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The Bioeconomics of Recirculating Aquaculture Systems



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Abstract

The goal of this study was to produce a detailed aquaculture production model incorporating constraints unique to closed system culture and to conduct a formal economic analysis of closed system operation. Results generated by this model indicate that less than perfect management ability can eliminate the normal advantages associated with using high protein feed. While higher protein levels produce faster growth, and for this reason are often used in the industry, the increased direct feed costs and indirect costs due to metabolic feedbacks produce lower daily returns if high protein feed use continues through harvest. This model showed that inefficiency in solids removal negatively affects returns, but the majority of negative impacts were linked to declines in biological filter efficiency. As biological filter efficiency falls, time to harvest increases at an increasing rate and returns decrease at an increasing rate. Results also indicate that as stocking density increased, direct increases in returns were assured only if no metabolic feedbacks occurred. If the filter technology is operated inefficiently, higher stocking density may actually lead to economic failure. Thus, a tradeoff exists between stocking density and management ability, with the tradeoff being substantially affected by levels of dietary protein. In essence, economically viable tradeoffs between dietary protein and stocking density occur over relatively narrow ranges of management ability. Without highly experienced and capable management, the biological realities of recirculating systems may preclude profitable system operation. These simulated observations may in part explain why recirculating systems have yet to demonstrate widespread success on a commercial scale.

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The Bioeconomics of Recirculating Aquaculture Systems

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Introduction

Similar to the "Green Revolution" of agriculture in the 1970s, aquaculture experienced a period of exponential growth in the 1980s referred to as the "Blue Revolution." The development of advanced production technologies resulted in higher yields through improvements in feed formulation, nutrition, water chemistry, disease prevention and treatment, and selection for commercially desirable traits. With the advent of these technologies came a focus on intensive culture operations that used closed, artificial confinement systems incorporating high input levels. Closed systems have numerous potential advantages over open pond production, with the most important being that the system's environment can be minutely controlled (Spotte 1979). Research on closed, or recirculating, technology has centered on general biophysical management practices, including the mechanical and biological aspects of water filtration (Brune and Tomasso 1991; Lawson 1991). However, the aquaculture industry has realized that the economic viability of recirculating systems cannot be solely assured by complex and innovative system designs:

"...the number one technical problem (in recirculating systems) is really a technical/economic problem... The proper technical solutions are too expensive for low-value food-fish products. All the technical problems are solvable, but not necessarily economically solvable" (Water Farming Journal, 1992).

As a result, research efforts are beginning to focus on the economics of recirculating technology. Of course, it can be difficult and expensive to conduct economic experiments on commercial-size recirculating systems. One way to avoid this problem and still generate the needed information is

through the use of bioeconomic models that accurately describe the underlying bioenergetic operation of the system (Allen et al. 1984).

Bioenergetic models have been widely used to examine the time dynamics of species growth in pond aquaculture systems (Paloheimo and Dickie 1965, 1966a, 1966b; Machiels and Henken 1986; Cacho 1990). Some investigations have even included the impact of metabolic feedbacks on growth (Cuenco, Stickney, and Grant 1985). Less common are bioeconomic models that combine bioenergetics and the economics of producer decision making. Cacho, Kinnucan, and Hatch (1991) developed a bioeconomic model of pond catfish production and used it to determine cost-effective feeding regimes. Researchers have also used bioeconomic models of varying degrees of sophistication to examine open system rearing of shrimp (Karp, Sadeh, and Griffin 1986), carp (Talpaz and Tsur 1982), lobster (Botsford, Rauch, and Shleser 1974), and tilapia (Liu and Chang 1992). To our knowledge, however, no study has examined a recirculating production system from a complete bioeconomic framework, incorporating not only realistic metabolite-constrained growth over time, but also the economic constraints faced by profit-seeking producers.

Objectives

The goal of this study was to produce a detailed production model incorporating constraints unique to closed system culture and to conduct a formal economic analysis of closed system operation. Specific objectives of the study included:

- 1) Develop and empiricize a conceptual biophysical model of an intensive recirculating system that realistically captures important interactions between technology and fish production;
- 2) Detail the theoretical relationship between the biophysical model and the optimal economic model of a recirculating system; and

- 3) Demonstrate the feasibility of using an empirical, bioeconomic model to analyze the impact of system technology on the optimal economic operation of a recirculating system.

Conceptual Model

Given the general features of a recirculating aquaculture system, a conceptual model can be developed using bioenergetic relationships and the principles of ecosystem dynamics (Figure 1). Although stylized and lacking specific reference to pH and water contaminants, this model includes the critical environmental components that affect the operation and management of a recirculating system. Considering only the bioenergetic portion of the model (shaded lower half of Figure 1), flows in the system are primarily driven by fish weight as mediated through metabolism and appetite. Variables potentially under producer control, such as water temperature and feed quantity and quality, can be used to adjust the various flows and thus the time path of fish growth. Feeding and growth lead to the generation of waste products and the consumption of oxygen, but most bioenergetic models assume that these components are assimilated or supplied by the open environment. Recirculating system models, however, need to fully account for these feedbacks because of their potential impact on individual fish growth, mortality, and the overall expansion of total biomass in the production system.

Metabolic waste products take two forms in the conceptual model; solids and total ammonia nitrogen (TAN) (Figure 1). The toxic portion of TAN, unionized ammonia nitrogen (UAN), serves as one component of a feedback mechanism that can inhibit fish growth through changes in appetite or, if large enough, cause fish mortality. Biological filtration controls the buildup of UAN in the conceptual model, but this activity adds bacterial respiration to the biological oxygen demand (BOD) generated by fish respiration and solids decomposition. Open flow-through systems mitigate both UAN and BOD buildup by water exchange, but recirculating and some pond systems must supply oxygen to

meet BOD through mechanical or liquid oxygen aeration. Suspended solids are removed from the system with mechanical filters. The operation of biological and mechanical filters are critical to the growth of fish and the stability of a recirculating system over the growout cycle. Only when both filters are perfectly efficient will there be no growth or mortality feedbacks. Failing adequate filtration, it may be possible to control the effects of UAN and BOD by emergency water exchange, depending on the laws and regulations governing a specific species culture.

Bioeconomic Model

The transition from a conceptual biophysical model to an empirical bioeconomic model that can be used to numerically investigate optimal system operation requires the identification of a specific culture species. Virtually any fish can be cultured in a closed system given successful approximation of the natural environment. However, commercial use of recirculating systems also requires consideration of economic factors. In short, a suitable species for food-fish culture must have an established market, sufficiently high value, be legal for culture, have tolerance for poor water quality and high stocking densities, thrive on pelleted food, exhibit an efficient feed conversion ratio (FCR), and be available from local sources (hatcheries or wild stocks). Given these features, tilapia is a fish that offers considerable potential for use in closed systems.

Tilapia as a Culture Species

Tilapia is the collective term for a group of warm water fishes belonging to the family Cichlidae. Native to Africa, tilapia have been cultured in open systems in the Middle East for centuries, a practice that has spread throughout the world. While tilapia production has traditionally been illegal in many areas of the U.S. because of concerns over the introduction of exotic species, tilapia evolved in tropical and subtropical areas and are not cold tolerant (Bowen 1982). In recent years, the culture of tilapia has been allowed in many states, with the 1991 Louisiana legislature

authorizing tilapia culture under restricted conditions. Among these restrictions was the requirement that tilapia be produced only in closed systems.

Researchers have identified tilapia as a prime species for use in recirculating systems because of their tolerance to crowding and low water quality (Drennan and Malone 1990). Tilapia also are well suited for closed systems due to their ability to adapt to changes in salinity, temperature, and dissolved oxygen. In addition to its hardiness, tilapia has great economic potential because of its ability to substitute for many high-valued fishes. Tilapia have mild white flesh that restaurants and retail consumers can use in place of increasingly scarce sea trout, redfish, and snapper. Because of its versatility, tilapia rapidly gained market acceptance in the U.S. In 1994, domestic production of tilapia was estimated at 6,818 metric tons (live weight), up 20% from 1993 (Figure 2a). This domestic production had a value at the farm-gate of approximately \$15.7 million (Figure 2b). In addition, 1994 U.S. imports of tilapia totaled 14,585 metric tons, up 29% from 1993 and representing a value of \$25.6 million.

Economic Framework

The empirical economic application of the conceptual model to a recirculating tilapia production system required specific bioenergetic and metabolic feedback sub-models, as well as the integration of these sub-models within an overall economic framework. This section describes the economic framework and presents the general management problem faced by recirculating system operators.

