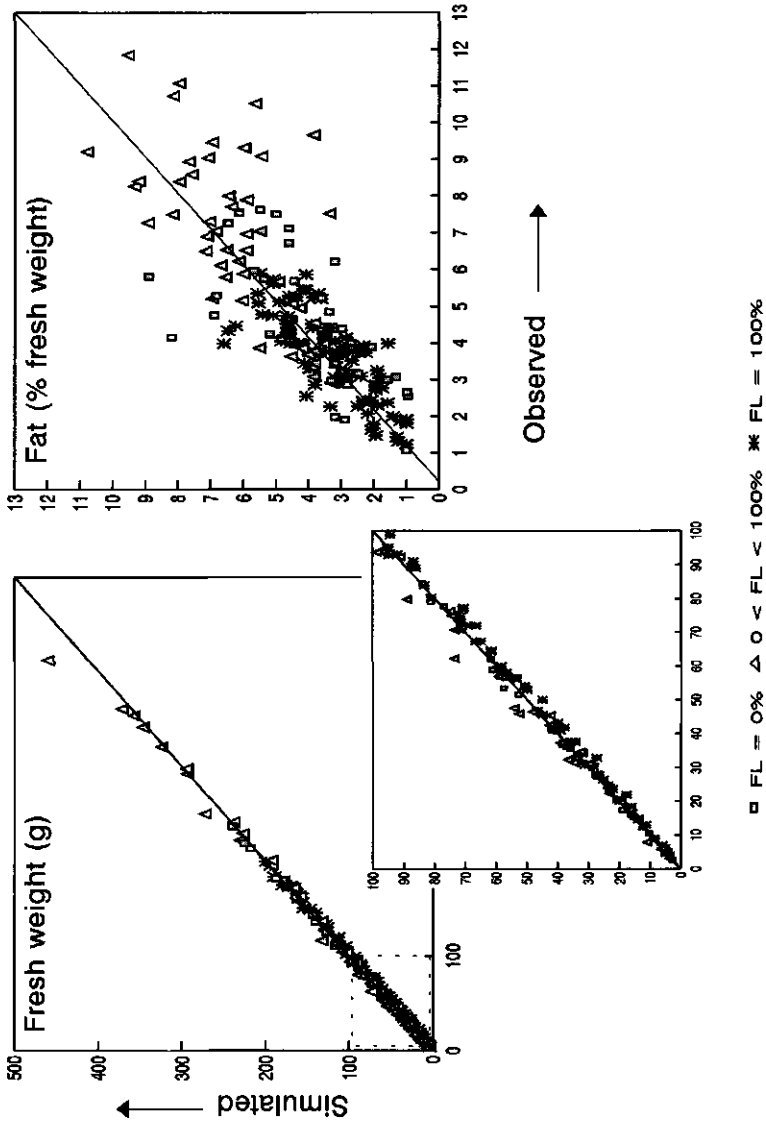
Figure 4.4. Calibration results for *Oncorhynchus mykiss*. The bisector represents perfect agreement between simulated and observed values. For parameter settings, see text. FL = feeding level. All data from From and Rasmussen (1984).
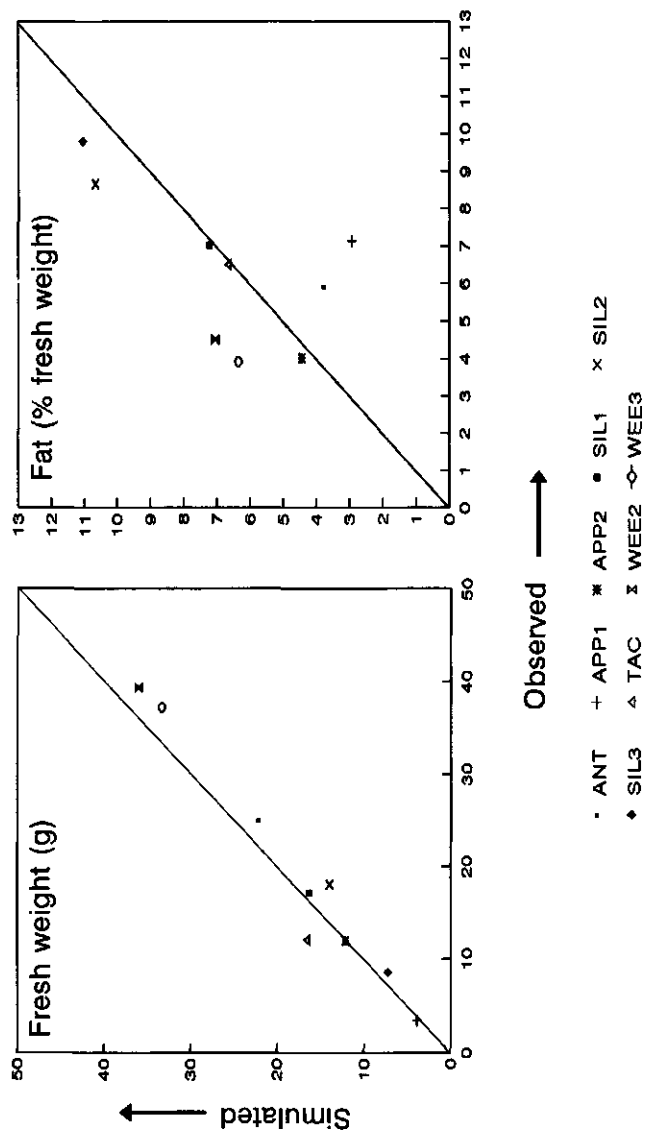
67

Figure 4.5. Validation results for *Oreochromis niloticus*. The bisector represents perfect agreement between simulated and observed values. For sources of data and further explanation see text.
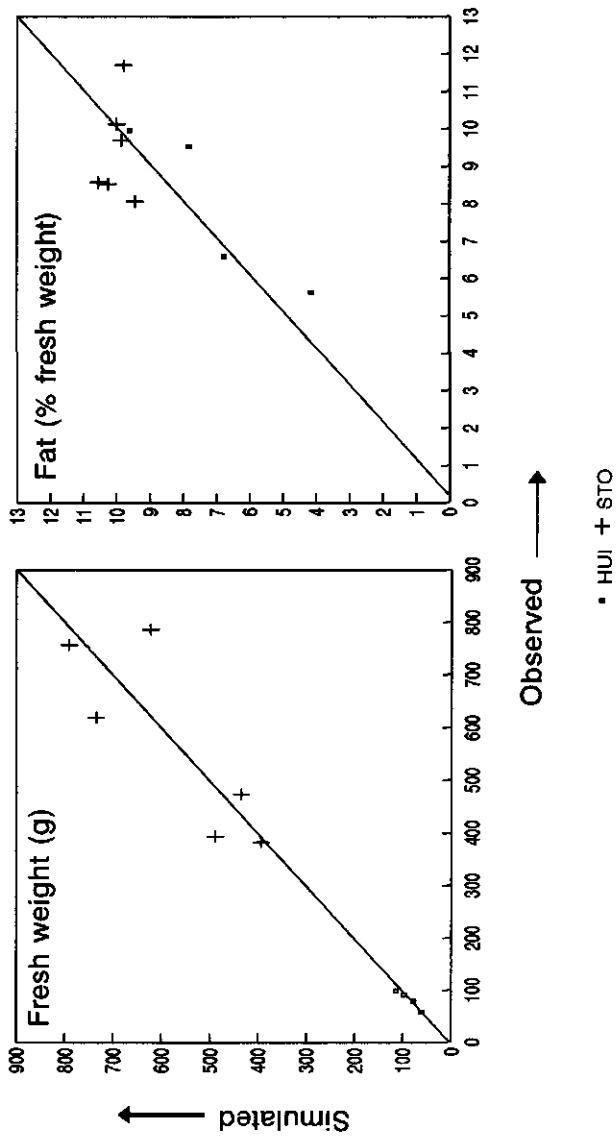
Figure 4.6. Validation results for *Oncorhyncus mykiss*. The bisector represents perfect agreement between simulated and observed values. For data sources see text.

The feeding rate as such is not the subject of this study. We divided the total amount of food into daily rations that were consumed fully in 12 hours. The feeding level was very important in determining the efficiency of protein conversion. If the model is used in studies of fish growth in ponds or natural waters, the feeding rate must be derived from natural feed availability and temperature.

Digestibility percentages were different for trout and tilapia. In FGS1, these were close to values commonly used in nutrition studies (Jobling 1983). In our model, the same values gave good results for rainbow trout, but for tilapia led to simulated body fat percentages that significantly exceeded observed values. Although tilapias and other herbivores have special adaptations for processing carbohydrates, this does not always result in high carbohydrate digestibility. The ability of tilapia to utilize lipids seems to be low compared to other species (Viola and Arieli 1983; Degani and Revach 1991). Protein digestibility is generally high, as most fishes are carnivores (Pandian and Vivekanandan 1985). Natural foods usually have proteins with good amino acid composition (Yurkowski and Tabachek 1979).

Oxidation rates are determined by the total energy requirement (metabolic rate) and the ratio of fat to protein oxidation. Routine metabolic rates can also be different between species: we found it 50% higher in the tilapia, and about twice as high in trout as in *C. gariepinus* (Table 4.3). This ranking agrees well with the typical "no swim" resting behaviour of the catfish and the active behaviour of the trout.

Feeding metabolism and energy cost of biosynthesis together account for what in the literature is called "specific dynamic action" (SDA) or "heat increment". SDA is usually estimated as a function of the protein or energy content of the feed. The relationship is indirect as SDA is probably linked directly to growth processes (Jobling 1981, 1985). In our model, the cost of biosynthesis is related directly to biomass synthesized, but the equation for feeding metabolism, although giving acceptable results, needs a more satisfactory formulation.

Comparison of simulation results for *O. niloticus* and *O. mykiss* with observations showed that the model can be applied to other fish species, provided that each species is characterized by its own set of parameters. Main differences among the species lie in the relative intensity of routine metabolism and in the relative digestibility of carbohydrates and

Table 4.3. Parameter values for *Oreochromis niloticus* (ON) and *Oncorhynchus mykiss* (OM) as used in this study. Values for *Clarias gariepinus* (CG) from Machiels and Henken (1986) are listed for comparison. For explanation, see text.

Parameter	Values			Source[e]	
	ON	OM	CG	ON	OM
Digestibility					
protein	80	80	80	see text	
carbohydrate	50	40	40	see text	
fat	50	80	80	see text	
Routine metabolism					
coefficient[a]	0.0018	0.0029	0.0012	1	2
exponent	0.8	0.76	0.8	1	2
Q10-value	2.0	2.0	2.0	3	3
Energy cost of biosynthesis[b]					
for protein	0.075	0.075	0.051	4	
for fat	0.015	0.015	0.014	4	
Protein content of fresh weight	0.160	0.156	note[d]	5	6
Oxycaloric equivalent[c]	14.0	14.0	14.3	7	

Notes:
[a] In mole ATP $g^{-0.8}$ d^{-1}
[b] In mole ATP g^{-1} protein or fat
[c] In kJ g^{-1} O_2
[d] Defined as 0.13 $W^{0.057}$

[e] Sources: 1: Becker and Fishelson 1990; 2: Winberg 1956; 3: Machiels and Henken 1986; 4: Jobling 1985; 5: based on various authors (see text); 6: based on From and Rasmussen (1984; see text); 7; Caulton 1982.

lipids. While the utilization of protein for energy generation was surprisingly similar for the two species, it is premature to conclude that trout and tilapia utilize feed protein in the same way, as only one feed type was used for trout. AALIRAT is the key parameter that determines the conversion of assimilated nutrients into fish biomass. The model supports our view that fasting fish derive ATP mainly from oxidation of fat, which is in agreement with observations of short-term (days) fasting in many species (Love 1980). Feeding fish increasingly use protein for ATP generation (Figure 4.2). A higher protein consumption, resulting from either a high protein content of the feed or from a high feeding level, results in less efficient protein utilization. The model also predicts that feeds with higher protein/energy ratios lead to more protein oxidation relative to fat.

The current computation of AALIRAT agrees well with observations in many species that increased protein consumption leads to a decrease in protein utilization (e.g. Nile tilapia: Magouz 1990; European eel *Anguilla anguilla* (L.): De la Higuera, Garcia Gallego, Sanz, Hidalgo and Suarez 1989; grass carp *Ctenopharyngodon idella* (Val.): Huisman and Valentijn 1981; rainbow trout: Huisman 1976). It also coincides with evidence about the regulatory influence of dietary protein on protein synthesis and degradation (Millward 1989; Houlihan, Hall and Gray 1989).

Reproduction affects growth through a loss of biomass during spawning and through energy expenditure on production of sex products, and on secondary sexual characteristics. As tilapia ovaries do not usually exceed 10% of total body weight (Peters 1983) and spawning intervals vary from 20 to 50 days (Mires 1982), the loss of biomass from spawned eggs is expected not to be a major factor. Estimates of the portion of the energy income of the fish devoted to reproduction are 10% at maximum (based on several species; Wootton 1985). We expect, therefore, that the absence of reproduction-related processes in the model will not significantly affect simulation results.

Although FGS2 has now simulated growth of three species with a set of specific parameters, we expect it to model other species as well since its theoretical basis is valid for a broad range of species. For other species, a set of parameters would have to be derived from the literature and relevant experimental data. If not all parameters for new species are available, a simplified version of the model, covering protein consumption, digestion,

synthesis and oxidation, would be adequate for the prediction of fresh weight. This would eliminate the need for estimation of carbohydrate and lipid digestibility parameters. The parameter for gluconeogenesis could be omitted and AALIRAT would be the only variable regulating protein use for non-growth purposes. Such a model could be easily derived from FGS2.

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Chapter 5

SIMULATION OF THE EFFECTS OF OXYGEN ON FOOD CONSUMPTION AND GROWTH OF NILE TILAPIA *OREOCHROMIS NILOTICUS* (L.)[*]

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 and Groves 1979): oxygen available for growth equals oxygen entering the body minus oxygen needed for metabolism (Pauly 1981; Longhurst and 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 and Henken 1986, 1987; Machiels and 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 and Penning de Vries 1995, Chapter 4). The objective of this study is to assess quantitatively the effect of oxygen limitation by incorporating a mechanism for oxygen limitation.

Material 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 (see 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 and Penning de Vries 1995, Chapter 4). 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: $kg^{0.8}$; 0.8 is the exponent from the relationship between fish weight and routine metabolism) (Winberg 1956; Becker and 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 (dataset OSM3, 0.5 - 4.0 g $kg^{-0.8}$ d^{-1}) and at higher feeding levels (dataset OSM4, 14-24 g $kg^{-0.8}$ d^{-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 (g O_2 $kg^{-0.8}$ 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 and 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 g dry feed $kg^{-0.8}$ d^{-1}). For the lower oxygen tanks (TSAD3, TSAD4 and TSAD5) we adopted the same feeding regime, but in the

Table 5.1. Glossary of variable and parameter names.

Name	Variable	Dimension
AAFDGL	fraction of digested protein used for gluconeogenesis	-
AAGLUC	rate of gluconeogenesis	g amino acid d^{-1}
AALIRAT	proportion of energy supplied by fat	-
AAOX	amino acid oxidation rate	g d^{-1}
DIGCA	carbohydrate digestibility	%
DIGLI	lipid digestibility	%
DIGPR	protein digestibility	%
DP	gill oxygen pressure gradient	mm Hg
DT	time step of integration	d
EFGSIZ	effective gill surface area	m^2
FEEDCA	feed carbohydrate	% in dry matter
FEEDDAY	daily ration	g
FEEDDM	feed dry matter	% of fresh weight
FEEDEN	feed energy content	kJ g^{-1}
FEEDLI	feed lipids	% in dry matter
FEEDMX1	feeding rate limited by O_2	g d^{-1}
FEEDMX2	feeding rate limited by feed	g d^{-1}
FEEDPR	feed protein	% in dry matter
FEEDRT	actual feeding rate	g dry matter d^{-1}
FEEMET	feeding metabolism	mole ATP d^{-1}
GARF	gill area reduction factor	-
GILCOR	effective gill surface area correction factor	-
GLULIP	rate of lipid synthesis from glucose	g d^{-1}
GSCF	coefficient of GILSIZ-W relationship	m^2 g^{-1}
GSEX	exponent of GILSIZ-W relationship	-
K	Krogh's permeability coefficient	g d^{-1} m^{-1} (mm Hg)$^{-1}$
LIATCO	cost of lipid synthesis	mole ATP g^{-1}
LENGTH	length of simulation	d
LIPOX	lipid oxidation rate	g d^{-1}
OLEF	empirical coefficient of O2MAX-W relationship	d^{-1}
O2FCP	scope for food consumption and processing	g d^{-1}
O2FDG	oxygen cost of 1 g feed dm	g O_2 g^{-1}
O2FMG	oxygen cost of feeding metabolism	g O_2 (g feed dm)$^{-1}$
O2LIG	oxygen cost of lipid synthesis	g O_2 (g feed dm)$^{-1}$
O2MAX	maximum oxygen supply rate	g d^{-1}
O2NEED	total oxygen demand rate	g d^{-1}
O2PRG	oxygen cost of protein synthesis	g O_2 (g feed dm)$^{-1}$
OXYCAL	oxycaloric equivalent	kJ (g O_2)$^{-1}$
PAMB	ambient oxygen pressure	mm Hg
PRATCO	cost of protein synthesis	mole ATP g^{-1}
PROLEV	protein feeding level	g protein $kg^{-0.8}$ d^{-1}
ROUMET	routine metabolism	mole ATP d^{-1}
SYNMET	biosynthesis metabolism	mole ATP d^{-1}
TAGSIZ	total anatomical gill surface area	m^2
TEMP	temperature	˙C
TIMFED	feeding period	d
WBD	water-blood distance	m
W	fish fresh weight	g

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 to the observed values. The initial fish fat percentage was assumed to be 3% of fresh weight.

To evaluate the simulation of maximum fish size, we used the largest reported size of *O. niloticus* as a lead: 63 cm (Lowe-McConnell 1982) or 5,700 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 g $kg^{-0.8}$ d^{-1}. The proximate composition of the bluegreen *Aphanizomenon flos-aquae* was taken as the diet composition (Yurkowski and Tabachek 1979). Average temperature was 30°C (Palomares 1991). Growth of a fish of 5 g initial weight was simulated for 5,000 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 5.1. Simulation conditions are summarized in Table 5.2.

Oxygen limitation module formulation

Oxygen demand

Most of the total oxygen demand (O2NEED, in g d^{-1}) is needed for aerobic energy generation through amino acid oxidation (1.25 g O_2 per g amino acid) and lipid oxidation (2.9 g O_2 per g lipid). The remaining oxygen is used for gluconeogenesis (0.68 g O_2 per g amino acid) and lipid synthesis from glucose (0.22 g O_2 per g glucose) (Machiels and Henken 1986; see Figure 5.1). Oxygen demand is therefore computed as:

$$O2NEED = 1.25 \times AAOX + 2.90 \times LIPOX + 0.68 \times AAGLUC + 0.22 \times GLULIP \quad (5.1)$$

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

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Table 5.2. Parameter settings and simulation conditions for simulation of *Oreochromis niloticus* growth in three different situations.