Over a growout cycle, management primarily affects the variable costs associated with short-run decision making. In addition to the direct monetary costs associated with stocking, feeding, and electrical power use, indirect costs can arise when a system's technology does not completely remove metabolic wastes. These indirect costs show up in the form of reduced fish growth and increased

mortality. Considering the short-run nature of the problem and the assumption that producers seek to maximize returns above variable costs (Π), the decision making problem can be expressed as

$$\text{maximize } \Pi = P_Q \cdot Q - C_f - C_e - C_s \quad (1)$$

here P_Q is the price of tilapia (\$/gram), Q is the quantity of fish harvested (grams/liter), C_f is total feed cost (\$/liter), C_e is total electricity cost (\$/liter), and C_s is total fingerling cost (\$/liter). The model was constructed on a per liter basis to avoid the need for explicit description of the types, sizes, and configuration of various physical system components. While this approach allows the study to proceed within a generic framework, it does assume an input divisibility and constant proportional returns that may not exist across the spectrum of real systems. As a result, this study cannot address questions concerning the economic viability of specific system designs. Instead, it focuses on the essentially continuous economic interactions between filtration efficiency, metabolic feedbacks, and fish growth. How the presence of lumpy inputs and variable proportional returns might affect the analysis of recirculating systems is uncertain and left to future research.

The growth function required for equation (1) can be expressed as

$$Q = W_H \cdot D_H = \left(W_0 + \int_{t_0}^{t_H} W_t dt \right) \cdot D_H \quad (2)$$

where W_H is the terminal fish weight at harvest (grams), D_H is the numerical density of fish in the system at harvest (numbers/liter), W_0 is the initial fish weight at stocking (grams), t_0 is the stocking day, t_H is the harvest day, and W_t is the growth rate on day t (grams/day). The variable production costs can be defined as

$$C_f = P_f \cdot \int_{t_0}^{t_H} R(t) \cdot F_t \cdot D(t) dt \quad (3)$$

$$C_e = P_e \cdot \int_{t_0}^{t_H} E_t dt \quad (4)$$

$$C_s = P_s \cdot D_O \quad , \quad (5)$$

where P_f is feed price (\$/gram), $R(t)$ is ration size relative to appetite on day t ($0 \leq R(t) \leq 1.0$), F_t is fish appetite on day t (grams/day), $D(t)$ is fish density on day t (numbers/liter), P_e is electricity price (\$/kilowatt hour), E_t is rate of electricity use for aeration and pumping on day t (kilowatt hours/liter day), P_s is fingerling price (\$/gram), and D_0 is the initial stocking density (numbers/liter). Prices were obtained from surveys of major suppliers, budget-based analyses of recirculating systems, trade journals, and industry reports (Table 1).

Given the desire to include UAN and dissolved oxygen feedbacks in the model, the technical relationships can be expressed as

$$W_t = g[UAN(t), DO(t), W(t), R(t), DC] \quad (6)$$

$$F_t = h[W(t)] \quad (7)$$

$$UAN_t = k[W(t), R(t), D(t), DC, BE] \quad (8)$$

$$DO_t = I[BOD(t), OC(t), SAE] \quad (9)$$

$$E_t = j[W(t), D(t), R(t), DC] \quad (10)$$

where UAN_t is the rate change in UAN concentration on day t (mg/liter/day), DQ is the rate change in DO concentration on day t (mg/liter/day), and other variables are defined in Table 1. The relationships that determine these equations of motion jointly compose the bioenergetic and metabolic feedback sub-models. Given that most recirculating systems are housed in climate controlled buildings, temperature was not included as a growth-related variable but assumed fixed at 30°C.¹ In addition, water exchange was excluded as a possible control variable because many state regulations governing tilapia culture (including Louisiana's) severely restrict water exchanges in order to prevent the escape of tilapia into natural fisheries.

Given the description of the bioeconomic model in equations (1)-(10), it is obvious that biological relationships significantly influence the ultimate economic operation of a recirculating system. Thus, a realistic economic analysis requires that the biophysical relationships embedded in the model be fully described and empiricized.

¹ While temperature can have important impacts on growth and other biophysical processes in both extensive and intensive aquaculture production, the model assumes a growout period over warm spring, summer, and autumn months when heating costs are not a factor. In addition, simulations with a fixed temperature assume that extremely high temperatures, and the resulting impairment of metabolic activity, are not encountered. In general, these conditions are met in recirculating aquaculture systems in the lower Southeast United States. Extensions of the current model can easily include explicit incorporation of fluctuating temperature in the bioeconomic model.

Bioenergetic Sub-Model

The bioenergetic model used in this study was an adaptation of Ursin's (1967) and Liu and Chang's (1992) generalized metabolic growth model. Physical growth was defined by the difference between energy intake and energy expenditure:

$$dw/dt = \beta \cdot dr/dt - \alpha \cdot \beta \cdot dr/dt - \kappa \cdot w^\eta \quad (11)$$

where dw/dt is the daily weight gain, β is the efficiency of food assimilation, dr/dt is the daily feed ration, α is the fraction of assimilated food lost to active metabolism, κ is the coefficient of resting metabolism, and η is an exponent relating body weight (w) to resting metabolism. Within this framework, daily ration can be described by

$$dr/dt = \delta \cdot f \cdot w^\mu \quad (12)$$

where δ is the coefficient of food consumption, f is the ration size relative to appetite, and μ is an exponent relating body weight to synthesis. Thus, the first term on the right hand side of equation (11) represents the amount of consumed food that is digested. The second and third terms of equation (11) measure the amount of digested food energy that is lost to active and resting metabolism, respectively. The growth model is quite flexible and capable of depicting concave, convex, or sigmoidal growth patterns over time depending on the specific parameter values. However, it is generally believed that unconstrained fish growth should follow a sigmoidal pattern from hatchling to maturity (Hopkins 1992).

Although equation (11) is capable of tracking the growth effects of different ration quantities, it does not explicitly incorporate feed quality. This can be partially accomplished by defining the tilapia-specific assimilation efficiency β as

$$\beta = (0.70 \cdot P:E + 0.51) / (P:E + 1) \quad (13)$$

where $P:E$ is the protein-energy to total-energy ratio contained in the food, with average tilapia assimilation efficiencies being approximately 70% for protein and 51% for total energy contained in a ration (Bowen 1982). Given this formulation, assimilation efficiency is primarily a function of feed protein levels.

Assuming a constant water temperature of 30° C, equations (11) and (12) were calibrated using a wide range of data from published and unpublished experiments (Caffey 1994). Final parameter values are presented in Table 2. Verification and validation of the bioenergetic model, a critical step in any simulation study, was accomplished with data used in model calibration and data independent of the model structure. Resulting simulations demonstrate that the bioenergetic model accurately depicts experimentally observed tilapia growth over a wide range of feeding conditions (Figure 3). The upper bound on modeled growth was approximately 1.45 kilograms over a 600 day period, a weight considered feasible under ideal conditions (Lutz 1994). Additional simulations suggest that the time path of individual tilapia growth was relatively insensitive to the range of feed protein levels commercially available (Figure 4a). This result might be expected for a fish like tilapia that feeds low in the food chain. However, changes in the allowed percent of satiation feeding had considerable effects on simulated growth (Figure 4b). In order to avoid protracted juvenile development, the high metabolic rates of fish under 50 grams needed to be satisfied by maximum, or satiation, feeding. Given its apparent importance in modeling fish growth, the daily feeding rate was one of the free control variables numerically optimized in this study.

UAN Feedback Sub-Model

The buildup of nitrogenous compounds in recirculating systems results from the accumulation of excreted metabolic byproducts, fecal waste, and uneaten feed. Speece (1973) demonstrated that TAN production can be directly calculated from the feed ration by using an ammonia conversion constant. Fivelstad et al. (1990) pointed out that this conversion constant will depend on the ration

quality, specifically the amount of protein in the diet. A convenient way to calculate the conversion constant for warm-water systems assumes that each kilogram of fish will daily excrete the same number of grams of TAN as the percent dietary protein in the ration (Meade 1973; Liao and Mayo 1974; Drennan and Malone 1990). But, TAN is only of interest because of its relationship to UAN, the most toxic form of aqueous ammonia. UAN levels are generally dependent on system pH and temperature, and are usually calculated as a fraction of the TAN in the system (Drennan and Malone 1990). Given a fixed pH of 8.0 and a temperature of 30° C, approximately 7.5 percent of TAN will be in unionized form (Emerson et al. 1975). Using this information and converting to an average daily concentration, a UAN production relationship was defined as

$$UAN_t = 0.075 \cdot CP \cdot D(t) \cdot dr/dt \quad (14)$$

where UAN_t is in mg/liter/day, CP is the percent crude protein of the ration, and D is the fish biomass load in g/liter.