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

Sources:
a. Osman 1988; b. Tsadik and Kutty 1987; c. Yurkowski and Tabachek 1979; d. van Dam and Penning de Vries 1994; e. Fernandes and Rantin 1986; f. Hughes 1966; g. Randall and Daxboeck 1984; h. Hughes and Morgan 1973.
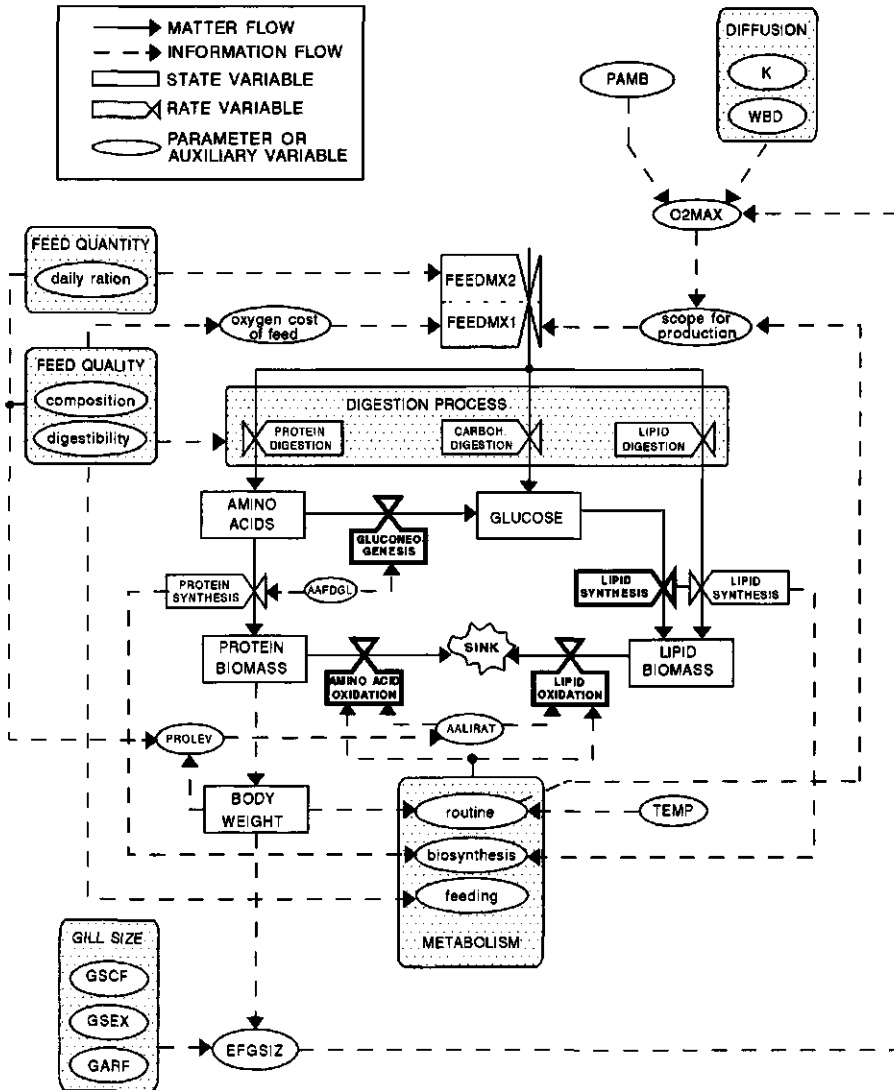
Figure 5.1. Relational diagram of FGS3. TEMP=temperature; PAMB=ambient oxygen pressure; O2MAX=maximum potential oxygen supply; AALIRAT= auxiliary variable determining the ratio of protein to fat oxidation; AAFDGL= parameter determining the proportion of amino acids that is converted to glucose; PROLEV=protein feeding level (in $g \cdot kg^{-0.8} \cdot d^{-1}$). 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 and Penning de Vries (1995).

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 en 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 and Hughes 1982). Also, experiments with carps and eels have shown that the rate of oxygen binding to haemoglobin is fast compared to diffusion (Hills, Hughes and Koyama 1982).

When diffusion is the limiting process, maximum potential oxygen supply to the fish (O2MAX in g d^{-1}) is given by Fick's law of diffusion:

$$O2MAX = \frac{DP \times K \times EFGSIZ}{WBD} \tag{5.2}$$

with DP = oxygen pressure gradient (mm Hg), K = Krogh's diffusion constant (g d^{-1} m^{-1} (mm Hg)$^{-1}$), EFGSIZ = effective surface area of the gills (m^2), and WBD = anatomical water-blood distance (m).

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

$$TAGSIZ = GSCF \times W^{GSEX} \tag{5.3}$$

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 and 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 and Daxboeck 1984). EFGSIZ (in m^2) is therefore defined as:

$$EFGSIZ = GARF \times TAGSIZ \qquad (5.4)$$

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 (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_2 d^{-1}):

$$O2FCP = O2MAX - 5.81 \times ROUMET \qquad (5.5)$$

where 5.81 converts routine metabolism from mole ATP d^{-1} to g O_2 d^{-1} (protein and fat oxidation both result in 0.172 mole ATP per g O_2 consumed).

The O_2 needs for consumption and processing of 1 g of feed dry matter (O2FDG, in g O_2 (g feed dm)$^{-1}$) can be computed from the reaction equations of the intermediary metabolism and the assumptions for feeding metabolism and costs of biosynthesis (Machiels and Henken 1986; van Dam and Penning de Vries 1995, Chapter 4). O2FDG is the sum of oxygen needed for protein synthesis (O2PRG), lipid synthesis (O2LIG) and feeding metabolism (O2FMG, all in g O_2 (g feed dm)$^{-1}$):

$$O2FDG = O2PRG + O2LIG + O2FMG \qquad (5.6)$$

where

$$O2PRG = 1.18 \times DIGPR \times (1 - AAFDGL) \times FEEDPR \times PRATCO \times 5.81 \qquad (5.7)$$

$$\begin{aligned} O2LIG = \ & (0.18 \times DIGPR \times FEEDPR \times AAFDGL + \\ & 0.32 \times DIGCA \times FEEDCA + \\ & 0.96 \times DIGLI \times FEEDLI) \\ & \times LIATCO \times 5.81 \end{aligned} \qquad (5.8)$$

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$$O2FMG = \frac{0.045 \times FEEDEN}{OXYCAL} \qquad (5.9)$$

The maximum feeding rate under an oxygen constraint (FEEDMX1, in g d^{-1}) is then given by:

$$FEEDMX1 = \frac{O2FCP}{O2FDG} \qquad (5.10)$$

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 d^{-1}) can be expressed as:

$$FEEDMX2 = \frac{FEEDDAY}{TIMFED} \qquad (5.11)$$

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) (see Figure 5.1). This is achieved by always choosing the lower feeding rate:

$$
\begin{aligned}
FEEDRT &= FEEDMX1 \quad when \ FEEDMX1 < FEEDMX2 \\
&= FEEDMX2 \quad when \ FEEDMX1 > FEEDMX2
\end{aligned} \qquad (5.12)
$$

Under low 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 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 5.2, 5.3 and 5.4:

$$O2MAX = OLEF \times W^{GSEX} \tag{5.13}$$

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

$$OLEF = DP \times \frac{GARF \times K \times GSCF}{WBD} \tag{5.14}$$

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

Parameterization for O. niloticus

The O_2-diffusion constant K was estimated at 5×10^{-6}, between its value in water (about 1×10^{-5}: Hughes 1966; Randall and Daxboeck 1984) and the values for eel skin and connective tissue (1.199×10^{-6}: Randall and Daxboeck 1984; and 2.980×10^{-6}: Hughes 1966, respectively) (all in g d^{-1} m^{-1} (mm Hg)$^{-1}$ 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^{-4} m^2 g^{-1} and GSEX = 0.75 were reported by Fernandes and 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 and Morgan (1973) was adopted here (3.6×10^{-6} m).

Simulation results

Oxygen demand

The average simulated values for the whole experiment agreed well with experimental results (Figure 5.2). The model predicted a constant weekly oxygen consumption at each feeding level while the observed values increased with time.
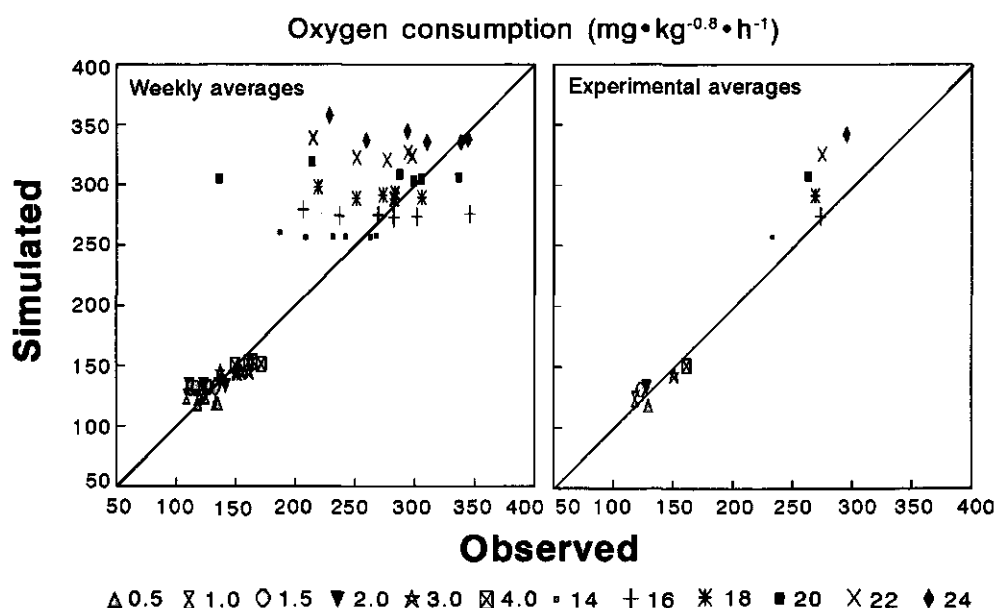
Oxygen consumption (mg•kg^-0.8•h^-1)

Δ 0.5   Ⴟ 1.0   Ο 1.5   ▼ 2.0   ★ 3.0   ⊠ 4.0   ▪ 14   + 16   ✳ 18   ■ 20   X 22   ♦ 24

Figure 5.2. Comparison of simulated and observed oxygen consumption (in mg•kg^-0.8•h^-1) at feeding levels ranging from 0.5-4.0 (experiment OSM3) and 14-24 (experiment OSM4) g•kg^-0.8•d^-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.

Lipid and protein oxidation accounted for 90-95% of total oxygen use. Amino acid oxidation replaced lipid oxidation as the feeding level increased (Figure 5.3).

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 (Figure 5.4).

Low ambient oxygen

For 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 5.70×10^{-2} (TSAD1) and 6.70×10^{-2} (TSAD2).
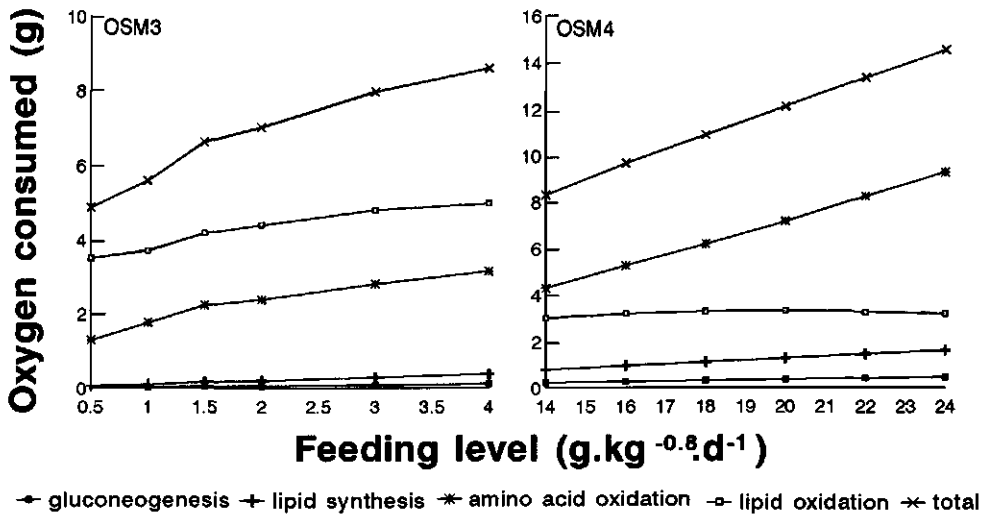
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Figure 5.3. Total simulated oxygen consumption (g) and its breakdown into gluconeogenesis, lipid synthesis, amino acid oxidation and lipid oxidation in relation to feeding level for the experiments OSM3 and OSM4. Amino acid and lipid oxidation together always account for at least 90% of total oxygen demand.
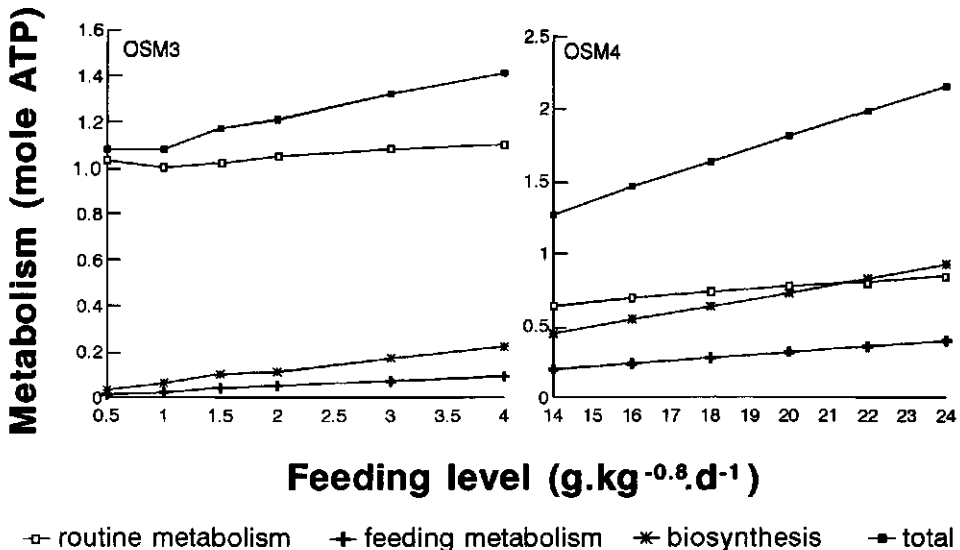

Figure 5.4. Total simulated energy metabolsim (mole ATP) and its breakdown into routine metabolism, feeding metabolism and biosynthesis in relation to feeding level for the experiments OSM3 and OSM4.
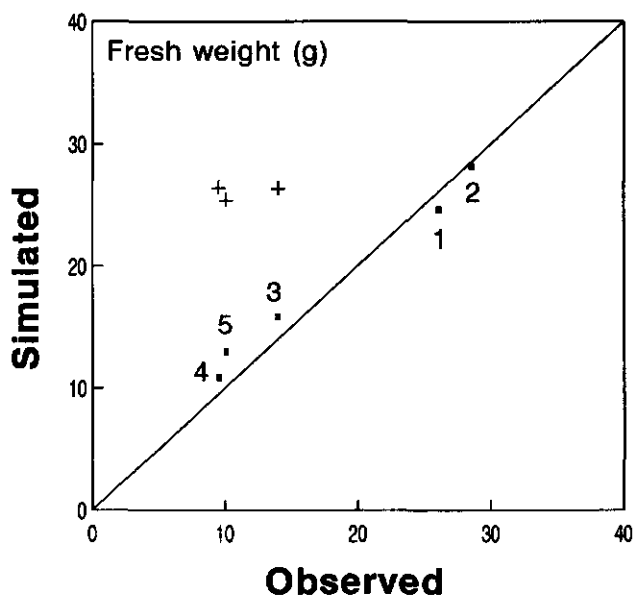
Figure 5.5. Comparison of simulated and observed fresh weight in the experiment of Tsadik and Kutty (1987). Numbers indicate the five tanks. The crosses show the simulated final weights of TSAD3-5 without oxygen limitation module.

In TSAD3, TSAD4 and TSAD5 the correct amounts of feed consumed were achieved with values of OLEF of 3.72×10^{-2}, 3.13×10^{-2} and 3.27×10^{-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 % (Figure 5.5).

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=6.80×10^{-2} at a feeding level of 7 g kg$^{-0.8}$ d^{-1}. With GSEX=0.75 (Fernandes and 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 to 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 (Figure 5.6A).

The effect of feeding level was assessed at GSEX=0.69 for feeding levels between 6.0 and 10.0 g kg$^{-0.8}$ d^{-1}. Final weight was independent of feeding level, as expected, and was reached in a shorter time at higher feeding levels (Figure 5.6B).

The effect of feed composition was assessed at GSEX=0.69 and feeding level = 8 g kg$^{-0.8}$ d^{-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 (Figure 5.6C).

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 (Figure 5.2).

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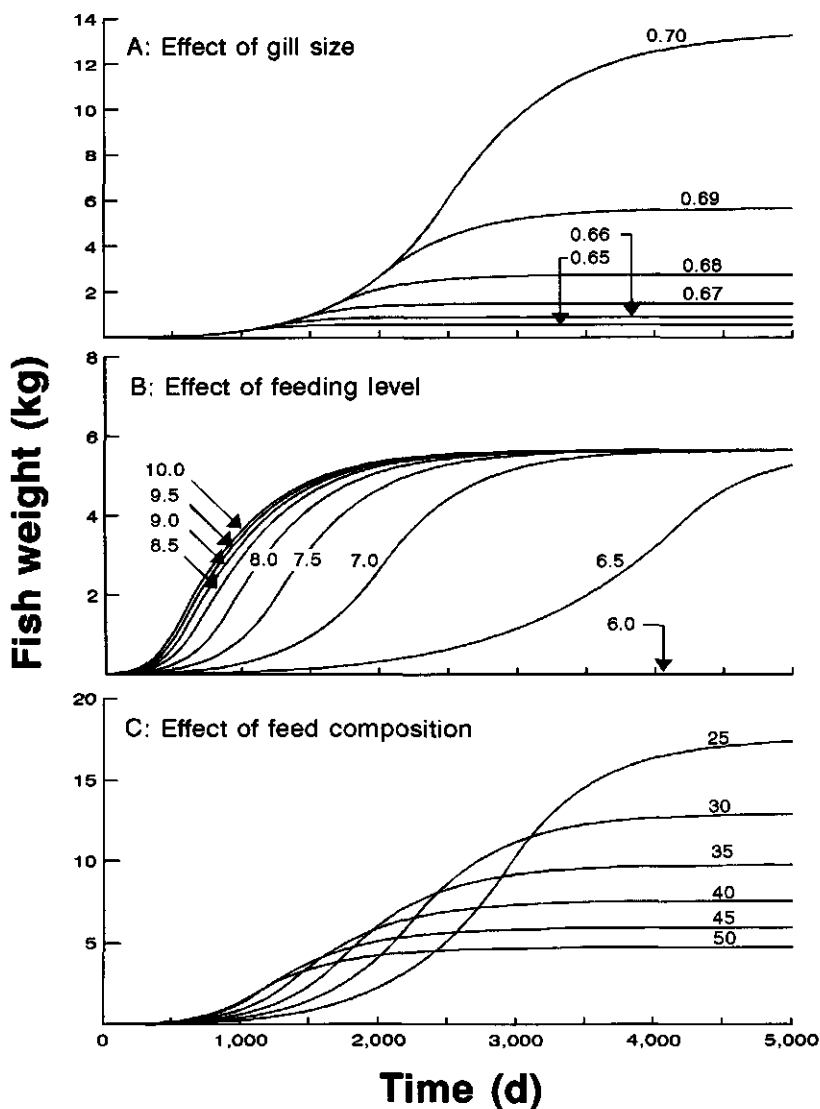
Figure 5.6. Simulation of final fish weight using data from Lake Turkana. **A:** Effect of varying the exponent (GSEX) of the allometric relationship between gill area and body weight between 0.65 and 0.70. Simulation conditions: OLEF=0.068, feeding level= 7 g•kg$^{-0.8}$•d^{-1}. **B:** Effect of feeding levels 6.0-10.0 g•kg$^{-0.8}$•d^{-1}. 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$^{-0.8}$•d^{-1}, GSEX=0.69, OLEF=0.068.

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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 activitity levels are 5-15% of total (i.e. routine) metabolism (Jones 1971; Farrell and Steffensen 1987). Sustained swimming does not increase the oxygen costs of breathing as efficiency of heart activity increases and the fish uses ram jet ventilation (Farrell and Steffensen 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 (Randall and Daxboeck 1984; Hughes 1984; Piiper and Scheid 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 g O_2 d^{-1} (Farmer and Beamish 1969). Using the parameters for *O. niloticus* and equations 5.2 and 5.4, O2MAX equals 0.0126 DP, which equals 0.879 at DP=69.8 mm Hg, a reasonable value for DP compared to measurements in other fish (Hughes 1972).

The analysis in Figure 5.3 stresses the importance of 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 and Doudoroff 1967; Adelman and Smith 1970; Doudoroff and Shumway 1970;

Brett and Blackburn 1981; Pedersen 1987; Tsadik and Kutty 1987; Pouliot and 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 and Valentijn (1981).

In some species, feeding can take up a large part of the scope for production (Jobling 1981). In *Gadus morhua*, feeding can even use up the entire scope for production, leaving no oxygen for non-routine swimming (Soofiani and 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 and 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 5.7) from the values of OLEF using parameter values of Table 5.2, 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 (Figure 5.1), low PAMB can affect growth at four levels: feeding, digestion, synthesis and oxidation. Experiments by Pedersen (1987) and Pouliot and 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 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 and 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 and 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 and Morgan 1973).

The van Bertalanffy parameters computed by Palomares (1991; $t_0 = -0.787$, $W_\infty = 5700$ g, $K = 0.176$) suggest that 95% of W_∞ is reached after about 20 years. A feeding level of 6.0 to 6.5 g $kg^{-0.8}$ d^{-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 maintenance 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 (Figure 5.7). 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 (O2FDG was 0.172 g O_2 (g feed)$^{-1}$ for the 25% protein feed, rising to 0.268 for the 50% protein feed; Figure 7B). In the natural environment or under culture conditions, factors affecting routine metabolism and aerobic
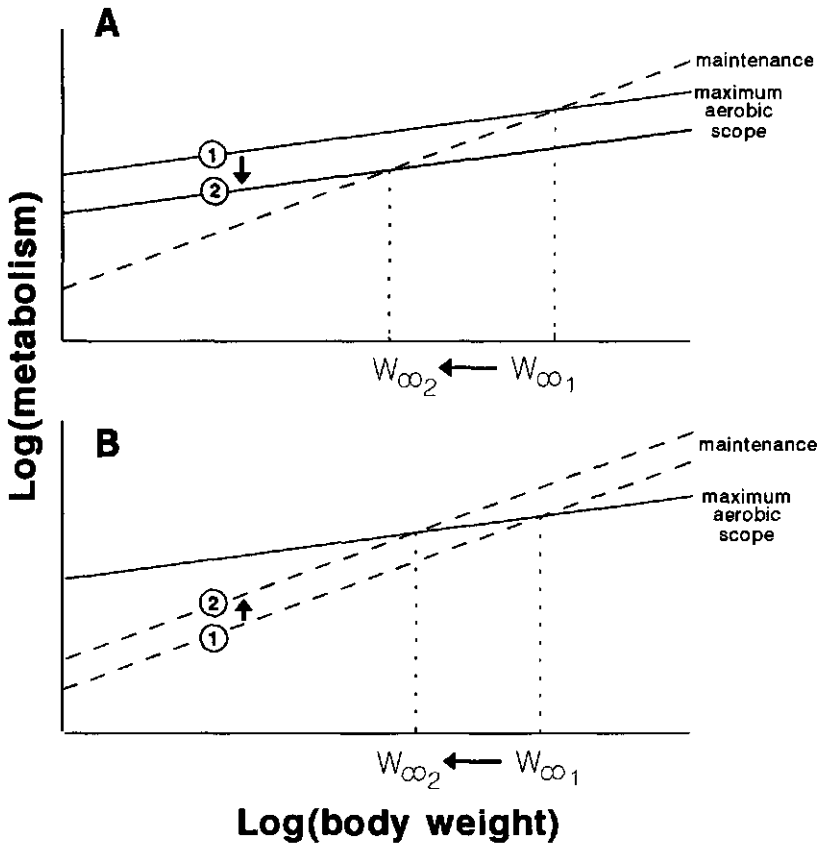
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Figure 5.7. Effect of changes in maintenance metabolism and maximum aerobic scope on the final weight of a fish. **A:** a decrease in maximum aerobic scope (e.g. caused by a reduction in ambient oxygen pressure) causes a decrease in final weight. **B:** an increase in maintenance metabolism (e.g. caused by an increase in temperature) causes a decrease in final weight.

scope may fluctuate, resulting in curves rather than the straight lines of Figure 5.7. 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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Chapter 6

SIMULATION OF FOOD AND OXYGEN LIMITATIONS ON THE GROWTH OF NILE TILAPIA *OREOCHROMIS NILOTICUS* (L.) IN FISHPONDS*

Abstract

A model for dynamic simulation of the growth of the Nile tilapia Oreochromis niloticus *(L.) in relation to food amount and composition, temperature and dissolved oxygen concentration was applied to tilapia ponds. To model food competition between stocked fish and fingerling recruits a pond food module was added.*

Data for model calibration were from uniform experiments with all-male O. niloticus *ponds fertilized with inorganic fertilizers and chicken manure in Honduras, Rwanda and Thailand. Calibration consisted of iterative determination of two model parameters: (1) CONLEV, the consumption rate without food or oxygen limitations; and (2) TPFS, the total daily food supply by the pond. Calibration results showed that in most ponds, final fish weight could be simulated with acceptable values for CONLEV and TPFS. Both CONLEV and TPFS were related to the natural productivity indicators (net primary production and chlorophyll a concentration). For each pond, an estimate of the degree of food and/or oxygen limitation could be given.*

Validation of the model with independent data from Indonesia and Panama was not successful. The relationships used to estimate values of CONLEV and TPFS from primary productivity measurements were not satisfactory. A more detailed approach to modeling food competition and oxygen limitation under these conditions is necessary. The model provides a conceptual framework for the analysis of fish growth in ponds, tying together effects of food quantity and composition, temperature and dissolved oxygen concentration.

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Introduction

Fish in waste-fed ponds or ricefields are subject to variable conditions. Temperature may be as high as $40°C$ in ricefields, and dissolved oxygen can vary from zero to above 200% saturation. Quantity and quality of food vary with pond inputs that are often protein-poor, cellulose-rich agricultural wastes. For their food intake, fish rely partly or completely on the natural food production in the pond. As pond inputs are meant to feed the microbial producers and consumers, pond management is focused on the effects of feeding and other inputs on the whole pond ecosystem, rather than on fish growth alone.

Faced with a wide variety of possible culture systems and environments, a systems approach may be used to obtain insight into the most important variables and their interactions. Several models have been constructed in attempts to conceptualize the complexity of the pond ecosystem (van Dam 1990). Part of such a model should be a fish growth module which deals with both the effects of the pond environment on the fish (food, temperature and oxygen) and the effects of the fish on the environment (faeces and ammonia production, oxygen consumption).

In culture systems that rely on hiqh-quality feed inputs, there is a direct relationship between the quantity and composition of the feed, over which the aquaculturist has full control, and fish production and water quality. In systems with organic or inorganic fertilization the effects of pond inputs on the fish are less direct. Control over water quality and natural feed availability is much less as they are affected not only by pond inputs but also by soil and water resources and by climate characteristics.

In a previous study, a dynamic simulation model was developed to predict fish growth on the basis of feed quantity and composition, temperature and dissolved oxygen concentration. The model, called Fish Growth Simulator 3 (FGS3) was based on a model for the African catfish *Clarias gariepinus* Burchell (Machiels and Henken 1986) and was parameterized for the Nile tilapia *Oreochromis niloticus* (L.) (van Dam and Penning de Vries 1995, Chapter 4; van Dam and Pauly 1995, Chapter 5). FGS3 computes weight gain and oxygen consumption on the basis of the major biochemical reaction equations of

the intermediary metabolism. FGS3 utilizes data on food composition and dissolved oxygen concentration and allows for computation of waste production (faeces, ammonia) by the fish. FGS3 may therefore be particularly useful in a whole-pond simulation model.

FGS3 was parameterized for *O. niloticus* with data from detailed experiments of fish growth in tanks with artificial, high density feeds, constant temperature and unlimiting, constant dissolved oxygen concentrations (van Dam and Penning de Vries 1995, Chapter 4). The objective of this study is to model fish growth under variable environmental conditions, as encountered in ponds fertilized with chemical fertilizers and organic manures. Once validated, such a model may be used for feasibility studies in other locations.

Material and methods

General

The theoretical effects of various combinations of temperature (TEMP) and dissolved oxygen concentration (DO) on fish growth were simulated for a Nile tilapia of 30 g growing for 150 days at consumption levels varying from 0 to 15 g $kg^{-0.8}$ d^{-1} ($kg^{0.8}$ is the dimension of metabolic weight, in which 0.8 is the exponent from the relationship between fish weight and routine metabolism; Winberg 1956; Becker and Fishelson 1990). First, final weight was simulated for all combinations of three fixed TEMPs (20, 25 and 30°C) and five DOs (1, 2, 3, 4 and 5 mg l^{-1}). Then, twelve diurnal DO regimes (at a constant TEMP of 25 °C) were created by combining three early morning (AM: 0, 2.5 and 5 mg l^{-1}) with four mid-afternoon (PM: 5, 10, 15 and 20 mg l^{-1}) DOs. DOs between AM and PM were computed by linear interpolation.

All ponds were stocked with all-male *O. niloticus* but due to errors in hand sexing reproduction occurred in most ponds. To model food competition in ponds between stocked fish and fingerling recruits a pond food module, developed below, was added to FGS3. The expanded model (FGS4) was calibrated using data from the Pond Dynamics/Aquaculture Collaborative Research Support Project (PD/A CRSP) in Honduras, Rwanda and Thailand (total of 106 ponds). From the calibration results, we

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derived a relationship between pond productivity parameters and fish consumption rate. Then, the model was tested with independent data from PD/A CRSP experiments in Panama and Indonesia (33 ponds).

Description of the datasets

O. niloticus growth data were from Honduras (Green, Alvarenga, Phelps and Espinoza 1989, 1990), Rwanda (Hanson, Ndoreyaho, Rwangano, Tubb and Seim 1991), Thailand (Diana, Kwei Lin, Bhukaswan, Sirsuwanatach and Buurma 1990, 1991), Panama (Teichert-Coddington, Peralta, Phelps and Pretto Malca 1990) and Indonesia (Batterson, McNabb, Knud-Hansen, Eidman and Sumatadinata 1989). A general description of these sites is given by Egna, Brown and Leslie (1987). There were two experimental cycles (Cycles 2 and 3), each with an experiment in the rainy and the dry season. In Cycle 2, the effects of organic (500 kg total solids ha^{-1} $week^{-1}$ of chicken manure or cow manure) and inorganic inputs (chemical fertilizer, at the levels of total phosphorous and nitrogen in the organic fertilizers) were compared. In Cycle 3, the effects of three or four levels (125, 250, 500 and 1000 kg total solids ha^{-1} $week^{-1}$) of chicken or cow manure were compared. Pond size was 1000 (Honduras), 600 (Rwanda), 250 (Thailand), 868 (Panama) and 200 (Indonesia) m^2 (see Table 6.1 for details).

Diurnal measurements of TEMP and DO were at fortnightly or monthly intervals. On a sampling day, measurements were taken at four-hour to five-hour intervals starting at about 6:00 a.m. In each pond, TEMP and DO were measured at 25 cm below the water surface (top), midwater (mid) and 25 cm above the bottom (bottom).

Chlorophyll *a* concentrations were measured once or twice weekly. Net primary productivity (NPP, in g C m^{-3} d^{-1}) was measured periodically using several methods: free-water diurnal oxygen curve method (Honduras, Panama); light and dark bottle method (Rwanda, Thailand); loss of dissolved inorganic carbon between dawn and dusk (Indonesia). Fish weight was sampled monthly. At the end of each experiment, all fish were weighed and counted to determine mean final weight and survival percentage. Total fingerling biomass was recorded.

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Food module formulation

The food available on one day to an individual stocked fish (FASF, in g d^{-1}) was calculated with

$$FASF = \frac{(TPFS \times AREA) - FDF}{NFISH} \tag{6.1}$$

in which TPFS = total daily pond food supply (g fresh weight m^{-2} d^{-1}), AREA = pond surface area (m^2), FDF = daily food demand of fingerlings (g fresh weight d^{-1}), NFISH = number of stocked fish (determined by linear interpolation between the number stocked and the number surviving on harvest day).

FDF was calculated with

$$FDF = NFING \times \left(\frac{CONLEV}{FEEDDM} \right) \times \left(\frac{WFING}{1000} \right)^{0.8} \tag{6.2}$$

in which NFING = number of fingerlings, CONLEV = consumption level without limitations (g dm kg$^{-0.8}$ d^{-1}), FEEDDM = feed dry matter (% fresh weight), WFING = individual fingerling weight (in g; in equation (6.2), it is converted to metabolic weight in kg$^{0.8}$). From the reports, we estimated the day when fingerlings first appeared in the pond as 15 days before the sampling day on which fingerlings were first spotted. Starting from zero on that day, the total biomass of fingerlings was determined by linear interpolation to the total biomass on harvest day. NFING was then estimated from total biomass by assuming a constant mean WFING of 5 g.

The food demand of an individual stocked fish (g d^{-1}) was expressed as:

$$FDSF = \left(\frac{CONLEV}{FEEDDM} \right) \times \left(\frac{W}{1000} \right)^{0.8} \tag{6.3}$$

where W = the weight of the stocked fish (in g, again converted to kg$^{0.8}$).

Table 6.1. Pond indicators by treatments in 13 datasets. All data are based on Green et al. (1989, 1990); Diana et al. (1990, 1991); Hanson et al. (1991); Teichert-Coddington et al. (1990); and Batterson et al. (1989). First two letters of names indicate country (HO=Honduras, RW=Rwanda, TH=Thailand, PA=Panama, IN=Indonesia); 2 or 3 indicates experimental cycle; DRY or WET the season type. Treatments (T) were: INO=inorganic fertilizer; CHI=chicken manure; COW=cow manure (see also text). IW = initial individual fish weight (g); FW = final individual fish weight (g); S = survival percentage (%); R = total biomass of recruits at harvest (g.m^{-2}). Dissolved oxygen concentration (DO, in mg.l^{-1}) and temperature (TEMP, in °C) were the mean of top and middle measurements (as used in the simulations, see text for details) and were averaged over the culture period. AM = early morning, PM = mid-afternoon (appr. 1400 hours). All figures are treatment means and superscripts are coefficients of variation (%). Hyphens indicate that data were not available.

| DATASET | | FISH | | | | | | WATER | | | |
| Name | T(N) | IW | FW | S | R | DO AM | DO PM | TEMP AM | TEMP PM | CHLa | NPP |
		(g)	(g)	%	g.m^{-2}	ppm	ppm	°C	°C	mg.m^{-3}	gC.m^{-3}.d^{-1}
HO2DRY	INO(4)	32.9^{7}	155.3^{25}	93.7^{4}	9.0^{25}	3.76^{15}	9.30^{14}	24.3^{0}	27.6^{1}	-	-
	CHI(4)	33.5^{8}	202.3^{8}	96.9^{1}	5.2^{60}	1.18^{9}	7.15^{8}	24.6^{1}	28.2^{1}	-	-
	COW(4)	32.3^{7}	175.3^{7}	95.7^{3}	1.4^{173}	0.81^{77}	4.97^{10}	24.8^{1}	28.1^{1}	-	-
HO2WET	INO(6)	15.7^{6}	132.1^{17}	92.9^{5}	8.7^{53}	2.01^{31}	6.33^{6}	24.8^{1}	27.9^{2}	122.0^{44}	1.94^{67}
	CHI(6)	16.8^{6}	183.1^{15}	93.0^{3}	11.6^{23}	0.58^{81}	6.22^{10}	25.1^{1}	28.2^{1}	102.5^{17}	3.69^{19}
HO3DRY	125(3)	36.0^{1}	116.7^{8}	92.9^{1}	4.3^{81}	2.88^{23}	5.02^{13}	25.1^{1}	28.6^{1}	47.6^{11}	0.86^{16}
	250(3)	37.1^{6}	142.9^{9}	95.9^{4}	3.5^{72}	2.30^{21}	5.75^{14}	25.3^{1}	28.6^{3}	56.6^{25}	1.11^{35}
	500(3)	36.9^{1}	202.6^{3}	91.1^{1}	4.1^{71}	0.84^{17}	6.78^{4}	25.2^{0}	29.0^{0}	106.6^{19}	2.07^{8}
	1000(3)	36.5^{1}	267.8^{4}	84.9^{1}	5.1^{121}	0.49^{5}	8.56^{5}	25.4^{0}	29.4^{0}	174.1^{25}	2.79^{4}
HO3WET	125(3)	26.0^{1}	114.6^{19}	94.1^{1}	6.1^{29}	2.75^{19}	5.07^{3}	25.1^{1}	28.1^{2}	30.6^{7}	0.55^{20}
	250(3)	26.4^{3}	154.8^{9}	92.7^{4}	15.8^{9}	1.60^{53}	6.51^{25}	25.2^{1}	28.5^{2}	70.0^{18}	1.24^{28}
	500(3)	24.4^{9}	177.1^{3}	93.0^{2}	18.5^{16}	0.65^{30}	6.98^{14}	25.4^{0}	28.7^{1}	115.9^{6}	1.51^{11}
	1000(3)	27.4^{4}	208.6^{5}	96.6^{1}	22.1^{43}	0.40^{23}	8.32^{12}	25.6^{0}	29.0^{0}	173.4^{14}	2.01^{16}
RW3DRY	125(3)	43.3^{3}	93.4^{10}	89.6^{3}	0.6^{72}	5.08^{8}	7.71^{8}	20.3^{1}	22.8^{1}	51.6^{10}	1.01^{43}
	250(3)	44.3^{6}	127.6^{10}	91.7^{1}	2.4^{57}	5.11^{11}	8.24^{7}	20.3^{0}	22.8^{0}	72.2^{20}	0.88^{9}
	500(3)	46.0^{4}	161.4^{14}	90.3^{2}	0.2^{82}	4.83^{5}	9.03^{7}	20.2^{1}	22.8^{1}	127.9^{20}	0.95^{34}

RW3WET	125(3)	37.3^3	47.6^9	92.9^7	1.5^{95}	5.04^9	6.09^7	21.3^0	23.1^0	20.6^{15}	0.71^2
	250(3)	39.7^7	63.7^{10}	92.9^{11}	1.8^{12}	5.14^5	6.60^7	21.4^1	23.0^1	29.7^{38}	0.96^{17}
	500(3)	42.7^8	76.4^{13}	94.6^2	2.5^{43}	4.97^6	6.56^5	21.2^1	23.0^1	44.5^{20}	1.21^{11}
TH2DRY	INO(4)	25.5^6	214.6^{10}	92.3^8	147.6^{21}	4.86^7	13.57^4	27.4^1	29.6^1	86.8^{21}	-
	CHI(4)	25.5^5	197.6^{13}	93.8^7	40.1^{83}	4.60^1	9.77^5	27.6^1	29.9^1	74.5^{21}	-
TH2WET	INO(3)	31.8^5	169.3^3	90.1^1	78.6^9	5.72^5	14.68^5	28.1^0	31.2^1	140.0^{29}	-
	CHI(4)	32.5^5	248.3^{10}	89.2^7	73.3^{21}	5.84^{11}	12.61^7	28.1^0	31.4^1	119.6^{22}	-
TH3DRY	125(3)	32.2^7	222.4^{17}	95.2^5	33.2^{77}	5.10^{16}	12.43^{13}	28.7^1	32.3^0	78.7^{18}	2.49^{16}
	250(3)	29.5^1	208.0^5	89.7^5	35.1^{42}	4.92^{25}	11.91^{10}	28.7^1	32.3^0	59.2^{12}	1.92^{12}
	500(3)	26.3^4	280.8^8	92.9^3	61.5^8	4.98^{11}	13.23^{14}	28.9^1	32.4^0	91.7^{20}	3.17^{22}
	1000(3)	27.3^2	259.2^{19}	94.4^5	48.0^{53}	3.94^{18}	10.86^9	28.7^1	32.3^0	66.5^{14}	2.14^9
TH3WET	125(3)	26.7^2	173.7^{25}	91.7^5	4.9^{69}	5.12^9	11.14^{10}	29.3^1	31.9^0	77.1^{32}	2.77^{20}
	250(3)	27.7^{11}	232.7^{16}	88.3^7	4.0^{88}	4.53^{22}	11.49^8	29.2^1	32.0^0	98.8^{26}	3.34^{16}
	500(3)	26.7^6	180.0^5	89.9^4	21.5^{21}	4.60^4	11.42^3	29.3^0	32.1^0	76.2^{15}	3.01^{20}
	1000(3)	26.3^2	247.0^{15}	91.1^4	24.9^{87}	4.13^{11}	12.54^5	29.3^0	32.1^1	108.3^{15}	3.95^{15}
PA3DRY	125(3)	36.6^2	87.0^{12}	92.6^1	40.6^{32}	7.07^8	11.53^{12}	27.8^1	30.8^1		1.84^{22}
	250(3)	36.0^6	114.2^7	88.4^7	80.6^{15}	6.91^5	13.31^6	27.9^1	30.7^1		2.64^8
	500(3)	36.4^2	136.4^6	95.6^3	93.7^6	5.69^{19}	14.24^8	27.8^1	30.4^0		3.14^{10}
	1000(3)	36.3^3	176.1^9	88.7^2	150.6^{15}	3.41^{67}	11.36^9	27.7^1	30.7^1		4.55^2
PA3WET	125(3)	24.3^5	69.8^{14}	84.6^7	22.4^{58}	6.02^4	9.34^7	28.1^1	30.3^1		1.44^{14}
	250(3)	23.7^1	85.9^{16}	90.3^7	49.9^{43}	6.31^2	11.35^5	28.2^1	30.1^1		2.19^{13}
	500(3)	23.5^4	113.8^4	85.3^2	74.0^{18}	4.37^9	13.05^5	27.0^5	29.8^1		3.24^9
	1000(3)	23.5^2	162.3^5	87.1^5	138.0^{12}	2.63^{87}	10.68^{13}	27.7^0	30.1^1		4.16^1
IN2WET	CHI(3)	39.1^{15}	83.9^4	86.3^5	46.7^{25}	5.24^2	7.47^6	27.6^0	29.2^1		1.21^{25}
	CHI†(3)	34.4^2	90.2^{15}	92.0^0	53.8^{42}	5.33^{11}	9.24^5	28.4^1	30.6^0		1.25^{12}
	INO(3)	39.7^7	80.2^8	87.5^7	19.5^{28}	6.00^4	7.22^4	27.4^1	29.3^0		0.70^{33}

†Treated with limestone to increase alkalinity

The amount of food consumable per day (FEEDDAY, g d^{-1}) by an individual fish was then determined by taking the smallest of the values of FASF and FDSF:

$$FEEDDAY = \begin{array}{l} FASF \text{ when } FASF < FDSF \\ FDSF \text{ when } FASF > FDSF \end{array} \qquad \textbf{(6.4)}$$

After this, the model computes the consumption rate of the fish taking into account the oxygen available for assimilation according to van Dam and Pauly (1995, Chapter 5).