Of course, recirculating systems employ biological filters to restrain the buildup of UAN. To represent the operation of the biological filter, a set percentage of UAN was removed from the system each simulated time period. This percentage was defined as the biological filter efficiency (BE). If management of the biological filter was less than 100 percent efficient ($0 \leq BE < 1.0$), UAN would carry over to the following day's simulation and provide a mechanism by which metabolites could build up in the system. Thus, the final relationship for UAN concentrations was defined as

$$UAN(t) = (1 - BE)(UAN_t + UAN(t-1)) \quad (15)$$

where $UAN(t)$ is the concentration at time t and $UAN(t-1)$ is the residual UAN carried over from the previous time period. BE can be interpreted either as the varying ability of producers to effectively manage a constant biological filter technology or as an index used to compare different types of filter technologies.

If the possibility of UAN buildup exists, then the resulting feedback effects need to be defined. Mortality from UAN toxicity varies significantly among warm-water fishes. Tilapia have survived at UAN levels as high as 3.4 mg/liter in studies involving long acclimation periods (Redner and Stickney 1979). While no complete information exists on tilapia mortality for various levels of UAN exposure over time, the acute toxic UAN levels for channel catfish (*Ictalurus punctatus*) closely resemble those reported for tilapia.² Using catfish data from Colt and Tchobanglous (1976), an expression for daily percent UAN-induced mortality (M_{UAN}) was derived:

$$M_{UAN(t)} = -100 \left(0.5^{\frac{1}{0.16 + 1420.5 e^{(-1.97 \cdot UAN(t))}}} - 1.0 \right) . \quad (16)$$

Given equation (16), mean daily mortality increases gradually as UAN concentrations rise to 3.0 mg/liter and then increases rapidly for UAN concentrations between 3.0 and 5.0 mg/liter (Figure 5a).

Colt and Tchobanglous (1978) provide data on catfish that can be used to estimate the impact of UAN concentrations on growth. Converting the authors' information into a relationship for the mean daily UAN-induced growth reduction (GR_{UAN}) yielded

$$GR_{UAN(t)} = 100(1.035 \cdot UAN(t)) . \quad (17)$$

With this relationship, growth reductions increase linearly for UAN concentrations between zero and 1.0 mg/liter (Figure 5b). While UAN concentrations leading to negative growth (individual fish weight loss) are mathematically possible, the suppression of UAN levels caused by falling growth rates and

² Tilapia are generally considered more tolerant than channel catfish of poor water conditions, both in terms of potential mortality and growth effects. Thus, use of catfish data for unavailable tilapia information would bias mortality rates towards the theoretical upper bounds, thereby making the economic analysis reflect a conservative, or worst case, scenario.

small levels of mortality prevents growth reduction from exceeding 100 percent as long as acute UAN shocks do not occur.

BOD Feedback Sub-Model

The consumption of oxygen in a recirculating system, or BOD, arises from three sources; fish respiration, oxidation of ammonia compounds by autotrophic bacteria, and the decomposition of organic solids by heterotrophic bacteria (Wheaton, Hochheimer, and Kaiser 1991). The BOD generated by fish respiration is usually determined by the sum of the oxygen required for active and standard metabolism. Using data in Watten, Colt, and Boyd (1992), total respiratory BOD for tilapia can be expressed as

$$BODf_t = 0.00443 \cdot D(t) \cdot W(t)^{-0.348} \quad (18)$$

where $BODf_t$ is grams of oxygen consumed/liter/day.

Additional oxygen demand can be linked to the nitrifying autotrophic bacteria that colonize available substrate within a recirculating system. Due to its high specific surface area, most nitrification occurs within the biological filter. Nitrifying bacteria require approximately 4.65 grams of oxygen for every gram of TAN oxidized (Wheaton 1977), or in terms of unionized ammonia, approximately 0.062 grams of oxygen for every milligram of UAN. Combining this information with equation (14) yields the relationship

$$BODn_t = 0.00465 \cdot CP \cdot D(t) \cdot dr/dt \quad (19)$$

where $BODn_t$ is in grams of oxygen consumed/liter/day.

The residual portion of BOD is associated with the oxygen demanded by heterotrophic bacteria that break down organic solids. Malone and Drennan (1994) developed expressions for oxygen consumed during filtration in experimental systems. Their studies suggest that $BODr$ can

range from one to four times the level of BOD_n depending on the solids removal efficiency (SRE) of a mechanical filter. Using this relationship and equation (19) yields

$$BODr_t = (0.00465 \cdot CP \cdot D(t) \cdot dr/dt) / SRE \quad (20)$$

where BOD_{r_t} is in grams of oxygen consumed/liter/day and $0.25 \leq SRE \leq 1.0$. Similar to BE, SRE can be interpreted either as the varying ability of producers to effectively manage a constant mechanical filter technology or as an index used to compare different types of filter technology.

The sum of equations (18)-(20) represent the daily per liter oxygen demand in the modeled system. In terms of validation, Colt and Orwicz (1991) developed a relationship between system oxygen demand and the feed ration, or oxygen:feed conversion ratio (OFR), from experimental data. They observed that oxygen demand was relatively constant for a given feeding regime, but negatively correlated to increases in the feeding rate. Figure 6 suggests that equations (18)-(20) correspond well with experimental data for tilapia. Given that two thirds or more of recirculating system BOD originates from the oxidation of organic compounds (Malone 1993), the efficiency of mechanical filtration greatly influences the OFR. Depending on the SRE, our model produced design OFRs between 0.25 and 0.75, a range that appears in the experimental literature and encompasses the suggested conservative design OFR of 0.60 (Liao and Mayo 1974).

The extent to which BOD affects the growth and mortality of tilapia is ultimately determined by the interaction of BOD, aeration, and the resulting residual dissolved oxygen (DO) in the system. Tilapia are among the most tolerant of warm water fishes, with survival reported for DO levels as low as 0.1 mg per liter (Caulton 1982). More conservative estimates suggest that tilapia growth reduction begins to occur at DO concentrations below 5.0 mg/liter, with mortality commencing at DO levels of 1.5 mg/liter (Caulton 1982). Unfortunately, almost no information exists concerning the functional relationship between DO and growth rates for tilapia or similar species. Thus, as a first

approximation, our model incorporates a sigmoidal relationship that was calibrated to the extreme values, but maintained a near linear relationship through much of the DO range. This produced a mean daily growth reduction relationship for DO (GR_{DO}) of

$$GR_{DO(t)} = 100 \left(0.5^{\frac{1}{2.22 \cdot (DO(t) - 2)}} - 1.0 \right) \quad (21)$$

where $DO(t)$ is the dissolved oxygen level in mg/liter at time t . Using this relationship, growth reductions expand rapidly as DO levels fall from 4.0 mg/liter to the minimum sub-lethal concentrations of 1.0 mg/liter (Figure 7a).

Unlike the case for DO-induced growth reductions, a range of data exists for DO-induced mortality in both tilapia and catfish (Caulton 1982; Tucker 1985). With this information, mean daily mortality relative to DO level (M_{DO}) was calibrated as

$$M_{DO(t)} = 100 \left(0.5^{\frac{1}{e^{19.0 \cdot (DO(t) - 0.6)}}} - 1.0 \right) \quad (22)$$

Equation (22) provides for subtle mortality effects just below the maximum lethal DO concentration of 1.5 mg/liter. These mortality effects increase gradually down to DO concentrations of 0.8 mg/liter and then increase rapidly as DO concentration falls below 0.7 mg/liter (Figure 7b).

As previously mentioned, DO concentrations are not just a function of BOD, but also of aeration technology. While there are a large number of mechanical and chemical aeration devices that could be used in recirculating systems, their operation is governed by the difference between the actual concentration of oxygen in the water and the theoretical saturation concentration. The relative rates at which aeration and degassing of water will occur can be described by a relationship for the oxygenation capacity (OC) of water that incorporates the standard oxygen transfer rate and the

standard aeration efficiency (SAE) of an aerator (Piedrahita 1991; Colt and Orwicz 1991; Caffey 1994):

$$OC(t) = 2884.62 \cdot SAE \cdot POWER(t) \cdot (C_i^* - C_i(t)) \quad (23)$$

where $POWER(t)$ is the amount of electricity used by the aerator at time t (kilowatt hours/day), C_i^* is the saturation concentration for oxygen at a given temperature (mg/liter), and $C_i(t)$ is the actual DO concentration at time t (mg/liter). Equation (23) describes the amount of oxygen that a given aerator can put into the water given the difference between ambient and saturation DO levels. Thus, OC can be used to meet BOD demand, with the remaining oxygen available to maintain a given DO concentration in the water. This relationship also points out the potential importance of $POWER$ as a control variable given a fixed SAE for a chosen aerator. SAE in this study was fixed at 2.0, a common value for commercially available aerators. Additional power needs are generated by pumps that circulate water through the system and filters, a demand that can be estimated assuming the need to circulate 0.6 liter/gram of fish/day (Caffey 1994).