Simulation conditions and parameterization

Time courses of TEMP and DO for each pond were constructed by linear interpolation between the diurnal sampling dates. For the TEMP and DO to which the fish were exposed, we took the mean of top and middle measurements assuming that the fish would utilize the water column rather than the bottom of the pond (except for the Panama data, where only middle measurements were available).

For each pond, we took the average fish weight at stocking as the initial weight. The values of TPFS and CONLEV that led to the best correspondence between simulated and observed fish weight at harvest (day 150) were iteratively determined. Mean observed weight at harvest was a more reliable calibration point than observed weights during monthly samples because it was determined from the whole population. Agreement between simulated and observed weight on days between stocking and harvest was assessed by calculating the relative error (RE) and the average relative error (ARE) against the mean of simulated and observed values:

$$RE_i = \frac{W_{sim,i} - W_{obs,i}}{\frac{1}{2}(W_{sim,i} + W_{obs,i})} \qquad \textbf{(6.5)}$$

$$ARE = \frac{\sum_{i=1}^{4} |RE_i|}{4} \qquad \textbf{(6.6)}$$

in which $W_{sim,i}$ and $W_{obs,i}$ are the simulated and observed fish weight at data point i. Fish sampling was done on days 30, 60, 90 and 120 (i=4).

Food limitation (LIMFD) was expressed as the percentage of total time that FASF was smaller than FDSF. Similarly, oxygen limitation (LIMO2) as the percentage of time that FEEDMX1 was smaller than FEEDMX2 (see van Dam and Pauly 1995, Chapter 5). The average consumption level (FEDLEV, in g $kg^{-0.8}$ d^{-1}) was computed as the mean of the consumption level at the four sampling days and at harvest. Thus, CONLEV is the consumption level that would be achieved in the absence of food or oxygen limitations, and FEDLEV is the consumption level computed daily by the model on the basis of actual amount of food consumed. TPFS can be seen as a measure of pond carrying capacity.

All simulations were done in Professional Dynamo Plus (Pugh-Roberts 1986). With the introduction of fluctuating DO-concentrations in the model, it was necessary to reconsider the time coefficient of the system and the corresponding time step of rectangular integration. Assuming an extreme linear DO increase from 1 to 20 mg l^{-1} between 6:00 and 14:00 hours, the rate of DO increase is constant at 2.4 mg l^{-1} h^{-1} and the relative rate of DO increase ranges from 2.4 h^{-1} (=2.4/1) to 0.12 h^{-1} (=2.4/20). The smallest time coefficient for this system would be 0.42 h (=1/2.4) or about 25 minutes. As a rule of thumb, the time step for rectangular integration should be one tenth of the time coefficient (de Wit and Goudriaan 1978). In our simulations, it was approximately equal to the smallest time coefficient. A further halving of the timestep resulted in very long computation times and final weights that were only a few percentages higher. Doubling the timestep to one hour resulted in a 10% weight decrease. As the extreme changes in DO only occurred in a few ponds during part of the culture period and a further reduction of the timestep did no affect simulated weights very much, our choice of timestep was justifiable. The time step was thus 1/48 day (Honduras, Rwanda, Panama, Indonesia) and 1/40 day (Thailand; the difference in time step is caused by a difference in sampling times).

The relationship between ambient oxygen pressure (PAMB) and the empirical oxygen limitation factor (OLEF; see van Dam and Pauly 1995, Chapter 5) was quantified using data from Tsadik and Kutty (1987) as OLEF = 0.0246 + 0.000251 P_{amb} (Figure
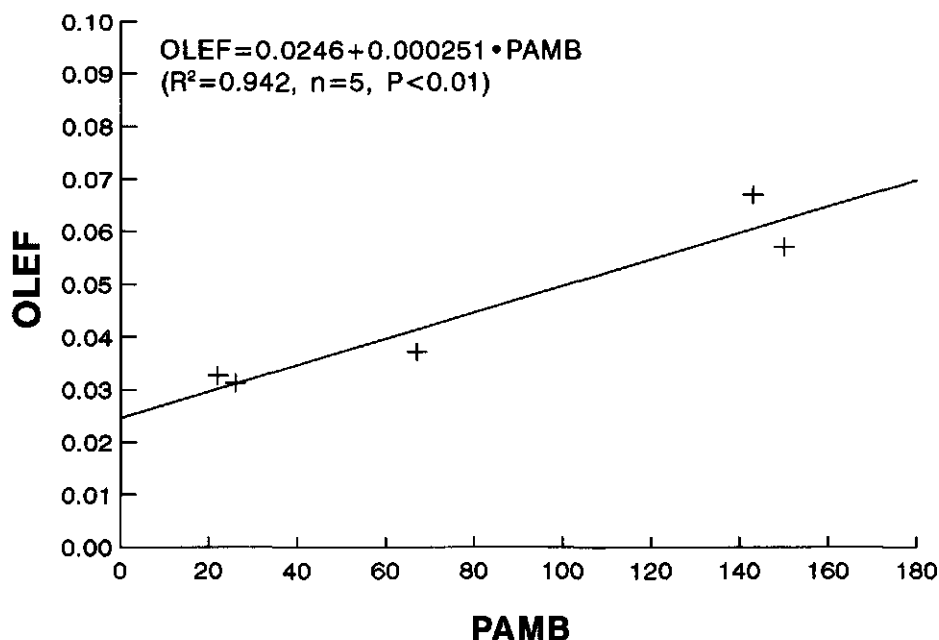
Figure 6.1. Relationship between the empirical oxygen limitation factor OLEF and the ambient oxygen pressure in the water PAMB. For explanation see text.

6.1). Conversion from oxygen pressure to concentration was done using oxygen solubility (μmol l^{-1} (mm Hg)$^{-1}$) as a function of temperature (Boutilier, Heming and Iwama 1984).

In all simulations, model parameters for digestion and metabolism were as in van Dam and Pauly (1995). The proximate composition of natural fish food was taken as 14.2% dry matter, 52.1% crude protein (dm), 7.7% lipids (dm) and 27.3% carbohydrates (dm) (Albrecht and Breitsprecher 1969 in Hepher 1988). Mean fingerling weight (WFING) was set at 5 g for all locations. A glossary of variable names is given in Table 6.2.

Table 6.2. Glossary of variable and parameter names

Name	Variable	Dimension
ARE	average relative error	-
AREA	pond surface area	m^2
CHLA	chlorophyll *a* concentration	mg m^{-3}
CONLEV	consumption level without limitations	g $kg^{-0.8}$ d^{-1}
DO	dissolved oxygen concentration	mg l^{-1}
DT	time step of integration	d
FASF	food available to individual stocked fish	g d^{-1}
FDF	daily food demand of fingerlings	g d^{-1}
FDSF	food demand of individual stocked fish	g d^{-1}
FEDLEV	average consumption level over whole culture period	g $kg^{-0.8}$ d^{-1}
FEEDDAY	daily ration	g d^{-1}
FEEDDM	feed dry matter	% of fresh weight
FEEDMX1	feeding rate limited by O_2	g d^{-1}
FEEDMX2	feeding rate limited by feed	g d^{-1}
FISMASS	total stocked fish biomass	kg
LIMFD	oxygen limitation	% of period
LIMO2	food limitation	% of period
NFING	number of fingerlings	-
NFISH	number of stocked fish	-
NPP	net primary production	g C m^{-3} d^{-1}
OLEF	empirical coefficient of O2MAX-W relationship	d^{-1}
O2MAX	maximum oxygen supply rate	g d^{-1}
PAMB	ambient oxygen pressure	mm Hg
RE	relative error	-
REPMASS	total fingerling biomass	kg
TEMP	temperature	$^\circ$C
TPFS	total pond food supply	g m^{-2} d^{-1}
W	fish fresh weight	g
WFING	mean fingerling weight	g

Results

Model performance

Results of the evaluation of model performance are shown in Figure 6.2. With increasing consumption level under constant DO, final weight increased to a ceiling where oxygen limited feed intake. At higher TEMPs, the ceiling value was lower because relatively more feed was used for metabolism. Under fluctuating DO at 25 °C, the theoretical effect of afternoon DO was the strongest at an early morning DO of 0 mg l^{-1} and was reduced as early morning DO increased to 5 mg l^{-1}.

Food consumption rates of wild *O. niloticus* vary from 4.7 (Lake Awasa, Ethiopia; Getachew 1989) and 6.3 (Lake Turkana, Kenya; Harbott 1976) to 10.5 (Lake George, Uganda; Moriarty, Darlington, Dunn, Moriarty and Tevlin 1973) (all converted by us to g kg$^{-0.8}$ d^{-1}). These differences coincide with differences in temperature among the locations, with consumption rates rising from approximately 4 to 10 g kg$^{-0.8}$ d^{-1} between 20 and 30 °C, respectively. Taking these rates as a maximum, the ceiling values will not be reached at the lower TEMPs (shaded areas, Figure 6.2) and DO limitation is only visible at high TEMPs.

Calibration

Table 6.1 summarizes information about the datasets. There were some clear differences between the experimental sites, expressed primarily in differences in water temperature. Rwanda was the coldest site with am and pm temperatures of around 20 and 23 °C, respectively. Thailand was warmest (am and pm TEMP of 29 and 32 °C). Honduras, Panama and Indonesia had intermediate temperature values.

For 103 out of 106 ponds, values of CONLEV and TPFS were determined that resulted in simulated final fish weights with $-0.01 < RE < 0.01$. Values of ARE varied from less than 0.10 to about 0.60 at maximum (Table 6.3; the 3 out of 106 ponds where the RE of simulated final fish weight was greater than 0.01 were excluded from Table 6.3). Generally, simulated values were lower than the observations and RE's were lower
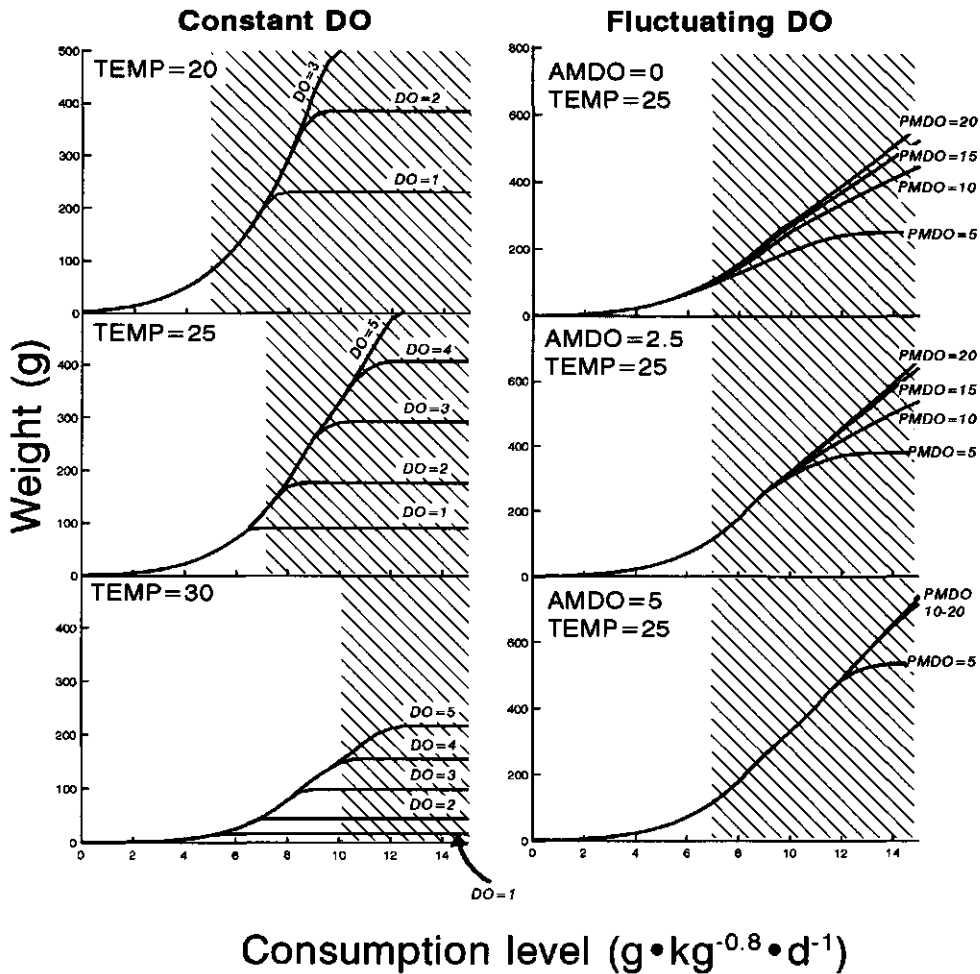
Figure 6.2. Model performance under constant and fluctuating dissolved oxygen (DO). Left: all combinations of three constant temperatures (20, 25 and 30 °C) and five constant DO concentrations (1, 2, 3, 4 and 5 mg·l⁻¹). The lines indicate the final weight of a 30 g fish growing for 150 days at consumption levels between 0 and 15 g·kg$^{-0.8}$·d^{-1}. Right: twelve diurnal DO regimes at a constant temperature of 25 °C. Regimes were combinations of an early-morning (AMDO) and a mid-afternoon (PMDO) oxygen concentration with values in-between estimated from linear interpolation. Shaded ares indicate consumption levels that are unlikely to occur at that temperature. Curves in those areas have only theoretical value. For further details see text.

for wet season than dry season simulations (Figure 6.3). In 76 out of 106 ponds, ARE was 25% or less.

At the low manure input levels in the Honduras dry season and in Rwanda, CONLEV was around 10 and 6.5, respectively (Table 6.3). In most other Honduras ponds and all Thailand ponds, even CONLEV = 20 led to negative RE's on days 30, 60 and 90. As we considered higher values of CONLEV unrealistic based on consumption levels found in experimental situations (Osman 1988; van Dam and Penning de Vries 1995, Chapter 4), we did not use higher values for CONLEV. FEDLEV varied between around 4 in Rwanda and around 15 in Thailand, with Honduras at intermediate levels. TPFS ranged from below 10 in the Rwanda ponds to about 50 g m^{-2} in some Thailand ponds and was, within experiments, related to input level (Table 6.3).

Oxygen limitation occurred in all ponds except in Rwanda. LIMO2 was related to manure input, being highest (50-80%) in the higher dosage chicken manure treatments. Food limitation was inversely related to treatments, being lower in the treatments with high dosage manure inputs (Table 6.3). Food limitation occurred everywhere except in the Honduras dry season experiment, Cycle II, and was lower in the high dosage manure treatments.

Some examples of simulations are given in Figure 6.4. In pond E06DRY (Rwanda; Figure 6.4A) reproduction was low and DO varied between 4.5 and 8 mg l^{-1}. Low pond productivity (mean NPP = 0.79) and low temperature (mean pm TEMP = 22.7) resulted in CONLEV = 6.5 and TPFS = 5.83. Food limitation started around day 20, resulting in a decrease of FEDLEV from the initial 6.5 to about 5 at the end of the culture period. In pond B06DRY (Honduras; Figure 6.4B), reproduction was also low but DO was much lower (mean am DO = 0.67) at a much higher mean temperature (mean pm TEMP = 28.7). The start of oxygen limitation coincided with the onset of early morning DO decline, around day 30, resulting in a decrease of FEDLEV. At the end of the culture period, some reproduction occurred resulting in some food limitation as well. The last example (pond D10DRY, Thailand; Figure 6.4C) shows a pond with a high reproduction and high pond productivity (mean NPP = 2.32). Although early morning DO was never under 4 mg l^{-1}, high temperatures (e.g., mean pm TEMP = 32.3) resulted in oxygen

Table 6.3. Calibration results for simulation of *Oreochromis niloticus* fresh weight in 10 datasets. Names of datasets and treatments as in Table 6.1. Oxygen limitation (LIMO2) and food limitation (LIMFD) are expressed as the percentage of total time that feeding was restricted by oxygen and food, respectively. Figures are treatment means. Superscripts are coefficients of variation. For further explanation, see text.

| Name	T	CONLEV	TPFS	LIMO2	LIMFD	FEDLEV	ARE
HO2DRY	INO	7.7^7	12.9^{23}	5.1^{124}	0.0^0	7.6^5	0.13^{19}
	CHI	9.0^4	17.3^9	26.0^{12}	0.0^0	8.1^4	0.12^{56}
	COW	10.0^{13}	16.9^{17}	51.9^{34}	0.0^0	7.7^3	0.13^{33}
HO2WET	INO	20.0^0	9.4^{25}	45.7^{33}	77.9^{17}	8.7^9	0.44^{30}
	CHI[a]	20.0^0	15.4^9	80.6^8	47.1^8	9.8^6	0.62^8
HO3DRY	125	9.3^{10}	7.8^7	9.5^{107}	78.8^6	7.0^2	0.07^{12}
	250	10.0^0	9.5^{10}	17.3^{30}	67.0^9	7.4^3	0.12^{30}
	500	20.0^0	12.8^4	47.4^6	93.2^2	8.1^2	0.07^6
	1000	20.0^0	16.6^2	48.8^6	81.5^1	9.4^4	0.15^{20}
HO3WET	125	20.0^0	7.6^{19}	23.2^{55}	97.1^4	7.1^9	0.11^{41}
	250	20.0^0	12.1^7	50.5^{33}	82.4^6	7.9^4	0.17^{35}
	500	20.0^0	14.8^2	61.4^{11}	69.9^3	8.6^4	0.30^{10}
	1000	20.0^0	17.7^{10}	58.2^7	65.1^9	8.9^4	0.36^9
RW3DRY	125	6.5^0	4.1^{14}	0.0^0	91.4^7	4.8^6	0.07^{23}
	250	6.5^0	5.8^{13}	0.0^0	67.2^{23}	5.4^7	0.08^{54}
	500	6.5^0	7.9^{23}	0.0^0	38.8^{70}	5.9^8	0.13^{46}
RW3WET	125	6.5^0	1.9^7	0.0^0	100.0^0	4.0^4	0.19^{17}
	250	6.5^0	2.5^5	0.0^0	100.0^0	4.4^5	0.14^{10}
	500	6.5^0	3.0^{16}	0.0^0	93.1^{10}	4.5^7	0.13^{29}
TH2DRY	INO	20.0^0	34.3^{21}	42.9^{13}	46.7^{15}	9.3^6	0.18^{19}
	CHI	20.0^0	20.0^{34}	50.1^{17}	57.5^{17}	10.5^5	0.14^{33}
TH2WET	INO	20.0^0	30.3^2	29.8^{15}	61.9^4	9.0^2	0.24^3
	CHI	20.0^0	29.1^{17}	37.2^{18}	50.8^{19}	10.8^3	0.29^{39}
TH3DRY	125	20.0^0	26.0^{27}	41.9^{41}	57.5^{17}	11.9^{11}	0.12^{28}
	250	20.0^0	23.7^{15}	51.2^{31}	54.9^{12}	11.5^3	0.15^{74}
	500	20.0^0	48.0^7	58.8^{13}	26.7^{20}	15.0^5	0.29^{33}
	1000[b]	20.0^0	39.2^{28}	64.2^{26}	38.0^{26}	12.6^2	0.23^{11}
TH3WET	125	20.0^0	11.9^{32}	32.8^{18}	77.1^{22}	11.2^{12}	0.19^{79}
	250	20.0^0	16.1^{12}	48.3^{22}	58.2^{23}	12.8^6	0.29^{67}
	500	20.0^0	17.3^4	46.4^6	56.2^5	11.6^3	0.29^{33}
	1000	20.0^0	26.8^{20}	52.4^{20}	38.2^{34}	13.4^7	0.52^{20}

[a]Two ponds excluded.
[b]One pond excluded.
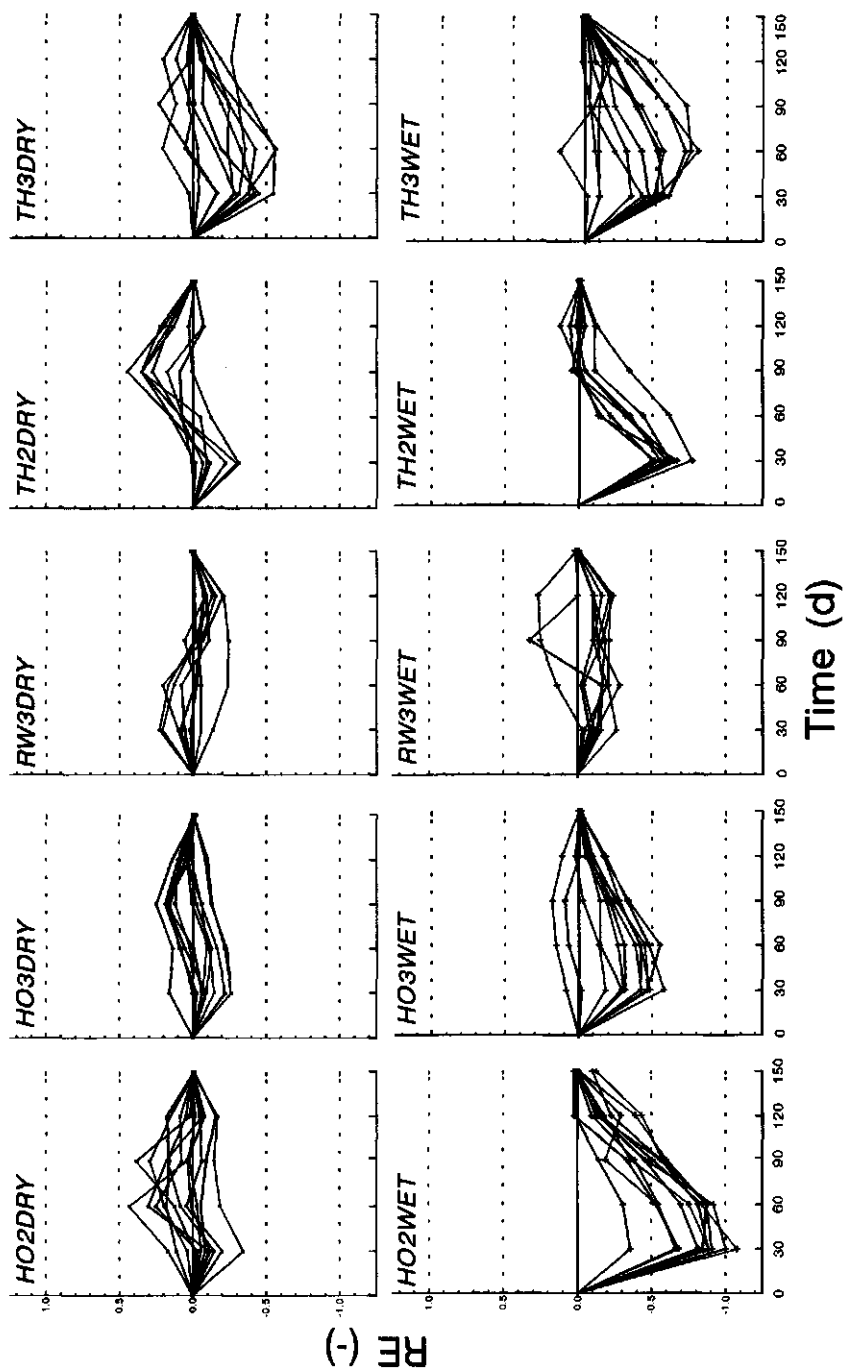
Figure 6.3. Relative errors (RE) of simulated fresh weight ([Wsim-Wobs]/½[Wobs+Wsim]) for a total of 106 ponds in Honduras, Rwanda and Thailand on 4 sampling days. For names of datasets see Table 6.1.
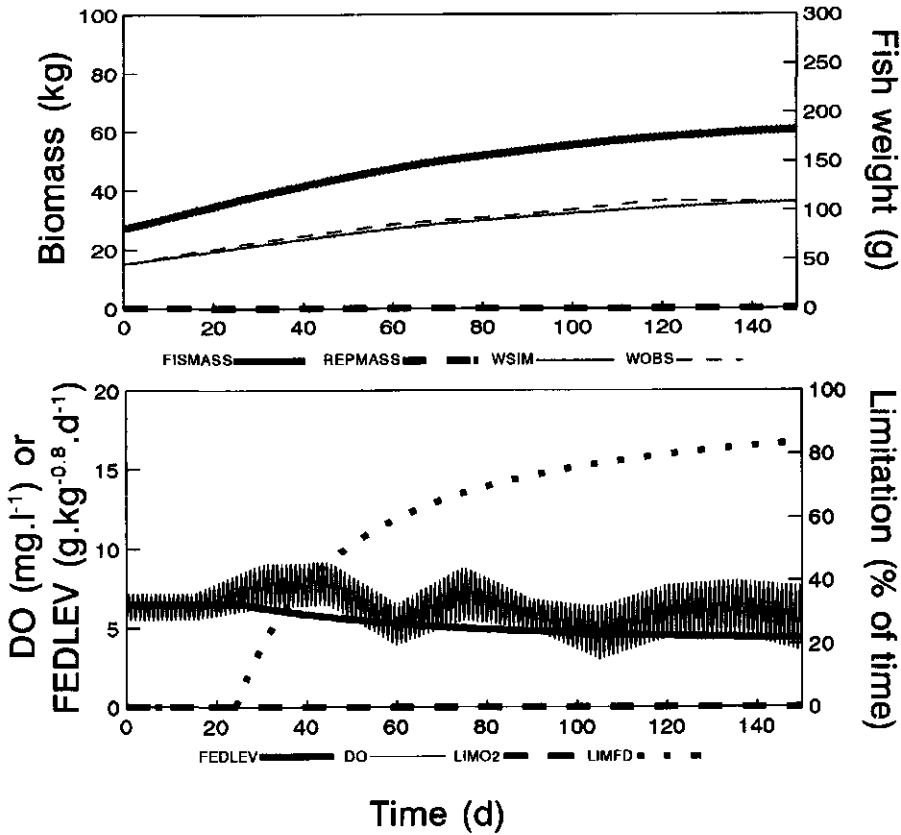
Figure 6.4A. Example of pond simulation: Rwanda.

limitation from the very first day (see also Figure 6.2) and a corresponding decline of FEDLEV. After the onset of reproduction around day 60, food limitation started on day 80 resulting in an even sharper decline of FEDLEV.

Validation

Low values of CONLEV only occurred in ponds that were at the bottom end of the productivity range (0-2 g C m^{-3} d^{-1}), although in some ponds high values of CONLEV
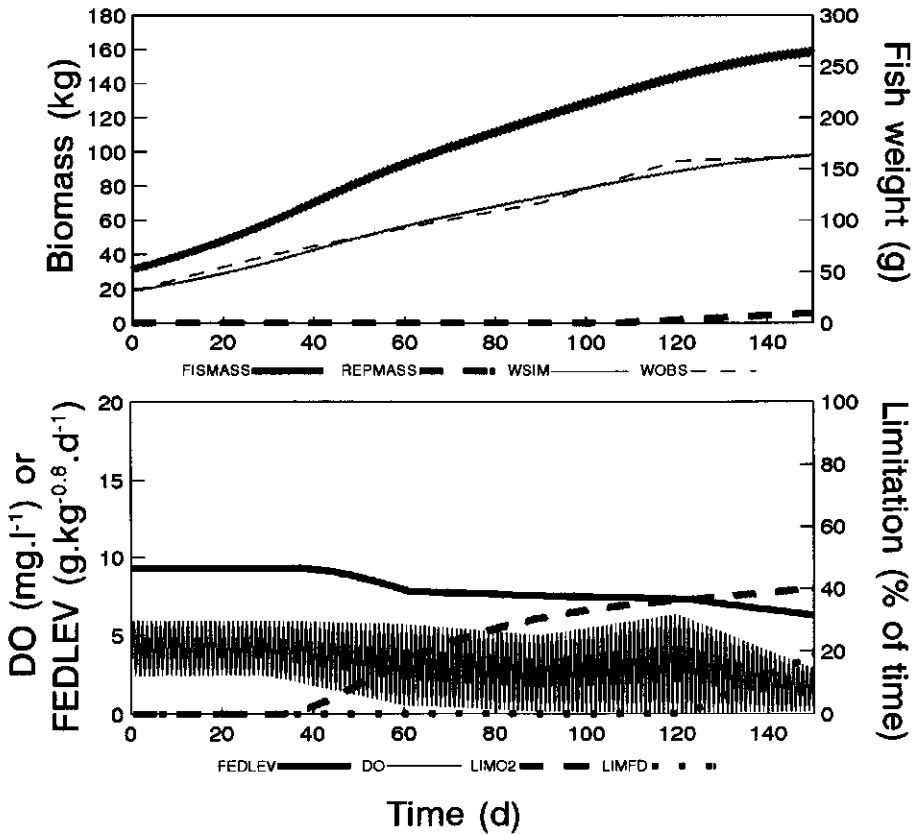
Figure 6.4B. Example of pond simulation: Honduras.

occurred also (Figure 6.5). Most of the lower CONLEV values also occurred at low chlorophyll *a* concentrations (Figure 6.6). TPFS increased with NPP to a ceiling of about 15 g m^{-2} at 3 g C m^{-3} d^{-1} (Figure 6.5). In a plot of TPFS against chlorophyll *a*, a country grouping emerged (Figure 6.6).

Based on these results, the model was validated by relating CONLEV and TPFS to the mean NPP of ponds in Indonesia and Panama and simulating fish weight under the local TEMP and DO-profiles. The relationships between NPP and CONLEV and TPFS
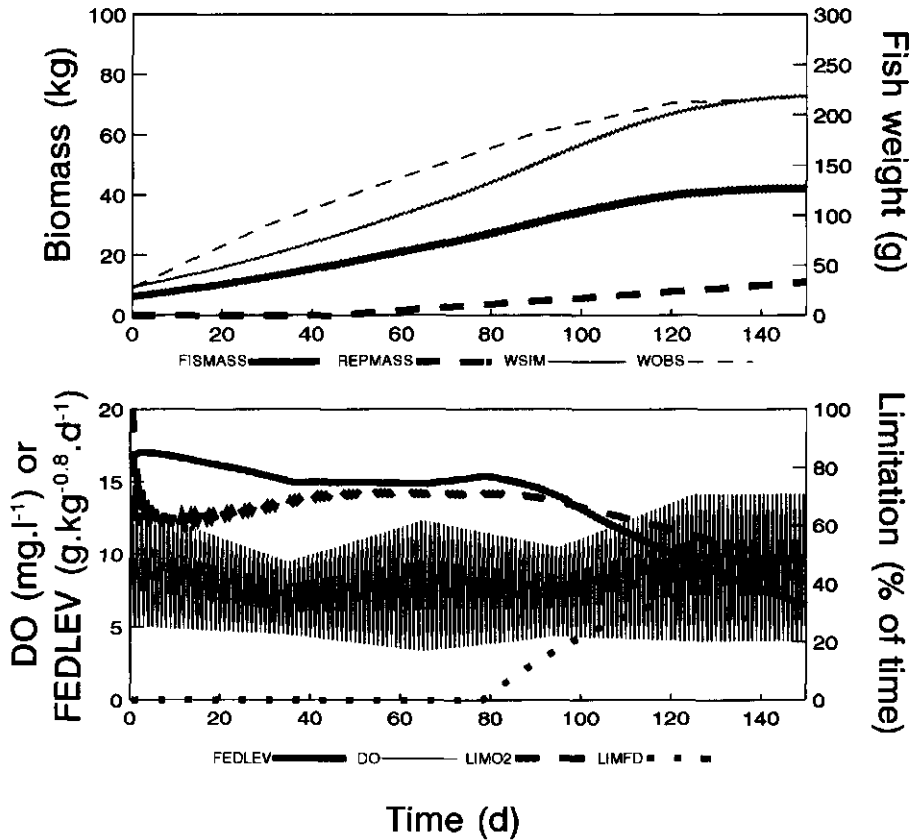
Figure 6.4C. Example of pond simulation: Thailand.

were based on the range of NPP values found in Indonesia and Panama (0 to 4 g C m^{-3} d^{-1}). CONLEV was assumed to increase linearly from 0 at NPP = 0 to 20 at NPP = 2 g C m^{-3} d^{-1}, and to remain 20 at higher NPP-levels (Figure 6.4). An equation for TPFS was derived by linear regression as TPFS = 2.65 + 4.77 × NPP (R^2 = 0.494, N = 49).

Results of this validation are summarized in Table 6.4. Simulated final fish weights generally had RE's of more than 0.35. ARE's for Indonesia were between 0.20 and 0.74

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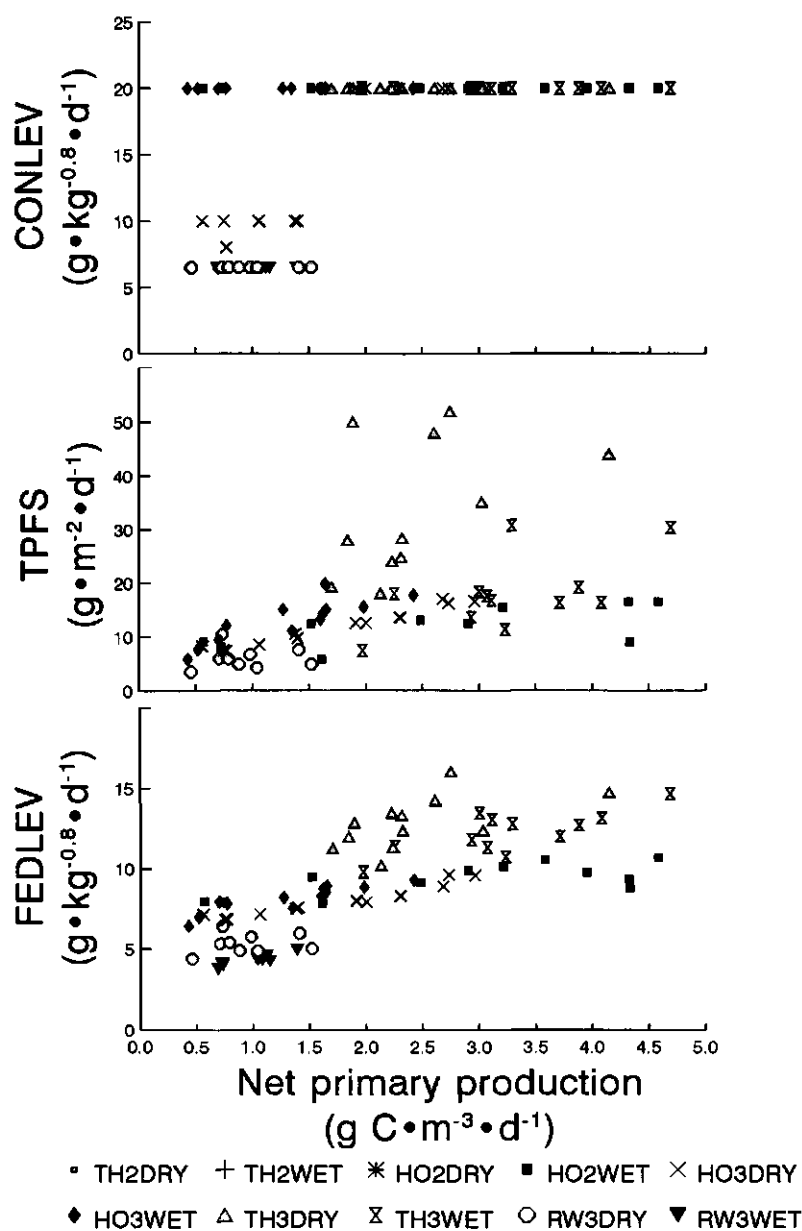
Figure 6.5. Relationship between net primary production (g C•m⁻³•d⁻¹) and CONLEV (in g•kg⁻⁰·⁸•d⁻¹, a model parameter setting the maximum food consumption level), TPFS (in g•m⁻²•d⁻¹, a parameter setting the maximum total pond food supply) and FEDLEV (in g•kg⁻⁰·⁸•d⁻¹, the mean of the actual food consumption level at 5 sampling days).
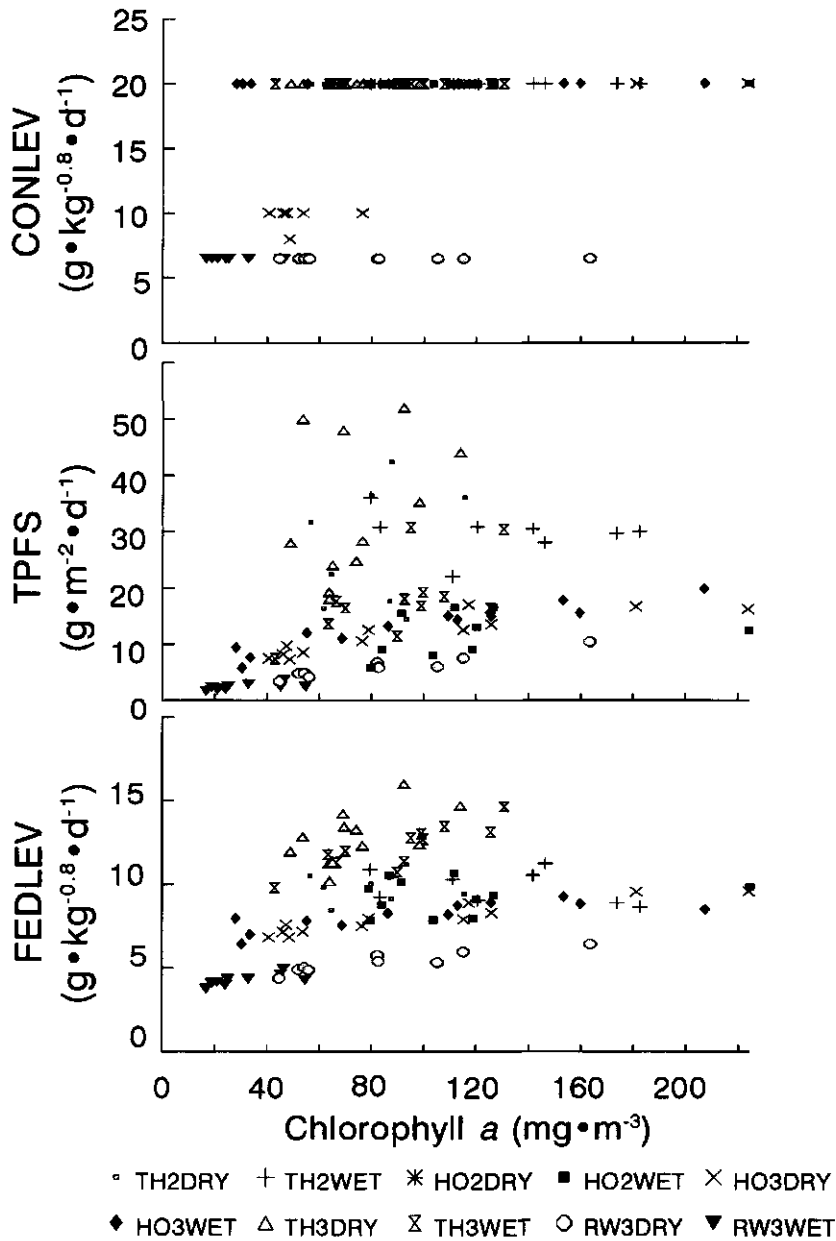
Figure 6.6. Relationship between chlorophyll-a concentration (mg•m⁻³) and CONLEV (in $g \cdot kg^{-0.8} \cdot d^{-1}$, a model parameter setting the maximum food consumption level), TPFS (in $g \cdot m^{-2} \cdot d^{-1}$, a parameter setting the maximum total pond food supply) and FEDLEV (in $g \cdot kg^{-0.8} \cdot d^{-1}$, the mean of the actual food consumption level on 5 sampling days).   121

(ARE for Panama could not be calculated because sample weights for days 30, 60, 90 and 120 were not reported). LIMFD was between 50 and 100 in most ponds.