Solution Algorithm

Having specified the bioenergetic relationships embedded in equations (6)-(10), the solution of equation (1) requires a strategy for dealing with the large number of potential control variables. For the purposes of this study, truly dynamic decision variables were restricted to the ration size relative to appetite (R) and electrical power use ($POWER$). Time to harvest (t_H) was treated as a static decision variable that was repeatedly adjusted to find the profit maximizing solution. A terminal individual fish weight of 700 grams was used as a boundary condition. This terminal weight falls within the range of marketable tilapia and represents the live weight required to produce the minimum 115 gram (approximately 4 ounce) fillets desired by the retail market. BE and SRE , the variables that represent the filter technology, were fixed for any given set of simulation optimizations over t_H , but

allowed to vary between optimizations. The results of different sets of simulation optimizations could then be compared and analyzed for the impact of technology on potential returns. Feed quality (DC) and initial stocking density (D_0) were similarly treated.

The complexity and non-linearity of the bioeconomic model suggests that solutions need to be approximated using a numerical optimization algorithm. Similar to Cacho, Kinnucan, and Hatch (1991), we employed a two-point boundary value shooting algorithm with a Brent maximization subroutine (Press et al. 1986). Two point boundary frameworks are used when ordinary differential equations are required to satisfy boundary conditions for more than one value of an independent variable. The most common case involves satisfying boundary conditions for starting and ending values of an integration. The primary feature of this approach is the ability to begin an acceptable solution at its initiation (initial conditions) and then develop a final value (terminal conditions) through integration. This process employs iteration to transform spatially scattered boundary conditions into a single global solution for a series of differential equations.

A standard two point boundary problem requires a solution to a set of N coupled first order ordinary differential equations, satisfying n_1 initial boundary conditions at x_1 , and a remaining set of $n_2 = N - n_1$ terminal boundary conditions at x_2 . The differential equations are

$$\frac{dy_i(x)}{dx} = g_i(x, y_1, y_2, \dots, y_N) \quad i = 1, 2, \dots, N \quad (24)$$

where at x_1 the solution must satisfy

$$B_{1j}(x_1, y_1, y_2, \dots, y_N) = 0 \quad j = 1, \dots, n_1 \quad (25)$$

and at x_2 it must satisfy

$$B_{2k}(x_2, y_1, y_2, \dots, y_N) = 0 \quad k = 1, \dots, n_2. \quad (26)$$

Thus, the shooting algorithm involves a series of iterations that begin by satisfying initial conditions and then integrate toward the terminal conditions. Resulting discrepancies from the desired terminal conditions are used to adjust the initial conditions, via a globally convergent variant of the Newton-Raphson method, until the boundary conditions are satisfied. The maximization subroutine was used to assure that the appropriate optimal control conditions were met each day in the time horizon. All simulation optimizations were conducted using the *Mathematica ver. 2.2.3* computer package (Wolfram Research, Inc., 1995).

Results and Discussion

The first part of this section presents the results from a numerical optimization of the bioenergetic model without any reference to economic variables in the system. This non-economic optimization is used both to examine the nature of the technology embedded in the simulation model and provide another means for examining the degree of model realism. Specifically, optimal trajectories of state and control variables are used to investigate the relationship between components of recirculating technology, and isoquant analysis describes the degree of substitution between the two variables (feed quantity and quality) most often used by producers to directly control the growth of fish in the systems. The second part of this section expands the bioenergetic analysis to include the economic objectives and constraints faced by producers in the real world. The results of numerical optimization of the constrained bioeconomic model are used to examine and formulate general management strategies for recirculating system operations.

Technology and the Bioenergetic Model

Given that the focus in recirculating system management is on filter technology, it was assumed that perfect biological filter ($BE=1.0$) and mechanical filter ($SRE=1.0$) operation would be required for maximum system performance regardless of feed quality. Operated without inefficiency,

the model indicates that production of 700 gram tilapia yields a terminal system fish density of approximately 50 grams/liter (0.4 pounds/gallon) for a wide range of feed quality (Figure 8a,b). However, the time to harvest decreases from 270 days using 20 percent crude protein feed to 230 days using 40 percent crude protein feed. This 40 day difference can be attributed to the increased growth provided by the high protein feed, even though tilapia in natural systems feed relatively low in the food web and are not generally fed high protein feeds in closed systems. The advantage of high protein feeds might also be expected under these perfect filtration scenarios because no metabolic feedbacks would be present to diminish the potential advantages of using high protein feeds.

Although theoretically feasible, few if any agricultural production systems are known to operate at perfect technical efficiency. Thus, it is useful to consider the effects of changing feed quality on days-to-harvest and maximum system density given less-than-perfect filter operation. As filter system efficiency falls, the number of days-to-harvest increase while the maximum system density decreases, with the effects more pronounced for higher quality feeds (Figure 8a,b). For example, as BE and SRE decrease to 0.95 and 0.50, respectively, terminal system density decreases to 48 and 47 grams/liter for 20 and 40 percent protein feeds, respectively. In essence, filtration inefficiency results in UAN accumulation, a reduction in system DO, and decreased growth rates and/or increased mortality. While these two terminal system densities are nearly equivalent, the days-to-harvest advantage for the 40 percent protein feed decreases from 40 to 25 days.

The negative effects of filter inefficiency become more evident as BE and SRE decrease. At a BE of 0.90 percent and an SRE of 0.33, terminal system density falls to near 45 grams/liter for both the low and high protein feed. However, the time advantage that existed for the high protein feed is now gone and it requires 10 more days at 40 percent protein feed to produce equal amounts of biomass. Thus, an emerging pattern of decreasing system densities appears for both feeds as the filtration efficiencies decrease. However, the rate of decrease in density is more rapid for the higher protein feeds. This pattern is further illustrated as filtration efficiency falls to a BE of 0.85 percent and

an SRE of 0.25 percent.³ For this level of technology, the terminal system densities decrease to 44 and 38 grams/liter for 20 and 40 percent protein feeds, respectively, and the time advantage associated with 20 percent protein feed increases to about 65 days.

While the growth in system biomass density follows some part of a sigmoidal trajectory for all efficiency combinations, the location and termination of each trajectory is influenced by accumulating metabolites. One point of particular interest appears at approximately 70 days for the 20 percent protein feeds and 50 days for the 40 percent protein feeds (Figure 8a,b). These points in time represent a density of approximately 1 to 2 grams/liter (15 to 30 grams per fish), or the point at which tilapia begin to grow rapidly and system biomass density diverges from what had been a nearly linear expansion path.

In earlier life stages, many fish exhibit an extremely high metabolic rate as suggested by increasing feed conversion ratios (FCR) (Figure 9a,b). High metabolic rates cause cumulative feed fed to rise sharply in proportion to body weight, causing FCRs to increase. As a result, the initial growth period from fry to fingerling is relatively linear compared to later growth. But, as fish enter the exponential growth phase, their ability to assimilate feed rises and weight increases rapidly, causing FCRs to decrease. Given that the exponential portion of the sigmoidal growth curve contains an inflection point where weight gain changes from increasing at an increasing rate to increasing at a decreasing weight, there will exist a biologically efficient minimum FCR. The implication is that it may be possible to accelerate the growth of very young tilapia with higher protein feeds, even in the presence of low levels of filtration efficiency, because concentrations of UAN are still extremely low (Figure 10a,b) while dissolved oxygen remains at adequate levels for a range of feed qualities. Simulated minimum FCRs for tilapia were approximately 2.4 for a 40 percent protein feed and efficient use of filter technology. The 40 percent protein feed produced the lowest FCRs for BE=0.95

³ Unless otherwise noted, subsequent discussion will refer only to the level of biological filter efficiency. However, it is understood that the following efficiency pairings are in effect: BE=1.0, SRE=1.0; BE=0.95, SRE=0.50; BE=0.90, SRE=0.33; BE=0.85, SRE=0.25.

cases, while FCRs converged at BE=0.90 for both protein levels and became less efficient for 40 percent protein feeds when BE fell to 0.85. These results correspond to observations of real commercial recirculating systems where the practice of feeding higher protein feeds to smaller fish is common. However, model results also suggest that advantages for this practice disappear rapidly as system biomass density expands beyond approximately 8 grams/liter (110 gram fish), indicating the need for different feeding strategies at different stages of crop development.

Because UAN concentrations are partially a function of feeding levels and therefore an indirect function of system density, UAN trajectories roughly follow density trajectories (Figure 10a,b). UAN effects can include both serious growth reduction and mortality for concentrations above 0.5 mg/liter and 1 mg/liter, respectively (Figure 5a,b). Thus, increases in UAN concentrations can generate a negative feedback relationship with system biomass density. As a result of this negative metabolic feedback, the family of UAN trajectories generally lies below 0.5 mg/l. Trajectories above this level are an indication of extremely inefficient protein-technology combinations.

As system biomass density increases, the increasing effects of fish respiration (BOD_r), ammonia production (BOD_n), and solids accumulation (BQD) cause increasing demands on the available oxygen in the system. The model takes these demands and, combined with the available aeration technology and the physical properties of the water, determines daily DO concentrations. While inefficient levels for BE and SRE were related to lower terminal DO concentrations with 20 percent protein feeds, the range for these terminal DO concentrations was relatively small, with all combinations of feed protein and technology efficiency producing terminal DO concentrations between 2.2 and 3.8 mg/liter. As with UAN, this system response reflects the negative feedback relationship between declining DO and system biomass density. Incremental decreases in DO cause incremental decreases in growth, which decreases feed demand, which reduces BOD production, which ultimately keeps DO concentrations from falling as fast or as far as would otherwise occur.

In summary, the simulated biological trajectories are dependent on feed quantity, quality, and the extent of technological inefficiency. In addition, the shape and divergence of system biomass density and FCR trajectories suggests that the feed quality/technology interactions are highly dependent on fish size, with metabolic feedbacks having a mitigating effect on the buildup of UAN and DO. While density reduction in these simulations can be primarily attributed to decreased growth, further increases in target harvest weight and/or decreased filter efficiency would eventually generate significant mortality responses.

Isoquant Analysis

Isoquants were obtained by plotting total feed consumed against the corresponding dietary protein from optimized simulations of the constrained biological growth model (Figure 11a,b). Points on the isoquants represent the combination of feed quantity and quality required to produce a given size tilapia at three levels of biological filter efficiency. While the actual distribution of feed throughout the growing season is not described by the isoquants, a number of observations are worth noting. First, the negatively sloped, convex portion of the isoquants suggests that a degree of substitution exists between feed quantity and quality. Secondly, the range of substitutability varies significantly with both harvest weight and biological filter efficiency. For example, a biological filter efficiency of $BE=1.0$ yields an isoquant for a 700 gram tilapia that exhibits substitution possibilities for feed quantities ranging from 1800-2300 grams and for feed qualities ranging from 10-37 percent crude protein (Figure 11a). Beyond protein levels of 37 percent, the isoquant begins to slope upward, suggesting that the marginal product of protein is negative. Cacho, Kinnucan and Hatch (1991) reported similar results for simulations of unconstrained 600 gram catfish production in ponds. This general trend also holds for the production of smaller sized tilapia, with the substitution possibilities occurring over a narrower range of feed quantity (Figure 11b).

When metabolic constraints are introduced by lowering biological filter efficiency, the range and degree of substitution narrows dramatically for large tilapia. For example, a BE=0.90 leads to a substitution range of 10-23 percent crude protein and 2450-2550 grams of total feed (Figure 11a). Although the substitution range narrows somewhat for the production of small tilapia as biological filter efficiency falls, the changes are not as dramatic (Figure 11b). This result may be partly a function of initial stocking density, as 50 gram tilapia do not correspond to enough system biomass density to generate significant metabolic feedbacks in the model when initial stocking density assumes growout to market size. Higher initial stocking densities that assume only the production of fingerlings do generate metabolic feedbacks and results similar to those illustrated in Figure 11a.

Another method of expressing this relationship is by using the elasticity of factor substitution (σ), calculated as the proportionate rate change of the input ratio divided by the proportionate rate change in the marginal rate of technical substitution. When σ is infinite, inputs are said to be perfectly substitutable. When $\sigma = 0$, inputs must be used in fixed proportions. For the isoquants in Figure 11a, the average calculated σ for the 25-35 percent protein range is 8.8 when BE = 1.0, indicating a significant degree of substitution. However, as BE decreases to 0.95, the σ falls dramatically to 2.4, indicating that the ability to trade feed quality for quantity is hampered by inefficiencies in biological filtration. This phenomenon is apparent in Figure 11a by observing the flattening of isoquant slopes as BE moves from 1.0 to 0.90. For 50 gram tilapia, the calculated σ for both BE=1.0 and BE=0.95 is 0.80, indicating relatively little substitutability but also little change in substitutability as filter efficiency changes. Thus, the combination of higher protein feeds and low biofilter efficiency is less limiting with 50 gram tilapia.

The implication of the isoquant analysis is that some degree of substitution exists between feed quantity and feed quality in the 20-40 percent crude protein range, with the exact magnitude affected by changes in filter efficiency as well as changes in the size of fish. In addition to lower overall system density, the increased protein assimilation efficiency of smaller tilapia may serve to

reduce the accumulation of metabolites from higher protein feeds at less than optimal levels of biological filter operation. However, as fish size increases, the range of benefits from higher protein feed becomes highly affected by filter efficiency. In the most inefficient case depicted ($BE = 0.90$), substitution of feed quantity and quality is practical only with low to medium levels of dietary protein.

Economic Impacts

Table 3 displays the results of economic optimization for seven levels of biological filter efficiency, four levels of mechanical filter efficiency, and three levels of dietary protein. Given the structure of the model, the optimum BE-SRE combination for all dietary protein levels occurs when no inefficiency exists, or where BE and SRE both equal one. Under these perfect management conditions, a 700 gram tilapia can be produced in 265 days using a 20 percent dietary protein. Net returns associated with this combination are 8.9 cents/liter, or 0.034 cents/liter/day. Movement away from this ideal management situation reduces returns, although the rate of decrease is relatively low for declines in SRE. For example, the time required to obtain a 700 gram fish increases by two days when $BE=1.0$ and $SRE=0.5$, resulting in a 3 percent decrease in daily returns to 0.033 cent/liter/day. This decline can be directly linked to solids removal inefficiency and the need for increased aeration. Further decreases in SRE cause additional increases in production time and decreases in net returns, with effects ranging up to a 15 percent decrease in net returns for an SRE of 0.25.

Although decreases in SRE produce lower returns for any specific level of BE, these changes are relatively small. However, declines in BE for any given level of SRE produce dramatic changes in returns and production times. When $SRE=1.0$ and $BE=0.95$ for 20 percent dietary protein, the time required for production increases by 14 days over the optimal BE-SRE combination, with returns decreasing by 12 percent, from 0.034 cents/liter/day to 0.030 cents/liter/day (Table 3). Additional declines in BE cause successively greater impacts, with returns falling over 80 percent from optimal

levels for BEs below 0.80, irrespective of the SRE level. No positive returns were observed for 20 percent dietary protein when BE was 0.70.

The model's apparent sensitivity to changes in BE can be linked to the nature of the BE-SRE feedback relationships in actual recirculating systems. Biological filter inefficiency leads to the gradual buildup of toxic UAN. UAN can cause mortality, but there is a fairly wide UAN concentration range over which the most immediate effect is to reduce growth to rates that allow the biological filter to assimilate the waste products. In turn, the reduction in growth rates tends to slow down the increase in UAN levels. The result is that rising UAN levels can occur without causing catastrophic system failure, but only at the ultimate loss of returns. When management ability is incapable of maintaining zero levels of UAN, optimal production time paths require less than satiation feeding and thus correspondingly longer production times. Given the model structure, declines in SRE levels do not have the same impact because they can be at least partially offset by increasing the power used in aeration. This latter process essentially mimics the way in which producers run additional aerators during periods of low DO. However, the observed small reductions in returns for higher values of SRE at any given BE suggests that the optimum level of power input to the system is somewhat less than 100 percent of the amount required for the elimination of DO growth effects.