Discussion

Comparability of datasets

Despite the uniform setup of the experiments throughout the various experimental sites, several site-specific effects hamper a straight comparison of results. Pond size varied from 200 m^2 in Thailand to 1,000 m^2 in Honduras, which may affect the comparability of ponds through differences in pond surface:volume ratio. The elevation of the sites (e.g., Rwanda: 1,500 m; Thailand: 5 m) caused important temperature differences. In addition, the alkalinity of the source water varied from about 18 (Rwanda, Panama) via 20-30 (Indonesia, Honduras) to 92 mg l^{-1} $CaCO_3$ (Thailand). During the experiments, these values increased to 25-50 (Panama, Indonesia), 30-60 (Rwanda), 50-200 (Honduras) and 100-250 (Thailand), explaining a large part of the higher productivity of the ponds in Honduras and Thailand. Increasing the alkalinity by limestone treatment in the Indonesia experiment increased fish yield immediately (Batterson et al. 1989).

Food limitation

In FGS4, the availability of food to the individual fish stocked is determined by CONLEV and TPFS. CONLEV is the maximum level of food consumption that is attained as long as the supply of natural food in the pond is sufficient. Below a certain density of natural food, consumption rate becomes density dependent. CONLEV is related to pond productivity (Figures 6.5 and 6.6). The relationship between CONLEV and NPP or CHLA is not clear. Obviously, relating a constant CONLEV to the mean NPP and CHLA values over the whole culture period obscures day-to-day variability. It is reasonable, however, to assume that the short-term variations in DO were more important than variations in pond productivity.

Table 6.4. Validation results for simulation of *Oreochromis niloticus* fresh weight in three datasets. Names of datasets and treatments as in Table 6.1. Oxygen limitation (LIMO2) and food limitation (LIMFD) are expressed as the percentage of total time that feeding was restricted by oxygen and food, respectively. Figures are treatment means, superscripts are coefficients of variation. For further explanation, see text.

Name	T	CONLEV	TPFS	LIMO2	LIMFD	FEDLEV	RE (150)	ARE
PA3DRY	125	17.0^{13}	11.4^{17}	1.0^{71}	90.0^{1}	6.3^{17}	-0.04^{1419}	-
	250	20.0^{0}	15.2^{6}	4.1^{47}	87.5^{3}	5.8^{18}	-0.45^{83}	-
	500	20.0^{0}	17.6^{8}	13.7^{34}	82.6^{1}	6.6^{10}	-0.35^{46}	-
	1000	20.0^{0}	24.4^{2}	20.7^{19}	70.3^{5}	6.5^{11}	-0.70^{52}	-
PA3WET	125	14.4^{14}	9.5^{10}	0.5^{71}	63.3^{10}	9.0^{5}	0.53^{36}	-
	250	19.8^{1}	13.1^{10}	11.4^{52}	73.6^{4}	8.8^{12}	0.39^{99}	-
	500	20.0^{0}	18.1^{7}	23.3^{38}	58.9^{5}	9.5^{2}	0.27^{61}	-
	1000	20.0^{0}	22.5^{1}	36.0^{10}	43.7^{6}	8.4^{2}	-0.48^{28}	-
IN2WET	CHI	10.3^{8}	7.6^{5}	0.0^{0}	75.9^{14}	5.4^{16}	-0.53^{40}	0.26^{29}
	CHI	14.3^{12}	9.5^{9}	6.4^{80}	83.7^{4}	4.4^{8}	-1.10^{14}	0.36^{13}
	INO	7.0^{33}	6.0^{18}	0.0^{0}	34.4^{99}	5.6^{19}	-0.58^{87}	0.42^{56}

CONLEV varied from 6.5 in Rwanda to 20 g $kg^{-0.8}$ d^{-1} in most ponds in Honduras and Thailand. The latter value seems to be high compared to reported values of 4-10 g $kg^{-0.8}$ d^{-1} in East African lakes (see Results section). Fishponds, however, are generally more eutrophic than lakes (Talling 1965; Oglesby 1977). Lake George, an exceptionally productive lake, is closest to a fishpond with an integral gross photosynthesis of 4-6 g C m^{-2} d^{-1} (Talling 1965); the consumption level of *O. niloticus* was 10 g $kg^{-0.8}$ d^{-1} here (Moriarty et al. 1973). The blue tilapia *Oreochromis aureus* (Steindachner) consumed the equivalent of 14-16 g $kg^{-0.8}$ d^{-1} when fed with fresh *Spirulina platensis* (Nordstedt) in aquaria at 21-26 °C (Stanley and Jones 1976). This shows that tilapias under culture conditions consume more than in natural waters. Thus, a value of CONLEV = 20 as an unlimited maximum appears to be acceptable.

The other parameter determining food availability is TPFS. TPFS should be seen as the productivity ceiling of the whole pond at the end of the culture period, when the stocked fish are joined by a growing number of fingerling recruits. Simulations without this ceiling would, in ponds where reproduction occurred, invariably lead to a much higher simulated than observed individual weight. Like CONLEV, TPFS is not really a constant. It may be expected to increase over time with the buildup of nutrients in the pond. Its value in the beginning of the culture period is of less interest because total food demand by the fish remains under TPFS.

TPFS values ranged from 2-50 (g fresh weight) m^{-2} d^{-1}. Assuming a dry matter percentage of 14.2 and 50% C in dry matter, this is equivalent to 0.14-3.6 g C m^{-2} d^{-1} available for fish consumption. TPFS was related to mean NPP and chlorophyll *a* levels (Figures 6.5 and 6.6) but in ponds with high manure loads, a large part of TPFS will consist of non-algal production and manure itself. The values for TPFS are below the upper limit for net algal productivity in fishponds of 4 g C m^{-2} d^{-1} (Colman and Edwards 1987).

In the food module, several simplifying assumptions were made. Fingerling total biomass was entered as a forcing function and FDF was always given priority (Equation 6.1). The fingerling population in a pond was assumed to consist of equal-sized fish with mean weight WFING. An improvement of the model would consist of a size-structured reproduction model based on the number of females and factors affecting fingerling growth and survival. To account for differences in competition between different ponds in this study, the current module was sufficient.

The datasets did not contain enough information to consider differences in food composition in the model. Different types of fertilizer inputs and differences in soil and climate can lead to different types of natural feeds. The accumulation of organic and inorganic nutrients during the culture period may cause shifts in species composition of the microbial populations (Colman and Edwards 1987). There are some marked differences in protein content between *Chlorophyta* and *Cyanobacteria* (Yurkowski and Tabachek 1979; Boyd and Goodyear 1971) that may affect the growth of fish.

Oxygen limitation

A better "fit" between simulated and observed fish growth was achieved in dry season ponds than in wet season ponds. In three ponds (two in HO2WET and one in TH3DRY) it was not possible to simulate the correct final weight on day 150. In a lot of these wet season ponds, simulated weight was lower than observed weight in the first half of the culture period (Figure 6.3). This may be due to a too strong feedback by the oxygen limitation mechanism. In most cases, LIMO2 was close to 100% at day 30, indicating that raising CONLEV even further would not solve the problem. Part of this must be ascribed to the limited number of observations underlying the relationship between OLEF and P_{amb} (Figure 6.1). Moreover, the formulation of the relationship, with OLEF incorporating several effects, is not satisfactory from a theoretical point of view. Nevertheless, the question remains why wet season simulations were less succesful.

A related issue is the estimation of the prevailing DO-concentration by taking the average of top and middle DO-measurements. A practical reason for doing this was that including the bottom DO-concentration in the computation resulted in too severe oxygen limitation. No information on fish behaviour in the ponds was available and indeed, very little is known at all about fish responses to variations in DO (Kramer 1987). Fish may choose to stay in the DO-rich layer, in which case including bottom and middle DO in the computation would lead to a too strong oxygen limitation. In an oxygen-stratified pond, the fish may be cut off from bottom food resources by low DOs.

In Honduras, oxygen limitation was primarily a result of low DOs. In subsequent experiments, DO was maintained above a prescribed minimum level using pump aerators, resulting in improved growth rates. These were attributed at least partly to increased feeding activity, as shown by decomposing feed in the unaerated control ponds (Teichert-Coddington and Green 1993). At higher temperatures, as in Thailand, fish growth was oxygen-limited even though mean early-morning DO was higher than 4 mg l^{-1} (Figure 6.4C). In this situation, routine metabolism is high and the scope for production (i.e., the difference between aerobic maximum metabolism and routine metabolism; Huisman and Valentijn 1981; van Dam and Pauly 1995, Chapter 5) is reduced, resulting in reduced feed consumption. Other causes of increased metabolism (e.g., bird predation pressure,

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diseases) may similarly lead to oxygen limitation. In situations of high temperature and "reasonable" DO, nocturnal feeders have an advantage over daytime feeders like *O. niloticus*, as they can utilize the cooler nightly hours for feeding and digestion.

This may be of importance for rice-fish culture. In experimental rice-tilapia fields in the Philippines, afternoon water temperatures ranged from 28 to 39 °C and DOs from 4 to 9 mg l^{-1} (Dela Cruz and Sevilleja 1990). At 35 °C and 5 mg l^{-1} (both constant), FGS4 predicts a ceiling fish weight of about 44 g; fish are probably oxygen-limited for most of the photoperiod and therefore don't feed. Under such conditions, feeding or applying manure to increase fish growth will have little effect. This was in fact experienced in rice-fish experiments (Sevilleja, Cagauan, Lopez, Dela Cruz and Van Dam 1992). Smaller fish are expected to do better than bigger fish because their scope for production is relatively greater. This may explain why rice fields in West Java, Indonesia are succesfully used as common carp (*Cyprinus carpio* L.) nurseries while growout is performed in other culture systems (Costa-Pierce 1992).

Potential for application of the model

Model performance confirms experimental results (Figure 6.2; Table 6.3), but failed to predict individual fish weight correctly in some independent datasets (Table 6.4). The estimation of CONLEV and TPFS from NPP apparently disregarded important site-specific effects. More experimental data on consumption levels of fish in ponds in relation to pond productivity and environmental factors are needed to improve the model. Nevertheless, FGS4 is a useful tool that may be used for estimations of fish production on the basis of local temperature, dissolved oxygen and food conditions.

Acknowledgements

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Chapter 7

FISH PRODUCTION IN INTEGRATED AGRICULTURE-AQUACULTURE
SYSTEMS: GENERAL DISCUSSION

Introduction

The general objective of the research described in this thesis was to obtain a better
understanding of fish production in integrated ponds and ricefields by formulating a
general model for these production systems.

In Chapter 1 it was argued that integrated culture systems produce fish without large
industrial energy inputs and have positive effects on the whole farm system. A main
characteristic of these production systems is the variability in environmental variables,
notably dissolved oxygen concentration and, to a lesser extent, temperature. A systems
approach using mathematical models was advocated because it can lead to insights that
have universal applicability while avoiding the pitfalls of site- and species-specific,
expensive experimental work.

In Chapter 2, previous pond modelling efforts were reviewed. Two modelling
approaches were distinguished: descriptive models, generally the result of statistical
analysis of datasets; and explanatory models, based on knowledge of the biological
processes underlying fish production.

In Chapter 3, multiple regression analysis (a descriptive modelling technique) was
used for the analysis of data from 15 integrated rice-fish production experiments with the
Nile tilapia *Oreochromis niloticus* (L.) in the Philippines. Results showed that this
technique led to insights in the data that had not been obtained through separate analysis
of the experiments. Main drawback of this method was that the models were not
applicable to other production environments.

Thus, in Chapter 4 an explanatory model for growth of *O. niloticus* was developed
on the basis of an existing simulation model for the African catfish *Clarias gariepinus*
Burchell (1822). After parameterization and calibration, the model gave good predictions
of fish growth in independent datasets. Parameterization and calibration of the same model
for the rainbow trout *Oncorhynchus mykiss* (Walbaum) demonstrated the generality of the

model and it was concluded that, provided that enough data are available, the model may be used to simulate growth in a wide range of fish species. Food amount and composition, and temperature were the environmental variables upon which the model based its predictions. The model was called Fish Growth Simulator (FGS).

In Chapter 5, FGS was expanded with a dissolved oxygen module to accomodate oxygen as an environmental variable. The module was based on the hypothesis that oxygen is needed in sufficient amounts for aerobic metabolism, and that gill surface area limits the supply of oxygen to fish. The resulting model allowed the simulation of fish growth under low dissolved oxygen concentration and also provided an explanation for differences in the final weight of fishes, both within and between species.

In Chapter 6, FGS was used for simulation of food and oxygen limitations in waste-fed fish ponds in Honduras, Thailand and Rwanda. The model simulated fish growth for various combinations of environmental conditions: temperature, food availability and dissolved oxygen concentration. Validation, using data from Indonesia and Panama, was not successful because the food consumption rate in these countries could not be estimated.

In this final chapter, the results of the preceding chapters will be discussed in view of the original objectives, taking into account relevant literature. The discussion is grouped around the following issues: (1) methodology; (2) the role of oxygen in fish metabolism and growth; (3) model implications for the management of integrated agriculture- aquaculture systems; (4) implications for further work. (A detailed description of the FGS computer program is in preparation. Interested persons may contact the author at the Agricultural University, Department of Fish Culture and Fisheries, P.O. Box 338, 6700 AH Wageningen, The Netherlands).

Methodology: systems approach or empiricism?
The traditional approach to studying agricultural (or aquacultural) production problems is empirical, using dose-response experiments. Some treatment of interest (e.g., the amount of food) is applied to an experimental unit (e.g., a group of fish) in various amounts,

while keeping all other conditions equal. This was the approach chosen in the 15 separate experiments at the Freshwater Aquaculture Center in the Philippines (see Chapter 3) and is chosen in dozens of research institutes around the world. Although this results in large amounts of raw data, the analysis often is not satisfactory. In the majority of the 15 rice-fish experiments, analysis of variance of the separate experiment did not result in a statistically significant effect of the variable studied. Generally, this was the result of large within-treatment variability. The number of replicates needed to gain sufficient statistical power can be very large in aquaculture pond research (van Dam 1990). Statistical analysis of accumulated data, as with multiple regression in Chapter 3, resulted in new insights without the need for new experiments. Conclusions about the effects of various management practices on fish and rice production could be drawn, resulting in suggestions for improved management.

Only data on fish and rice at stocking and at harvest were available in Chapter 3. The main reason for this is the difficulty in sampling fish, especially tilapia, from ricefields (van Dam and Dela Cruz 1992). As a result, the analysis has a strong input-output character. In fishponds, where a sufficient fish sample can be taken periodically, the culture period can be divided into sub-periods of 2-4 weeks. Fish growth in each sub-period can be related to data on inputs and water quality in the same period. This approach, first proposed by Pauly and Hopkins (1983), was applied successfully to several pond experiments (Costa-Pierce, van Dam and Kapeleta 1993; Prein 1990; see also several papers in Prein, Hulata and Pauly 1993) and may become a standard method for analysis of pond experiments.

A disadvantage of the models in Chapter 3 is their specificity for the conditions in which the data were collected. Application of the fish yield models to rice-fish systems in e.g., Northeast Thailand or West-Java will fail because the climatic and geographic conditions are entirely different. Provided that sufficient data from different locations are available, descriptive models of fish growth across sites can be constructed. In Chapter 4 however, another approach was chosen. An explanatory model, based on knowledge of the biological processes underlying fish production, was applied to the Nile tilapia. The model integrated information from various disciplines such as physiology, ecology and

Table 7.1. Availability of data for parameterization of Fish Growth Simulator model for some species of interest to tropical pond/ricefield aquaculture. + = available; - = not available to our knowledge. Superscripts refer to some relevant literature sources. A: consumption rate; B: digestibility; C: food conversion and growth; D: routine metabolism and SDA; E: haemoglobin; F: gill size; G: effect of hypoxia; H: experimental data for calibration/validation?

Species	A	B	C	D	E	F	G	H
Cyprinus carpio	+[11,20]	+[6]	+[47,49]	+[12,13]	+[14,19]	+[15]	+[16,32]	+
Ctenopharyngodon idella	+[17,18]	+[21,22]	+[23,24,25]	-	-	-	-	?
Oreochromis niloticus	+[1,2,3,4]	+[5,6]	+[33]	+[7,48]	+[8]	+[9]	+[10,46]	+
Oreochromis mossambicus	-	+[34,36,38]	+[35,37]	+[39,40]	-	-	-	+
Tilapia rendalli	+[26,27]	+[28]	+[44,45]	+[29]	-	-	-	?
Clarias gariepinus	+[41,42]	+[43]	+[30,31]	+[31]	-	-	-	+

References: 1. Getachew 1989; 2. Moriarty et al. 1973; 3. Harbott 1976; 4. Chapman and Fernando 1994; 5. Getachew 1988; 6. Degani and Revach 1991; 7. Becker and Fishelson 1990; 8. Verheyen et al. 1985; 9. Fernandes and Rantin 1986; 10. Tsadik and Kutty 1987; 11. Garcia and Adelman 1985; 12. Winberg 1956; 13. Hamada and Maeda 1983; 14. Salama and Nikinmaa 1988; 15. Hughes and Morgan 1973; 16. Hughes et al. 1983; 17. Cui et al. 1993; 18. Bonar et al. 1990; 19. Speckner et al. 1989; 20. Zur 1980; 21. Lesel et al. 1986; 22. Das and Tripati 1991; 23. Carter and Brafield 1992; 24. Huisman and Valentijn 1981; 25. Cui et al. 1994; 26. Caulton 1977a; 27. Chifamba 1990; 28. Caulton 1976; 29. Caulton 1977b; 30. Machiels and Henken 1985; 31. Hogendoorn 1983; 32. Christiansen et al. 1982; 33. Meyer-Burgdorff et al. 1989; 34. Mathavan et al. 1976; 35. Jauncey 1982; 36. de Silva et al. 1984; 37. Bowen 1976; 38. Bowen 1981; 39. Job 1969; 40. Caulton 1978a; 41. Hogendoorn et al. 1983b; 42. Machiels and Van Dam 1987; 43. Henken et al. 1985; 44. Caulton 1978c; 45. Caulton 1978b; 46. Fernandes and Rantin 1989; 47. Huisman 1976; 48. Ross and McKinney 1988; 49. Sondermann et al. 1985.

biochemistry. By formulating mathematical equations at the level of the basic processes using biologically meaningful parameters, it was possible to predict behaviour at a higher aggregation level (in this case: an "average" fish in a fish tank or pond). Thus, this approach is fundamentally different from a descriptive approach, where the equations describe the higher aggregation level. Parameters of descriptive models may be interpreted biologically but they do not represent separate biological processes.

The simulations reported in Chapters 4-6 have demonstrated that an explanatory model could simulate fish growth over a wide range of environments. One of the main drawbacks of this approach is the need for data for parameterization, calibration and validation of models. Table 7.1 summarizes the availability of published information on the major processes represented in FGS for a few tropical aquaculture species. Studies on digestibility and utilization of nutrients and energy are available for most of the species. By contrast, information on respiratory physiology (oxygen affinity of hemoglobin, gill surface area measurements, oxygen pressure gradients across gills, effects of hypoxia) is much scarcer. Studies on respiratory physiology are often conducted under artificial laboratory situtations, but this should not be problematic as these basic physiological processes are expected to be similar under culture conditions. Some of the information on basic processes can even be used across fish species. Therefore, it will generally be possible to parameterize models for the species listed in Table 7.1. For calibration and validation, complete datasets on fish growth, amount and composition of feed, temperature and dissolved oxygen concentration and, ideally, fish body composition are needed from a wide range of environments. This kind of raw data, if available, is often not published in the primary literature and therefore hard to retrieve.

The comparison of descriptive and explanatory models stresses one difference between data-driven and theory-driven research. Descriptive models (data-driven) are useful when large amounts of data are available. They result in hypothesis development and suggestions for further research. Explanatory models integrate available knowledge, leading to understanding of system behaviour. A comparison of predicted system behaviour with observations helps to identify knowledge gaps, resulting in research geared specifically at filling these gaps (theory-driven). Descriptive and explanatory models can

complement each other. Then, existing information (accumulated data and basic biological information) is utilized in an optimal way, research priorities can be identified at an early stage and experimental work can be most effective, leading to acceleration in research.