As previously mentioned, negative returns were observed for every level of SRE when BE=0.70. This region of negative returns expanded to include higher levels of BE efficiency as the percent dietary protein increased (Table 3). For example, negative daily returns for 30 percent dietary protein developed at levels of $BE \leq 0.80$. Given the model relationships for metabolite production, the results indicated that an increase in food quality from 20 to 30 percent protein causes an approximate 33 percent increase in TAN production and the corresponding increased growth and mortality effects as mediated directly through UAN and indirectly through DO. Thus, at higher dietary protein levels, more UAN was present to ultimately reduce returns when management of filter technology was not perfect. This phenomenon was even more pronounced in the simulations using

a dietary crude protein level of 40 percent (Table 3). While increasing dietary protein may be a desirable production strategy in the absence of metabolic feedbacks, careful consideration must be given to the costs and benefits of doing so in a recirculating system. This is especially important for tilapia culture given that the fish has a relatively low protein requirement and may not exhibit large protein-related growth responses (Figure 4a). Simulation results further suggest that feeding high protein feeds to tilapia in closed systems is even less advantageous because increased problems with metabolite feedbacks counteracts potential production benefits for all but the perfectly managed systems.

Another important component associated with optimal recirculating system management concerns the initial stocking density. Stocking density can directly affect all aspects of system operation, from the way in which UAN and BOD concentrations develop to the ultimate number of fish available for harvest. Table 4 presents economically optimal simulation results using the same parameters as the simulations in Table 3, but fixing dietary protein at 20 and 40 percent, SRE at 0.50, and allowing a range of stocking densities and biofilter efficiency levels. Because SRE is fixed, management ability is entirely focused on the choice of stocking level and the biological filtration process.

As expected under perfect biological filter management, increases in stocking density produce no additional increases in the optimal 267 days required to produce a 700 gram tilapia (Table 4). The relative absence of metabolic feedbacks when $BE=1.0$ (some BOD effects still exist given $SRE=0.50$) allows returns to increase as stocking density increases, up to a maximum of 0.061 cents/liter/day for an initial density of 0.13 fish/liter. This density represents a recommended upper bound on the stocking density in real systems in order to reach harvest biomass concentrations of 0.25 to 0.50 lbs/gallon. But, as before, changes in BE have dramatic effects on returns and time to harvest, with the impact of stocking density becoming increasingly important as biological filter efficiency decreases. For example, a decrease in BE from 1.0 to 0.95 leads to an approximate 20 day increase

in the time to harvest for all levels of stocking. However, decreasing BE from 0.95 to 0.90 causes a 10 day harvest time increase for a density of 0.07 fish/liter, but an 18 day increase for an initial stocking density of 0.09 fish/liter. Furthermore, the same BE reduction causes increases of 29 and 41 days for densities of 0.11 and 0.13, respectively. The impacts of less than perfect biological filter management are further magnified in the 40 percent dietary protein simulations (Table 4).

Figure 12 provides an illustration of the trade-off that exists between management ability and stocking density. Daily returns are presented for a range of biological filter efficiencies over four initial stocking densities and two dietary protein levels. At a BE=1.0, the economic returns for 20 percent protein feed increase by nearly 100% per day as stocking densities increase from 0.07 to 0.13 fish/liter (Figure 12a). However, decreases in BE lead to metabolic feedbacks that cause growth reduction and mortality, decreasing the range of returns. For example, at BE=0.90 no economic advantage exists for a density of 0.13 over a density of 0.11 fish/liter. In addition, only slightly higher returns exist for a density of 0.09 over a density of 0.07 fish/liter. As biological filter efficiencies fall below 0.85, the economic advantages of stocking rates higher than 0.07 fish/liter completely disappear. The interaction between dietary protein level and management ability is even more obvious when comparing simulations for 20 and 40 percent protein feeds. Not only do the advantages of higher stocking levels decrease for 40 percent dietary protein even under perfect management ability, but higher protein feeds become a substantial negative influence on returns for even small decreases in biological filter efficiency (Figure 12b).

Conclusions

Aquaculture producers face an array of decision making responsibilities that determine the ultimate success of their operation. As producers intensify resource use, the role of management ability becomes critical. Recirculating systems may be the most vulnerable to small management mistakes. The nature of recirculating system operation dictates that producers stock their systems

at high densities to overcome the higher fixed and variable costs normally associated with closed system operation. But, higher levels of biomass imply narrower margins for error in managing the biophysical environment. As a result, management ability becomes extremely important to the economic success of recirculating system operations.

Results generated by this model indicate that less than perfect management ability can eliminate the normal advantages associated with using high protein feed. While higher protein levels produce faster growth, and for this reason are often used in the industry, the increased direct feed costs and indirect costs due to metabolic feedbacks produce lower daily returns if high protein feed use continues through harvest. This model showed that inefficiency in solids removal negatively affects returns, but the majority of negative impacts were linked to declines in biological filter efficiency. As biological filter efficiency falls, time to harvest increases at an increasing rate and returns decrease at an increasing rate. Results also indicate that as stocking density increased, direct increases in returns were assured only if no metabolic feedbacks occurred. If the filter technology is operated inefficiently, higher stocking density may actually lead to economic failure. Thus, a tradeoff exists between stocking density and management ability, with the tradeoff being substantially affected by levels of dietary protein. In essence, economically viable tradeoffs between dietary protein and stocking density occur over relatively narrow ranges of management ability. Without highly experienced and capable management, the biological realities of recirculating systems may preclude profitable system operation. These simulated observations may in part explain why recirculating systems have yet to demonstrate widespread success on a commercial scale.

Limitations and Future Research Directions

As with all simulation studies, limitations inherent in the preceding analyses can be traced to the assumptions used to define the model, the choice of input and output variables, and the need to develop a simplified representation of the complexity of the real-world system. As a result, it cannot

be assumed that the model will reproduce real-system performance for any specific recirculating aquaculture operation. Instead, the model can be described as representing a general, simplified recirculating system where the emphasis of study is on the relationships between major variables that affect economic outcomes. Ultimately, these types of simulation studies can be valuable for identifying the important variables that affect system productivity, thus leading to recommendations on how the systems might be improved for commercial production purposes. In its present form, the model should not be used to determine specific production actions taken by individual aquaculturalists.

There are a number of ways that this study could be expanded to further examine the role of management on the economics of recirculating system operation. A more complete characterization of the metabolic sub-models awaits additional biological research, but modeling of the biological filtration process could be improved by incorporating growth relationships for the resident bacterial colonies. This addition is suggested by the often stated industry observation that recirculating system operators are actually producing at least two crops simultaneously; harvestable fish biomass and non-harvested, but critically important, bacterial biomass. The modeling framework of this study could also be used to examine the economic impact of biological production shocks (acute over-feeding, disease related mortality) and price risk (both input and output) under varying levels of management ability. Other useful avenues of research would modify the model to examine the use of non-divisible inputs, variable proportional returns to scale, and differential growth across individual fish.

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Table 1 Description of Constant, State, Fixed, and Free Control Variables for any Individual Simulation Scenario	
Variables	Variable Description (value where appropriate)
Constants^a	
P_Q	Price of harvestable tilapia (\$0.00287/gram for a 700 gram fish, live weight)
P_f	Feed price (\$0.00026/gram, \$0.00030/gram, and \$0.00034/gram for low, medium, and high protein feeds, respectively)
P_e	Electricity price (\$0.07/kilowatt hour)
P_s	Fingerling price (\$0.05/one gram fish)
States	
$W(t)$	Individual fish weight on day t (grams)
$UAN(t)$	Concentration of unionized ammonia nitrogen on day t (mg/liter)
$DO(t)$	Concentration of dissolved oxygen on day t (mg/liter)
$BOD(t)$	Biological oxygen demand on day t (mg/liter)
$OC(t)$	Oxygenation capacity of the water on day t
$F(t)$	Individual fish appetite on day t (grams)
$D(t)$	Numerical fish density on day t (numbers/liter)
D_H	Numerical fish density at harvest (numbers/liter)
Fixed Controls	
W_0	Individual fish stocking weight (1 gram)
W_H	Terminal fish weight at harvest (700 gram market size, live weight)
D_0	Initial numerical stocking density (0.07, 0.09, 0.11, or 0.13 fish per liter, depending on the simulation)
DC	Feed quality (20%, 30%, or 40% crude protein feed, depending on the simulation)
BE	Biological filter efficiency (0.7 to 1.0, depending on the simulation)
SAE	Standard aeration efficiency (2.0)
Free Controls	
$R(t)$	Ration size relative to appetite on day t ($0 \leq R(t) \leq 1.0$)
$E(t)$	Electricity used for aeration and pumping on day t (kilowatt hours/liter day)

^a Prices obtained from a telephone survey of major industry suppliers.