Role of oxygen in fish metabolism and growth

Studies of fish bioenergetics are usually based on quantifying energy budgets or a balanced energy equation (Webb 1978; Brett and Groves 1979; Brafield 1985; Jobling 1994). All terms of the budget (consumption, faecal and urinary losses, gain and metabolism) are expressed in energy equivalents. The effects of temperature, body weight and feeding level on energy budgets have received considerable attention (Heinsbroek 1987). Because of the focus on energy in growth studies, oxygen has received much less attention. By comparison, metabolic studies in homeotherms rarely address the oxygen supply to the organism because the constant, high oxygen content of air ensures an abundant oxygen supply to the animal. The oxygen content of water equilibrated with air is only about one thirtieth that of air; and oxygen diffuses roughly a million times faster in air than in water; also, water is much more dense and viscous than air (Steen 1971). The oxygen supply to fish, therefore, cannot be taken for granted.

Energy budgets can be established at feeding levels ranging from fasting to maximum feeding. It is difficult, however, to measure feed consumption in fish accurately. All feed administered is not necessarily consumed; some may be wasted in the water. Furthermore, the concept of an energy budget does not provide an upper limit, be it to consumption or to metabolism. Maximum feed consumption has been explained using rates of stomach evacuation (Jobling 1981a) or the energy content of the feed (Lovell 1979), but this has never led to a satisfactory general model. Taking oxygen into account provides an alternative concept for a limit to the energy budget and has been elaborated here.

In many fish species (and also in terrestrial animals), the exponent of the allometric relationship between metabolism and weight was observed to be greater at fasting or maintenance level than at maximum feeding. This phenomenon might account for the fact

that fish do not grow indefinitely (Hogendoorn 1983; Heinsbroek 1987). The hypothesis about oxygen limitation (Chapter 5) suggests that the weight exponent at maximum feeding is identical to the exponent of the allometric relationship between body weight and gill surface area. The biochemical model first proposed by Machiels offered an opportunity to test this hypothesis because this model makes a distinction between the energy and oxygen demands of the fish. The simulation results in Chapter 5 support this theory. Unfortunately, there are not many species for which data are available to investigate this (Table 7.1).

Within a fishpond, dissolved oxygen concentration and temperature are the main causes of environmental variability. Studies on fish bioenergetics are generally conducted under constant temperature and oxygen conditions. The consequences of using parameter values which were determined under constant conditions for pond situations are not clear. An example is feeding metabolism. In the model, energy demand in response to feeding is instantaneous, as is the subsequent oxygen consumption. In reality, oxygen consumption after a meal rises to a peak and then slowly declines; the peak is usually observed within 12 hours after the meal (Jobling 1981b). With constantly changing oxygen concentrations in a fish pond, the interaction between the time of a meal and the duration of the associated oxygen demand may be important.

The oxygen limitation hypothesis brings up questions about the regulation of food intake in fish. Optimal foraging theory states that individuals attempt to maximize a goal function that is linked to fitness. The goal function comprises both costs (e.g., energy expended in looking for food and processing it) and benefits (e.g., energy and nutrients gained) (Townsend and Winfield 1985). Various "fitness currencies" can be maximized, e.g., the ratio of energy gained over energy spent in foraging (currency is efficiency) or the net rate of energy gain (currency is rate) (Ydenberg, Welham, Schmid-Hempel, Schmid-Hempel and Beauchamp 1994).

Tolkamp and Ketelaars (1992), in a study in ruminants, defined oxygen consumption as the cost because the use of oxygen by tissues causes damage to cell structures, loss of vitality, ageing and a limited life span. Using a model based on maximization of the efficiency of oxygen utilization they were able to predict the voluntary intake of a variety

Table 7.2. Estimation of oxygen utilization efficiency for an experiment by Osman (1988). First three columns show original data. Net energy was computed as the sum of net energy for maintenance (35.3 kJ $kg^{-0.8}$ d^{-1}) and net energy for growth. O_2 consumption was converted to liters per day assuming 1.43 g O_2 l^{-1}.

feeding level	O_2 con-sumption	Net energy for growth	Net energy	O_2 con-sumption	NE/O_2
g $kg^{-0.8}$ d^{-1}	мg $kg^{-0.8}$ h^{-1}	kJ $kg^{-0.8}$ d^{-1}	kJ $kg^{-0.8}$ d^{-1}	l $kg^{-0.8}$ d^{-1}	kJ $(1\ 0_2)^{-1}$
0.5	128.9	-28.1	7.2	2.16	3.33
1.0	118.3	-20.1	15.2	1.99	7 64
1.5	122.4	-21.7	13.6	2.05	6.63
2.0	128.0	-17.0	18.3	2.15	8.51
3.0	151.1	-8.8	26.5	2.54	10.43
4.0	161.7	-7.0	28.3	2.71	10.44
14	233.0	72.3	107.6	3.91	27.5
16	273.6	83.9	119.2	4.59	26.0
18	269.1	86.7	122.0	4.52	27.0
20	279.6	91.2	126.5	4.69	27.0
22	274.8	95.1	130.4	4.61	28.3
24	295.7	98.7	134.0	4.96	27.0

of feeds by ruminants. The maximum oxygen utilization efficiency in sheep ranged from about 15 to 20 kJ net energy $(1\ O_2)^{-1}$.

The oxygen utilization efficiency for the Nile tilapia, *Oreochromis niloticus* increased from about 3.3 to 10.4 kJ $(1\ O_2)^{-1}$ at consumption levels from 0.5 to 4.0 g $kg^{-0.8}$ d^{-1} and were around 27.5 kJ $(1\ O_2)^{-1}$ at consumption levels 14-24 g $kg^{-0.8}$ d^{-1} (estimated from Osman (1988); see Table 7.2). A simple quadratic model fitted to these data is shown in Figure 7.1. There is a large gap between 30 and 110 kJ $kg^{-0.8}$ d^{-1} and the scatter
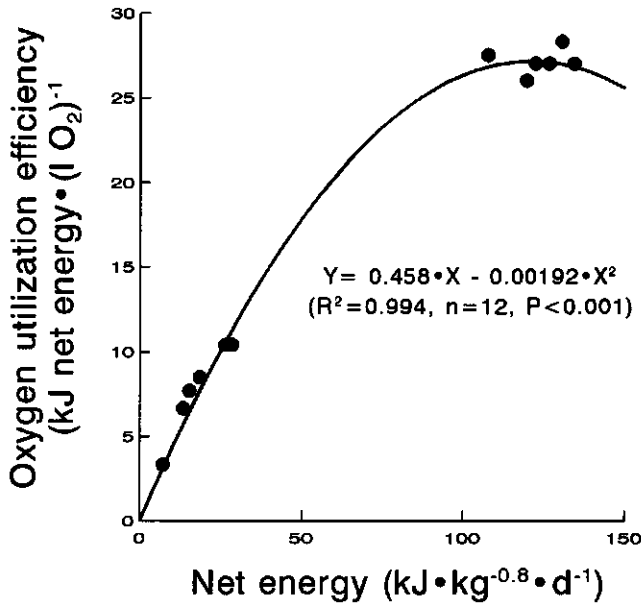
Figure 7.1. Simple quadratic model fitted to the data from Table 7.2. Maximum oxygen utilization efficiency appears to occur at the observed ad lib feed intake. For discussion, see text.

around the maximum is considerable; therefore, no definite conclusions can be drawn from this curve. Nevertheless, a quadratic curve through the origin seems to be the obvious model here. The maximum oxygen utilization efficiency coincided with the ad lib feed intake. As in the analysis of Tolkamp and Ketelaars (1992), these fish may have been feeding at their optimum oxygen utilization efficiency.

The central question is: what is the strategic goal of food consumption in fish? The differences between water-breathing poikilotherms and air-breathing homeotherms were

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already pointed out. It is likely that the anatomy of organisms has evolved to fit their physiological requirements. Gill size, oxygen affinity of hemoglobin, heart capacity, etc. are all geared for each other because it is expensive to maintain unnecessary machinery. Still, food intake is flexible. Consumption rates of wild fish are generally lower than fish under culture conditions (Chapter 6). Apparently, environmental conditions can shift the feed intake within a genetically determined range (Calow 1985). Food under culture conditions is generally more abundant and of a higher quality, resulting in changes in the cost-benefit trade-off determining feed intake. The analysis in Table 7.2 and Figure 7.1 suggests that tilapias are also maximizing their oxygen utilization efficiency, albeit at a higher level than sheep. Under natural conditions, the limits of the metabolic scope may not always be reached, and where lifestyle or environment do pose limits fish have adapted, e.g. by developing very large gills (as in the tunas) or by developing accesory respiratory organs for air-breathing (as e.g. in in the largest freshwater fish *Arapaima*). Under culture conditions that result in increased feed intake, oxygen may be limiting more often. Priede (1985) argues that research on fish energetics has over-exposed species that swim well in respirometers. These species happen to be mostly salmonids with large gills and a high proportion of dark, aerobic muscle. The majority of fish species (probably more than 50%, according to Priede) cannot maintain high swimming speeds and are of the "viscerally dominated type". In these species, locomotor activity has to be fitted in between peaks of feed utilization activity that occupy the entire metabolic scope. This suggests that oxygen limitation can actually occur in the natural environment.

Implications for the management of integrated agriculture-aquaculture systems

Integrated fishponds can be linked to the agriculture components of the farm system in various ways. In integrated rice-fish culture, fish and crops can be integrated most closely, sometimes sharing the same water. However, in most cases integration is realized by applying waste materials from animal and crop production to fish ponds. In some cases, these materials are utilized by the fish directly as a feed (e.g., rice or maize bran, grasses, vegetable leaves). Then, protein and cellusose contents will affect the fish

production that can be realized. Most often, waste materials serve as "feeds" for the microbial pond organisms which then serve as fish feeds. In these cases, waste inputs have an effect on both microbial productivity and on water quality. Large amounts of organic matter input will raise oxygen consumption in the detrital foodweb, thereby lowering the dissolved oxygen concentration. Waste materials containing soluble inorganic nutrients will stimulate phytoplankton production, leading to increased oxygen production during the photoperiod and increased respiration at night. Also, photosynthesis affects water pH through the uptake of carbon dioxide from the water, leading to diurnal pH flucutations. Thus, pond inputs have a strong effect both on water quality and on fish feeding.

The current model suggests that *O. niloticus* in ponds eat the maximum amount of food that can be fitted into their scope for production (defined as the difference between maximum aerobic and routine metabolism). Growth is primarily determined by the size of the scope for production and by the quality of the food. Growth rates can be maximized by maximizing the scope for production and ensuring a high food quality.

The first option for maximizing scope for production is to increase maximum aerobic metabolism. Maximum aerobic metabolism depends primarily on the size of the gill surface and, in ponds, may be limited by the dissolved oxygen concentration, which is the result of oxygen production (by photosynthesis) and consumption (by respiration processes). The minimum dissolved oxygen concentration needed for unlimited growth depends strongly on temperature. An increase in temperature will raise routine metabolism and also reduces oxygen solubility in water. Minimum dissolved oxygen concentrations in ponds in Thailand and Rwanda were around 5 mg l^{-1}, but in Thailand oxygen limitation only occurred because of the higher temperature (Chapter 6). At higher temperatures, a higher dissolved oxygen concentration will be needed to maintain the scope for production. Figure 7.2 summarizes the combined effects of temperature and oxygen on fish growth.

In fishponds, there are limited possibilities for manipulation of dissolved oxygen concentration. Intermediate phytoplankton densities should be maintained because then, net oxygen production is highest and highest dissolved oxygen concentrations can be achieved (Colman and Edwards 1987; Smith and Piedrahita 1988). If technically and
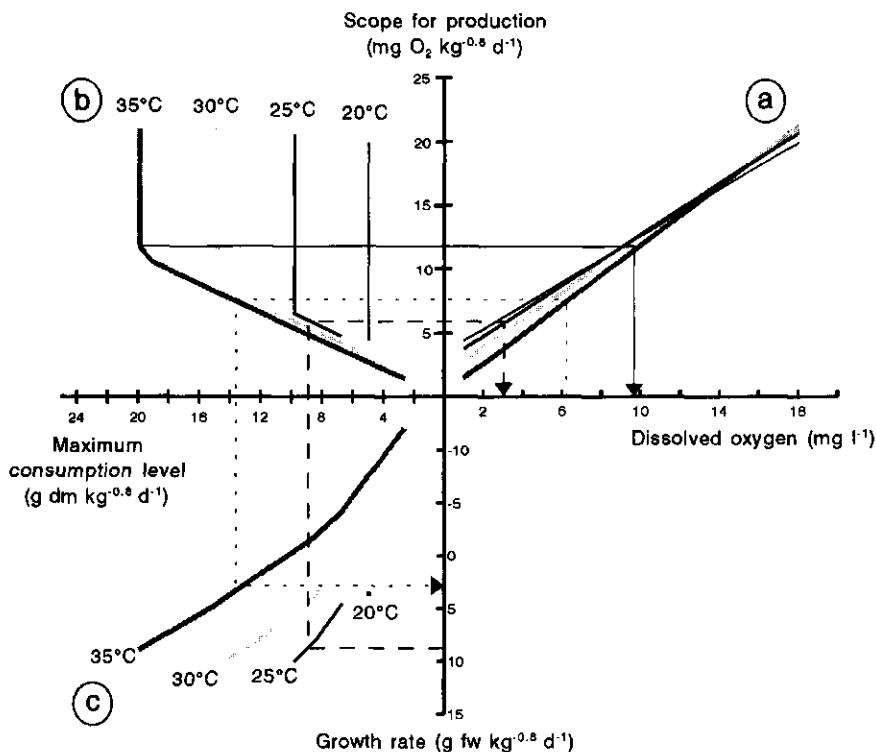
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Figure 7.2. Summary of FGS simulation results at constant dissolved oxygen (DO) concentrations and four constant temperatures (TEMP).
Quadrant a: Relationship between DO and scope for production at four TEMP's.
Quadrant b: Relationship between scope for production and maximum consumption level. Maximum consumption levels in the absence of oxygen limitation were assumed to be 5, 10, 15 and 20 g kg$^{-0.8}$ d^{-1} (dry matter) at 20, 25, 30 and 35 °C, respectively.
Quadrant c: Relationship between consumption level and fish growth rate.
All data are from simulations with a 30 gram Nile tilapia in a 7-day period.
Feed composition was 14.2% dry matter (dm), 52.1% protein (in dm), 7.7% lipids (in dm) and 27.3% carbohydrates (in dm).
Relationships between environmental factors (DO, TEMP) and fish growth can be evaluated in various ways:
1. Effect of TEMP and DO on fish growth: start with DO in quadrant a and trace scope for production, maximum consumption level and growth rate for each temperature (see dotted arrow).
2. Minimum DO required to realize a certain growth rate. From the growth rate, trace consumption level, scope for production and DO (dashed arrow).
3. DO concentration at which growth becomes oxygen-limited: from the bend in the curve of quadrant b, trace scope for production and DO (e.g., solid arrow at 35°C).

economically feasible, aeration may be applied when oxygen is limiting. The model can be used to compute the minimum oxygen concentration in relation to fish species and local conditions.

Another option to maximize scope for production is the choice of the right fish strains and species. There is a considerable variation in intensity of routine metabolism, both between and within species (Chapter 4; Winberg 1956; Becker and Fishelson 1990). Relatively little is known about gill surface area in species for pond aquaculture, but some variability in gill size within species may be expected. It may be feasible to select for this trait in fish breeding programs, provided that reliable and simple methods for gill area measurement are available. It is possible that current selection programs are already indirectly selecting for high scope for production. Air-breathing fish species have a natural advantage in this respect.

Apart from scope for production, food quantity and quality are important. Food quantity is determined by the level of primary production reached and by possible additional feed inputs. The rate of primary production depends strongly on temperature and should be supported by sufficient nutrient inputs into the pond. In tilapia culture, fish stock density is of special importance because of the prolific reproduction that may occur. Simulations (Chapter 6) showed that food limitation occurred in almost all ponds. In Rwanda, this was due to low primary productivity. In Honduras and Thailand, food limitation started after reproduction had occurred.

Protein is the most important component of feeds, because increases in body weight are primarily due to protein gain and because protein is an important substrate for energy generation in fish (Chapter 4). Most natural fish feeds have a high protein content of good amino acid composition (Yurkowski and Tabachek 1979; Hepher 1988). The only exception are green algae (Chlorophyceae) and diatoms. Manipulation of phytoplankton in fishponds may not be practically feasible, especially in on-farm situations. The model can be used for a theoretical evaluation. Although the low dry matter content of natural feeds appears to be a disadvantage, *O. niloticus* are well adapted for extracting dry matter from the aqueous environment (maximum dry matter consumption rate about 15 g $kg^{-0.8}$ d^{-1} in natural feeds (14% dry matter) versus 24 g $kg^{-0.8}$ d^{-1} in pelleted feed (90 % dry matter).

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More attention is needed for the effect of oxygen stratification on fish behaviour and their access to food resources in the pond. If fish do prefer to stay in the oxygen-rich upper layers of the water column, they may be separated from the detritus on the pond bottom. Bottom feeders in polyculture have been employed to remobilize nutrients from the sediment. Stirring of the pond bottom using rakes has also been suggested as a means of breaking stratification (Costa-Pierce and Pullin 1989; Beveridge, Wahab and Dewan 1994). This may be an option in combination with aeration.

Summarizing the options for management of integrated fishponds, it can be concluded that most options require a high research input (genetic improvement of fish, manipulation of natural food production) and that some options may be feasible in on-farm situations (aeration). A model such as FGS may help in assessing the options before implementing experiments, so that unviable options such as feeding fish in high-temperature ricefields (see Chapter 6) can be avoided.

Implications for further work

All data used in this thesis, whether for parameterization, calibration or validation, were from experiments originally conducted for other purposes. The choice for this approach was deliberate. However, there are some knowledge gaps. Some of these gaps concern basic fish physiology, such as the relationship between ambient oxygen pressure and the pressure gradient across fish gills. The empirical equation used to estimate the effect of ambient oxygen concentration (Chapter 6) is not satisfactory. Solving these problems would require basic experimentation in a well-equipped physiological laboratory.

Some other problems are more specific for aquaculture. An example is the consumption behaviour of fish in ponds. Very little information about the spatial distribution of fish in relation to water quality (especially dissolved oxygen) exists. Experiments to shed some light on this problem would have to involve fish monitoring techniques that could register fish movements continuously. Possibly echo sounding and video could be used for this (Floen, Totland and Ovredal 1988; Juell, Fernö, Furevik and Huse 1994).

The size-distribution of the fish population is not considered in the current version of the model, which simulates the growth of an average, sexless fish. The model could be refined by applying the 'boxcar train' method to simulate the dispersion in size distribution (de Wit and Goudriaan 1978). This would be especially useful for simulation of the growth in size and numbers of tilapia recruits that compete with the stocked fish for food.

Little information exists about the consumption rate of fish in ponds. Good methods for the estimation of daily ration based on quantitative analysis of stomach contents exist (Jarre, Palomares, Soriano, Sambilay and Pauly 1989, 1990) and should be applied to pond fish. Unfortunately, there seems to be a reluctance among scientists and funding agencies to apply sophisticated research techniques to low-input production systems, such as integrated fishponds. Little progress in pond culture can be expected if this situation does not change.

In the current model, temperature and oxygen are forcing functions. Predictive simulation models for water temperature and dissolved oxygen have been constructed (Chapter 2) and may be integrated with FGS. The biochemical modelling approach has been applied succesfully to crop production (Penning de Vries, Brunsting and van Laar 1974), pig growth (Oko 1979) and fish growth (Machiels and Henken 1986, 1987; chapter 4, this volume). The principle can be applied to other biotic groups in the pond ecosystem (phytoplankton, zooplankton, etc. See Chapter 1, Figure 1.2). A dynamic nutrient balance could be derived from the manuring/feeding rates and from the biomass of the various biotic groups. At the same time, water quality could be computed from the gaseous exchange (carbon dioxide, oxygen) and metabolic waste production (ammonia). Such a general model may help in identifying the most promising experiments that ultimately lead to improvements in productivity.

Acknowledgements

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SUMMARY

Modelling studies of fish production in integrated agriculture-aquaculture systems

Total world fish production in 1990 was around 104 million tonnes, of which 14 million tonnes were from aquaculture. Capture fisheries production is suffering from overfishing and environmental degradation, and the contribution from aquaculture to total fish production is expected to increase further. For aquaculture in developing countries, earthen fishponds are often recommended because they can produce fish without high investments in energy, facilities and fish feeds. In fishponds agricultural wastes and byproducts, such as grasses and manures, can be mineralized by heterotrophic microorganisms. The anorganic nutrients that result from this process can be utilized by primary producers (especially phytoplankton) or accumulate in the pond sediment. Both heterotrophic and autotrophic biomass can serve as natural fish feeds.

Apart from the benefits of fish as a source of human protein consumption, fishponds can contribute to the improvement of farming systems. Research has shown that integrating fishponds with other agricultural enterprises can increase whole farm productivity and sustainability by enhancing the cycling of nutrients through the farm system.

On research stations with integrated fishponds high yields can be obtained, but it has proved difficult to repeat these successes on-farm. Technical reasons for this are the complexity of integrated farming systems and the large variety of fish species, farming systems and climates. Classical agricultural experimentation with dose-response tests and statistical analysis can yield important information about the whole production system under specific conditions, but it is difficult to extrapolate research results to other areas and climates. Moreover, the number of potential combinations of species, feeds and other resources is vast, making research expensive.

The similarity of fishponds in ecological structure offers possibilities for a systems approach using mathematical models. Construction of general pond models increases the understanding of the pond ecosystem. A general model will allow comparisons of pond systems that display different behaviours but share important common features. Such a model can be used for developing management strategies and for extrapolation of research results to other locations. In this way, models can help accelerate research, saving both time and money.

In this thesis, a general model for fish growth in ponds is developed. After an introduction (Chapter 1), the thesis starts with a review of existing pond models (Chapter 2). A distinction is made between descriptive models, that describe the relationships between the system variables but do not explain the mechanisms underlying these relationships; and explanatory models, that quantify the system on the basis of knowledge about the system variables and their relationships with each other and with external variables. Both types of models have their own strengths and may complement each other.

In Chapter 3, a descriptive model was used to analyze the effects of various management practices on yields and growth of fish and rice in an integrated rice-fish production system. Data from 15 rice-fish experiments, conducted at the Freshwater Aquaculture Center of Central Luzon State University, Philippines between 1976 and 1983, were analyzed using multiple linear regression with the objective to explain the variation in fish production from input and climate data. The experiments dealt with the effects of various management practices on the production of Nile tilapia, *Oreochromis niloticus* (L.) in concurrent culture with several varieties of lowland irrigated rice, *Oryza sativa* (L.).

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Significant models (P < 0.001) were derived for gross fish yield (kg ha^{-1}), net fish yield (kg ha^{-1}), fish recovery (%), fish growth rate (g day^{-1}) and rice yield (kg ha^{-1}). For gross fish yield, 66% of the variation could be explained by seven explanatory variables: length of the culture period, fish stocking weight and density, nitrogen and phosphorous application rates, insecticide application and air temperature. The analysis offered new insights into the functioning of the system. It also showed that the models could not be extrapolated to other situations. Therefore, an explanatory model for growth of the Nile tilapia was made on the basis of the biochemical growth model for the African catfish *Clarias gariepinus* (Burchell 1822) by Machiels and co-workers (Department of Fish Culture and Fisheries, Wageningen Agricultural University).

The biochemical model predicts fish weight and fat percentage from the amount and composition of the feed and water temperature on the basis of the biochemical reaction equations of the intermediary metabolism. In Chapter 4, this model (called FGS, Fish Growth Simulator) was parameterized and calibrated for the herbivorous Nile tilapia and for the carnivorous rainbow trout *Onchorhynchus mykiss* (Walbaum). The major factor determining the efficiency of feed conversion is the proportion of energy provided by protein oxidation. In the model, this proportion is positively related to the protein feeding level and the protein/energy ratio of the feed. FGS predicted fresh weight of *Oreochromis niloticus* in an independent dataset with a mean deviation of -2.1% (range -22.7 to +37.1) of observed values (fish weights 10-40 g). For *Oncorhynchus mykiss*, the mean deviation was 4.8% (range -20.8 to +24.2, 50-800 g). Thus it was shown that FGS can predict the growth of fish on the basis of knowledge about the basic biochemical and physiological processes.

The most important environmental factor in FGS is water temperature. In fishponds, however, oxygen is also of major importance. 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. In Chapter 5, it is hypothesized that the maximum rate of feed intake is related to the capacity to take in oxygen for processing of this feed and that the maximum rate of feed intake relative to body size decreases with increasing body size to a point where feeding stops, and therefore growth is zero. An oxygen limitation module based on this theory was incorporated into FGS. 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. This extended FGS was used to simulate feeding and growth of *O. niloticus* in two situations. First, growth under reduced ambient oxygen pressure was simulated. FGS simulated reduced feed intake and the resulting reduction in growth rate quite accurately. Then, growth under natural (assumed unlimiting oxygen) conditions in an East-African lake was simulated. With realistic values for the model parameters, simulated final weight for *O. niloticus* agreed well with observed weight. Simulation results thus provided strong support for the oxygen limitation theory. Hence, FGS 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.

In Chapter 6, FGS was used to simulate food and oxygen limitations of *O. niloticus* under pond conditions using data from the world-wide, standardized CRSP-project. Data were from Rwanda, Thailand, Indonesia, Honduras and Panama. In each country, ponds were stocked with monosex male tilapias for 150 days. Ponds were fertilized with chemical fertilizers and with chicken manure. For the simulations, the stocking weight of the fish and the temperature and oxygen measurements were used as forcing functions. To model food competition between stocked fish and fingerling recruits a pond food module was added. Calibration consisted of iterative determination of two model parameters: CONLEV, the consumption rate without food or oxygen limitations; and TPFS, the total daily food supply by the pond. Calibration results showed that in most ponds, final fish weight could be simulated with acceptable values for CONLEV and TPFS. Both CONLEV and TPFS were related to the net primary production and to the chlorophyll *a* concentration. For each pond, an estimate of the degree of food and/or oxygen limitation (expressed as the percentage of time that food or oxygen limitation existed) could be given. Validation of the model with independent data from Indonesia and Panama was not successful. The relationships used to estimate values of CONLEV and TPFS from primary productivity measurements were apparently not applicable to the conditions of Panama and Indonesia. When the model is to be used for *prediction* of fish growth, a more detailed, explanatory approach of the relationship between CONLEV and TPFS and primary production is necessary. Nevertheless, the model provides a conceptual framework for the analysis of fish growth in ponds, tying together effects of food quantity and composition, temperature and dissolved oxygen concentration.

In Chapter 7, the results are discussed in the light of the original research objectives and implications for pond management and further research are given. Main conclusions are: (1) Research into fish production in integrated agriculture-aquaculture systems should take a systems approach, using both descriptive and explanatory models in combination with well-targeted experimentation. This ensures optimal utilization of available information and effective use of expensive research funds/facilities; (2) It is possible to predict the growth of a broad range of fish species using a general simulation model based on the physiological processes underlying fish growth. In the absence of limiting water quality factors (such as unionized ammonia or dissolved oxygen), the factors affecting fish growth are temperature, food quantity and food composition (i.e., protein, fat, carbohydrate and dry matter content). For each species, a set of biologically meaningful parameters is needed that may be derived from the literature or from relevant experimental data; (3) The amount of food fish can process is limited by their ability to take in oxygen. The oxygen available for food processing and locomotion is equal to the difference between maximum metabolism (defined by the gill surface area, except in air-breathing fish) and routine metabolism. Factors that reduce this difference (which can be called "scope for production"), either by reducing maximum metabolism or by increasing routine metabolism, will reduce growth through a reduction of food intake; (4) The model developed in this study may be used to analyze food and oxygen limitations to fish growth for a wide range of conditions.

SAMENVATTING

Modelonderzoek naar visproduktie in geïntegreerde visteeltsystemen

De totale visproduktie in de wereld in 1990 was ongeveer 104 miljoen ton, waarvan 14 miljoen ton werd geproduceerd in de aquacultuur (visteelt). De visserij kampt op het ogenblik met problemen, zoals overbevissing en milieu-degradatie, en het aandeel van de visteelt in de totale visproduktie zal naar verwachting stijgen in de komende jaren. Voor visteelt in ontwikkelingslanden worden aarden visvijvers vaak aanbevolen, omdat daarin vis geproduceerd kan worden zonder hoge investeringen in energie, infrastructuur en voeders. In visvijvers kunnen agrarische afvalstoffen en bijprodukten, zoals grassen en dierlijke mest, gemineraliseerd worden door heterotrofe microörganismen. De vrijkomende anorganische nutriënten kunnen worden benut door de primaire producenten (met name fytoplankton) of accumuleren in de vijverbodem. Zowel de heterotrofe als de autotrofe biomassa kan dienen als natuurlijk visvoedsel.

Naast de voordelen van vis als eiwitbron in de humane voeding kunnen visvijvers een bijdrage leveren aan het verbeteren van agrarische bedrijfssystemen. Uit onderzoek is gebleken dat het integreren van visvijvers met andere landbouwactiviteiten bedrijfssystemen produktiever en duurzamer kan maken, o.a. door het bevorderen van de circulatie van nutrienten door het systeem.

Op proefstations met geïntegreerde visvijvers kunnen hoge opbrengsten gehaald worden, maar het is moeilijk zulke successen op het boerenbedrijf te realiseren. Op het biologisch/technische vlak zijn de complexiteit van geïntegreerde systemen en de grote variatie in vissoorten, bedrijfssystemen en klimatologische omstandigheden belangrijke hindernissen voor doelmatig onderzoek. Klassiek landbouwonderzoek met dosis-respons proeven en statistische analyse kan belangrijke informatie opleveren over het produktiesysteem als geheel onder specifieke omstandigheden, maar de resultaten zijn moeilijk te extrapoleren naar andere lokaties en klimaatsomstandigheden. Bovendien is het aantal te onderzoeken combinaties van vissoorten, voeders en andere hulpbronnen groot, waardoor het onderzoek duur en tijdrovend wordt.

De overeenkomsten in ecologische strucuur van visvijvers bieden mogelijkheden voor een systeembenadering met wiskundige modellen. Algemene vijvermodellen vergroten het begrip van het vijverecosysteem en maken een vergelijking mogelijk van systemen die op het oog verschillend zijn, maar toch belangrijke overeenkomsten vertonen. Zulke modellen kunnen worden gebruikt voor het ontwikkelen van beheerstrategieën en voor het extrapoleren van onderzoeksresultaten naar andere locaties. Op deze wijze kan onderzoek sneller verlopen, waardoor zowel tijd als geld bespaard wordt.

In dit proefschrift wordt een algemeen model voor visgroei in vijvers ontwikkeld. Na een inleiding (Hoofdstuk 1) begint het onderzoek met een overzicht van bestaande vijver-modellen (hoofdstuk 2). Daarbij wordt een onderscheid gemaakt tussen beschrijvende modellen, die relaties tussen systeemvariabelen aangeven maar niets zeggen over de oorzaken van die relaties, en verklarende modellen die het gedrag van een systeem voorspellen op basis van kennis over de relaties tussen de variabelen van het systeem. Beide typen modellen hebben hun eigen toepassingsmogelijkheden en kunnen elkaar aanvullen.

In hoofdstuk 3 wordt een beschrijvend model gebruikt voor het analyseren van een geïntegreerd rijst-visteeltsysteem, waarbij de effecten van beheersmaatregelen voor rijst en vis op de groei en overleving van de vis worden onderzocht. Gegevens van 15 rijst-visteelt experimenten, die werden uitgevoerd bij het Freshwater Aquaculture Center van de Central

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Luzon State University in de Filippijnen tussen 1976 en 1983, werden geanalyseerd met meervoudige regressie-analyse. Het doel daarvan was om de variatie in visproduktie te verklaren uit input- en klimaatsvariabelen. Met behulp van de experimenten werden de effecten onderzocht van een aantal beheersmaatregelen op de produktie van de Nijltilapia *Oreochromis niloticus* (L.) in gecombineerde teelt met verschillende natte rijstvariëteiten *Oryza sativa* (L.). Statistisch significante modellen (P < 0.001) werden afgeleid voor bruto en netto visproduktie (kg ha^{-1}), visoverleving (%), visgroeisnelheid (g d^{-1}) en rijstproduktie (kg ha^{-1}). Voor de bruto visproduktie kon 66% van de variatie verklaard worden met zeven onafhankelijke variabelen: duur van de groeiperiode, begingewicht van de vis, bezettingsdichtheid, stikstof- en fosfaat gift, insecticide-toepassing en luchttemperatuur. De analyse leverde nieuwe inzichten op over het functioneren van dit systeem die uit de afzonderlijke experimenten niet naar voren waren gekomen. Tegelijkertijd wordt echter duidelijk dat de modellen niet van toepassing zijn op andere situaties. Daarom werd een verklarend simulatiemodel voor de Nijltilapia gemaakt op basis van het biochemische groeimodel voor de Afrikaanse meerval *Clarias gariepinus* (Burchell 1822) van Machiels en medewerkers (vakgroep Visteelt en Visserij, Landbouwuniversiteit Wageningen).

Het biochemische model berekent het visgewicht en vetpercentage uit de hoeveelheid en samenstelling van het voer en de watertemperatuur op basis van de biochemische reactievergelijkingen van de intermediaire stofwisseling. In hoofdstuk 4 werd dit model (dat hier FGS, Fish Growth Simulator wordt genoemd) geparameteriseerd en gecalibreerd voor de herbivore Nijltilapia en voor de carnivore regenboogforel *Oncorhynchus mykiss* (Walbaum). De belangrijkste factor die de efficiëntie van de voeromzetting bepaalde was het aandeel van de energievoorziening waarin door eiwitoxidatie werd voorzien. In het model was dit aandeel gekoppeld aan het eiwitvoederniveau en aan de eiwit/energie verhouding in het voer. FGS voorspelde het gewicht van *Oreochromis niloticus* in een onafhankelijke set gegevens met een gemiddelde relatieve fout van -2,1% (uitersten: -22,7 tot +37,1%) ten opzichte van de waargenomen waarden (visgewicht tussen 10 en 40 g). Voor *Oncorhynchus mykiss* was deze fout 4,8% (uitersten -20,8 tot +24,2%, visgewicht 50-800 g). Hiermee was gedemonstreerd dat FGS de groei van vissen kan voorspellen op basis van kennis over de basale biochemisce en fysiologische processen.

De belangrijkste omgevingsfactor in FGS is de watertemperatuur. In visvijvers is echter het zuurstofgehalte van het water ook zeer belangrijk. Vissen hebben zuurstof nodig voor de aërobe produktie van energie voor lichaamsonderhoud, beweging, voedselopname en biosynthese. De opnamesnelheid van zuurstof wordt bij de meeste vissen bepaald door de diffusiesnelheid door het kieuwoppervlak. Het kieuwoppervlak groeit langzamer dan het lichaamsgewicht. Hieruit volgt de hypothese, dat de maximale voeropnamesnelheid evenredig is met de zuurstofopnamecapaciteit en dat de maximale voeropnamesnelheid per gram lichaamsgewicht afneemt met toenemend lichaamsgewicht totdat de groei tot nul gereduceerd is. In Hoofdstuk 5 werd een module voor zuurstofbeperking, gebaseerd op deze theorie, ingebouwd in FGS. De module berekent de maximale potentiële zuurstoftoevoer door de kieuwen op basis van de diffusiewet van Fick en de allometrische relatie tussen lichaamsgewicht en kieuwoppervlakte. De totale vraag naar zuurstof wordt berekend als de som van zuurstof nodig voor routinestofwisseling, zuurstof voor voederopname en vertering (specifieke dynamische actie) en zuurstof voor biosynthese. De voedselopname wordt beperkt tot een zodanig niveau dat de vraag naar zuurstof nooit de toevoer overstijgt. Dit uitgebreide

model werd gebruikt voor simulatie van de groei van *O. niloticus* in twee situaties. Eerst werd de groei onder lage zuurstofconcentraties gesimuleerd. FGS simuleerde de reductie in voeropname en de als gevolg daarvan lagere groei in een experiment met drie verschillende zuurstofgehalten goed. Vervolgens werd de groei onder natuurlijke omstandigheden zonder zuurstofbeperking in een Oost-Afrikaans meer gesimuleerd. Met realistische parameterwaarden kon het eindgewicht van de Nijltilapia gesimuleerd worden. De simulatieresultaten ondersteunen de zuurstofbeperkingstheorie. FGS kan dus gebruikt worden voor het analyseren van de effecten van voederhoeveelheid en voedersamenstelling, en milieufactoren (temperatuur, zuurstofconcentratie) op de visgroei. FGS verklaart ook verschillen in eindgewicht tussen verschillende soorten, en binnen soorten onder verschillende omstandigheden.

In Hoofdstuk 6 werd FGS gebruikt om voedsel- en zuurstofbeperkingen van *O. niloticus* onder vijveromstandigheden te simuleren met behulp van gegevens van een wereldwijd, gestandaardiseerd onderzoeksproject. De gegevens kwamen uit Rwanda, Thailand, Indonesië, Honduras en Panama. In elk land werden de vijvers bezet met handgesexte tilapia's (alleen mannelijke vissen werden gebruikt, maar enkele vrouwtjes kwamen toch in de vijvers terecht) gedurende 150 dagen. De vijvers werden bemest met kunstmest en met kippemest. Voor de simulaties werden het begingewicht van de vis en de gemeten temperatuur- en zuurstofwaarden in het model ingevoerd. Voor voedselcompetitie tussen de oorspronkelijke vissen en gedurende de groeiperiode geproduceerde recruten werd een module aan het model toegevoegd. Calibratie van het model bestond voor iedere vijver uit een iteratieve bepaling van de waarde van twee modelparameters: CONLEV, de voedselconsumptiesnelheid zonder voedsel- of zuurstofbeperking; en TPFS, het totale dagelijkse voedselaanbod in de vijver. In de meeste vijvers kon een goede overeenstemming tussen het gesimuleerde en het waargenomen gemiddelde eindgewicht bereikt worden met acceptabele waarden voor CONLEV en TPFS. Zowel CONLEV als TPFS lieten een verband zien met de netto primaire produktie en de chlorophyll *a* concentratie. Voor elke vijver kon een schatting van de voedsel- of zuurstofbeperking (uitgedrukt als het percentage van de tijd dat een voedsel- of zuurstofbeperking bestond) worden gegeven. Validatie van het model met gegevens uit Indonesië en Panama was niet succesvol. De beschrijvende relaties tussen CONLEV en TPFS enerzijds en primaire produktie anderzijds waren kennelijk niet van toepassing op de situaties in Panama en Indonsië. Wanneer het model voor *voorspellen* van de visgroei gebruikt moet worden is een meer gedetailleerde, verklarende benadering van de relatie tussen CONLEV en TPFS en primaire produktie nodig. Niettemin kan het model kan gebruikt worden voor de analyse van visgroei in vijvers, waarbij het de effecten van voederhoeveelheid en -samenstelling, temperatuur en zuurstof in onderlinge samenhang analyseert.

In Hoofdstuk 7 worden de resultaten van de voorgaande hoofdstukken besproken in het licht van de oorspronkelijke onderzoeksdoelstellingen en worden implicaties voor het beheer van visvijvers overwogen. De belangrijkste conclusies zijn: (1) Onderzoek naar visproduktie in geïntegreerde visvijvers kan het beste een systeembenadering kiezen, waarbij zowel beschrijvende als verklarende modellen gebruikt worden in combinatie met doelgericht experimenteel onderzoek. Hierdoor wordt optimale benutting van reeds beschikbare informatie en een effectief gebruik van fondsen en faciliteiten gewaarborgd; (2) Het is mogelijk de groei van een groot aantal vissoorten te voorspellen met een algemeen simulatiemodel op basis van

de fysiologische processen in de vis. Bij afwezigheid van limiterende milieufactoren (zoals ammoniak of zuurstof) zijn de belangrijkste factoren die de visgroei beïnvloeden: temperatuur, en voedselhoeveelheid en -samenstelling. Voor iedere vissoort kunnen de waarden van de benodigde biologische parameters worden afgeleid uit de wetenschappelijke literatuur of uit relevante experimentele gegevens; (3) De hoeveelheid voedsel die een vis kan assimileren wordt beperkt door zijn zuurstofopnamecapaciteit. De zuurstof die beschikbaar is voor assimilatie en lichaamsbeweging is gelijk aan het verschil tussen maximale stofwisseling (die evenredig is aan het kieuwoppervlak, behalve in vissen die zuurstof uit de lucht kunnen opnemen) en routinestofwisseling. Factoren die dit verschil (hier "scope for production" genoemd) verkleinen, door ofwel de maximumstofwisseling te verlagen, ofwel de routinestofwisseling te verhogen, verlagen de groei door een verlaging van de voedselopname; (4) Het in dit onderzoek ontwikkelde model kan gebruikt worden voor het analyseren van voedsel- en zuurstofbeperkingen voor visgroei onder uiteenlopende omstandigheden.

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