Table 2

Final Parameter Values Used in the Bioenergetic Model ($\frac{dw}{dt} = \beta \cdot \frac{dr}{dt} - \alpha \cdot \beta \cdot \frac{dr}{dt} - \kappa \cdot w^\eta$, $\frac{dr}{dt} = \delta \cdot f \cdot w^\mu$).			
Parameter	Definition	Value in Model	Source
μ	Exponent of synthesis	0.67	Calibration; Liu and Chang 1992
η	Exponent of resting metabolism	1.00	Calibration; Liu and Chang 1992
δ	Coefficient of food consumption	0.98	Liu and Chang 1992
κ	Coefficient of resting metabolism	$0.018 + 0.034 \operatorname{sech}[0.01 W(t)] + 0.018 \tanh[100 - 0.01 W(t)]$	Calibration (see Caffey 1994)
α	Fraction of assimilated food lost to active metabolism	$0.269 + 0.513 \operatorname{sech}[0.141 W(t)] + 0.017 \tanh[0.141 W(t)]$	Calibration (see Caffey 1994)

Table 3

Optimal Simulated Returns Per Liter, Days to Harvest, and Returns Per Liter Per Day For Varying Biological Filter Efficiency, Mechanical Filter Efficiency, and Percent Dietary Protein^a

Biological Filter	Mechanical Filter Efficiency											
	1.00			0.50			0.33			0.25		
Efficiency												
----- 20 Percent Dietary Protein -----												
	¢/liter	days	¢/liter/day	¢/liter	days	¢/liter/day	¢/liter	days	¢/liter/day	¢/liter	days	¢/liter/day
1.00	8.9	265	0.034	8.7	267	0.033	8.4	273	0.031	8.0	280	0.029
0.95	8.3	279	0.030	7.9	287	0.028	7.6	291	0.026	7.3	295	0.025
0.90	7.6	294	0.026	7.4	297	0.025	7.2	300	0.024	6.8	304	0.022
0.85	6.5	318	0.020	6.2	322	0.019	5.9	325	0.018	5.6	329	0.017
0.80	4.8	351	0.014	4.6	354	0.013	4.3	359	0.012	4.0	362	0.011
0.75	2.3	405	0.006	2.0	411	0.005	1.4	420	0.003	0.8	432	0.002
0.70	-0.8	478	-0.002	-1.4	481	-0.003	-1.8	489	-0.004	-1.8	495	-0.004
----- 30 Percent Dietary Protein -----												
	¢/liter	days	¢/liter/day	¢/liter	days	¢/liter/day	¢/liter	days	¢/liter/day	¢/liter	days	¢/liter/day
1.00	8.7	245	0.036	8.4	247	0.034	8.2	250	0.033	7.9	253	0.031
0.95	7.8	261	0.030	7.6	263	0.029	7.4	265	0.028	6.5	267	0.024
0.90	5.8	291	0.020	5.4	293	0.018	5.2	294	0.018	4.9	296	0.017
0.85	3.4	331	0.010	3.1	333	0.009	2.7	337	0.008	2.3	340	0.007
0.80	-0.6	403	-0.002	-0.9	403	-0.002	-1.2	404	-0.003	-1.5	405	-0.004
0.75	-5.0	501	-0.010	-5.3	502	-0.011	-5.6	502	-0.011	-5.9	502	-0.012
0.70	-7.9	603	-0.013	-8.0	603	-0.013	-8.4	603	-0.014	-8.8	603	-0.015
----- 40 Percent Dietary Protein -----												
	¢/liter	days	¢/liter/day	¢/liter	days	¢/liter/day	¢/liter	days	¢/liter/day	¢/liter	days	¢/liter/day
1.00	8.4	230	0.037	8.1	233	0.035	7.8	236	0.033	7.4	238	0.031
0.95	7.1	253	0.028	6.9	255	0.027	6.4	261	0.025	5.9	265	0.022
0.90	4.6	291	0.016	4.3	291	0.015	4.2	292	0.014	3.9	293	0.013
0.85	0.6	365	0.002	0.3	368	0.001	-0.2	373	-0.001	-0.6	375	-0.002
0.80	-5.1	478	-0.011	-5.2	480	-0.011	-5.4	481	-0.011	-5.7	481	-0.012
0.75	-8.5	595	-0.014	-8.6	595	-0.015	-8.6	596	-0.015	-8.9	596	-0.015
0.70	-10.2	698	-0.015	-10.3	698	-0.015	-10.3	698	-0.015	-10.3	699	-0.015

^a Shaded table entries denote regions of negative returns.

Table 4

Optimal Simulated Returns Per Liter, Days to Harvest, and Returns Per Liter Per Day For a Fixed Solid Removal Efficiency of 0.50 and Varying Biological Filter Efficiency, Initial Stocking Densities, and Percent Dietary Protein^a

Biological Filter	Initial Stocking Density (1 gram fish/liter)											
	0.07			0.09			0.11			0.13		
Efficiency	----- 20 Percent Dietary Protein -----											
	¢/liter	days	¢/liter/day	¢/liter	days	¢/liter/day	¢/liter	days	¢/liter/day	¢/liter	days	¢/liter/day
1.00	8.7	267	0.033	11.2	267	0.042	13.7	267	0.051	16.2	267	0.061
0.95	7.9	287	0.028	10.2	287	0.036	12.3	287	0.043	14.2	291	0.049
0.90	7.4	297	0.025	8.9	305	0.029	10.0	316	0.032	10.5	330	0.032
0.85	6.2	322	0.019	6.7	342	0.020	6.0	368	0.016	4.0	399	0.010
0.80	4.6	354	0.013	3.2	397	0.008	0.0	449	0.000	-4.2	507	-0.008
0.75	2.00	411	0.005	-1.3	479	-0.003	-5.8	554	-0.011	-10.3	622	-0.017
0.70	-1.00	4481	-0.002	-5.3	574	-0.009	-9.7	657	-0.015	-13.5	727	-0.019
	----- 40 Percent Dietary Protein -----											
	¢/liter	days	¢/liter/day	¢/liter	days	¢/liter/day	¢/liter	days	¢/liter/day	¢/liter	days	¢/liter/day
1.00	8.1	233	0.035	10.1	238	0.042	11.8	245	0.048	11.1	271	0.041
0.95	6.9	255	0.027	8.1	266	0.031	8.8	278	0.032	8.7	294	0.030
0.90	4.3	291	0.015	3.2	331	0.010	0.4	371	0.001	-3.8	416	-0.009
0.85	3.0	368	0.008	-4.6	443	-0.010	-10.1	521	-0.019	-15.0	588	-0.026
0.80	-5.2	480	-0.011	-10.3	581	-0.018	-15.0	663	-0.023	-19.0	731	-0.026
0.75	-8.6	595	-0.015	-13.0	698	-0.019	-16.8	781	-0.022	-19.9	848	-0.024
0.70	-10.3	698	-0.015	-13.9	801	-0.017	-17.2	882	-0.020	-20.0	949	-0.021

^a Shaded table entries denote regions of negative returns.

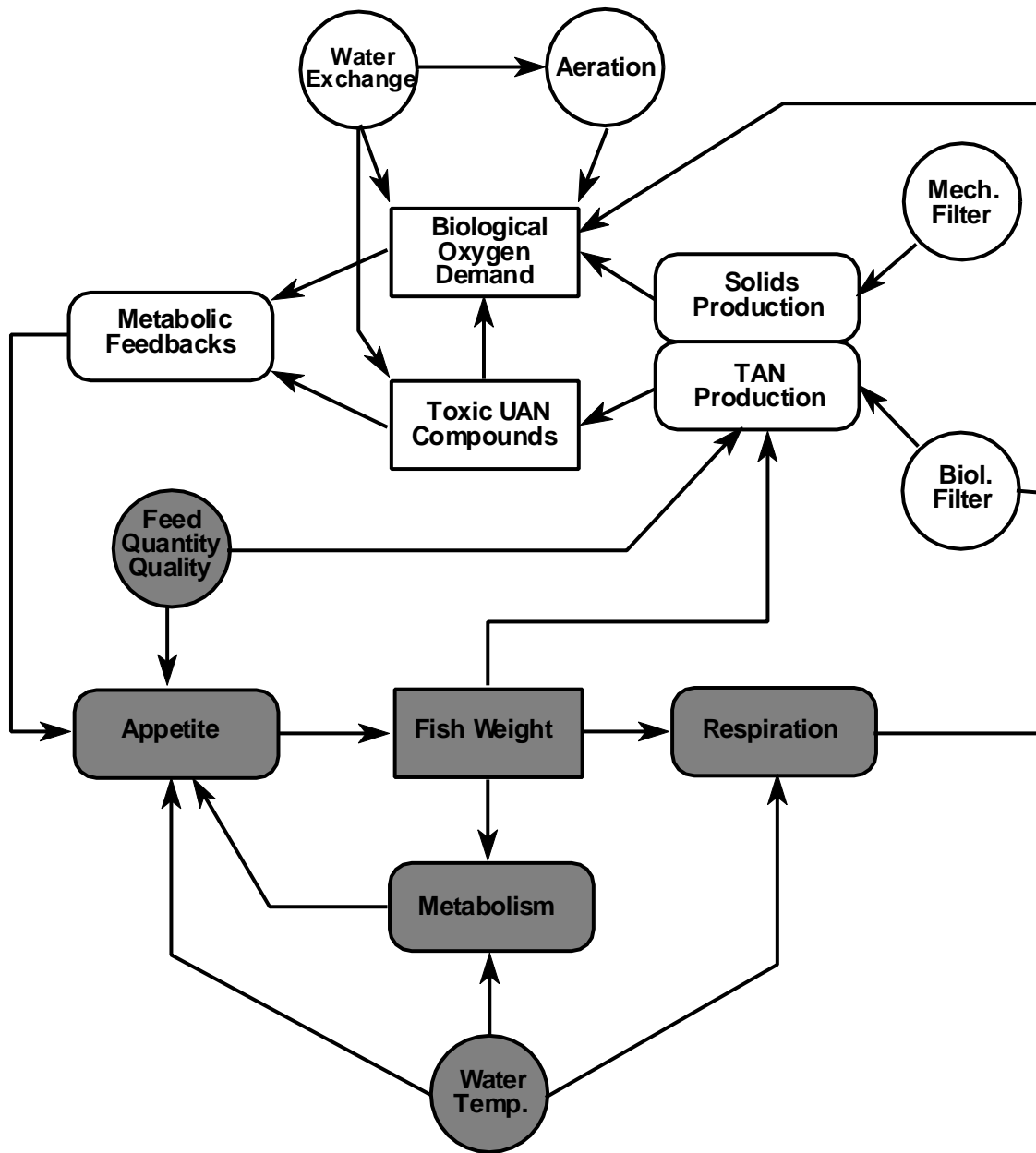


Figure 1. Conceptual Model of the Interactions Among Control Variables (circles), Process Variables (rounded polygons), and Storage Variables (rectangles) in a Recirculating Fish Production System (Shading denotes the bioenergetic components of the model).

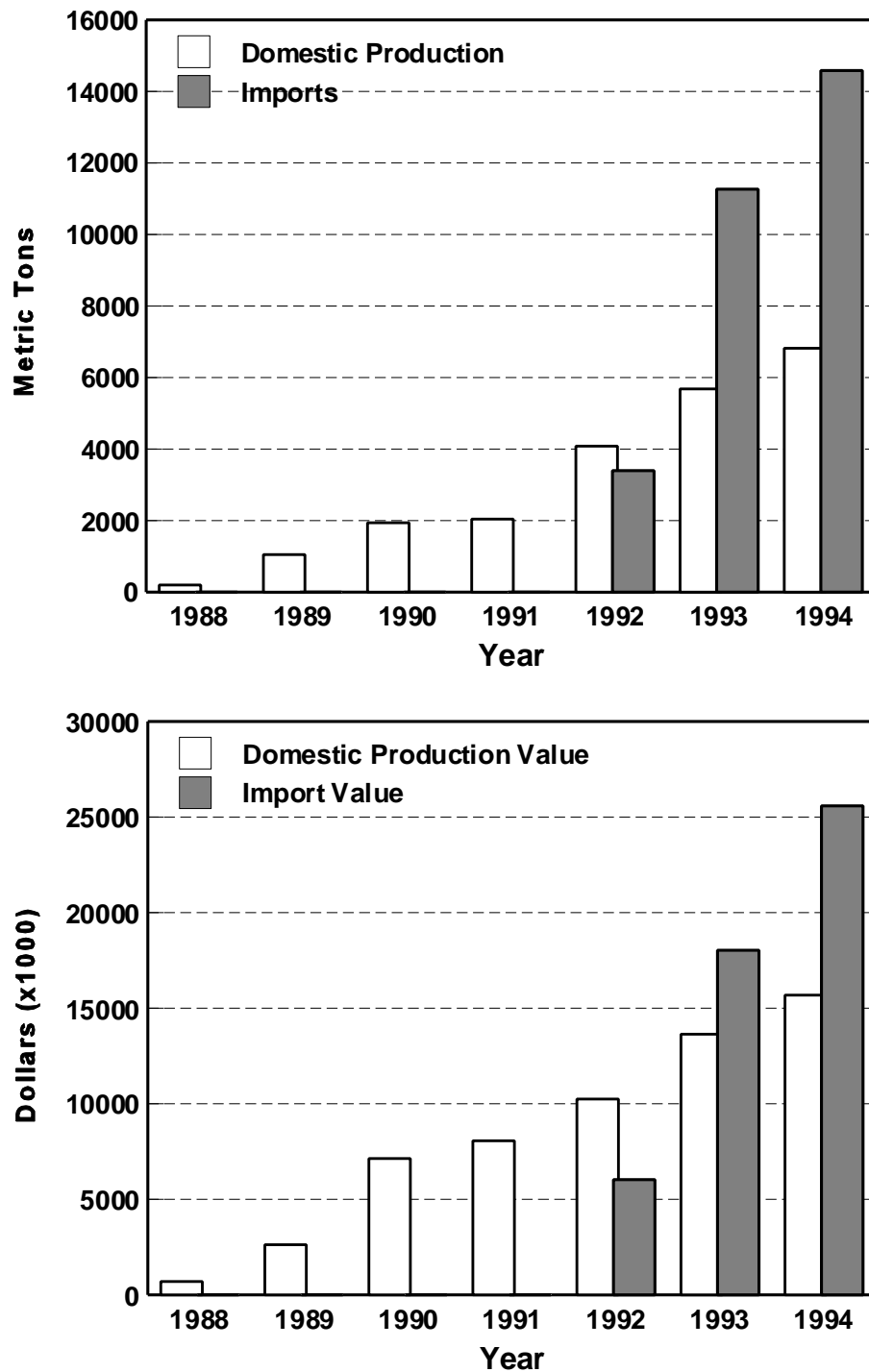


Figure 2. Tilapia Production and Farm-Gate Value From Domestic and Imported Sources (Data from *Aquaculture Situation and Outlook*, various dates, and *Fisheries Information, Data, and Statistics: Foreign Agricultural Organization*, 1995 Internet Database).

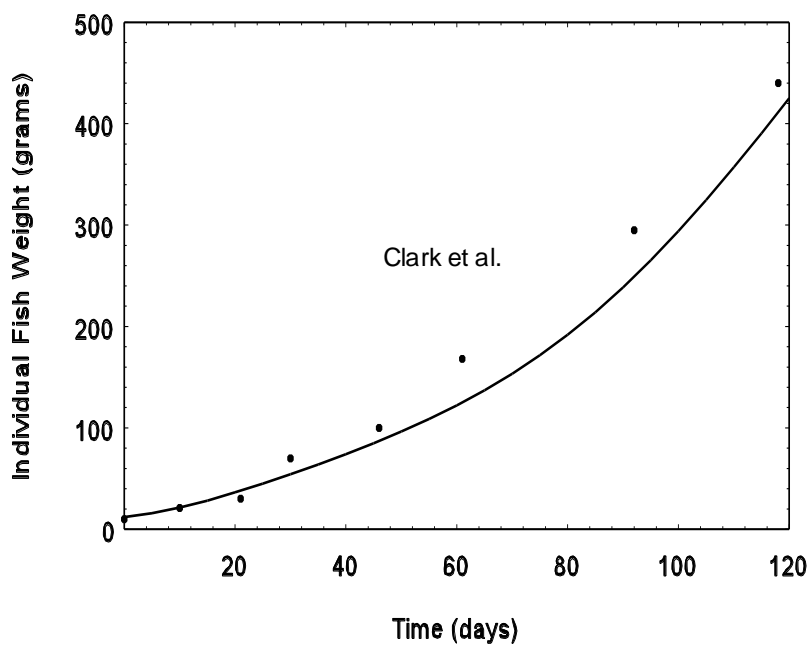
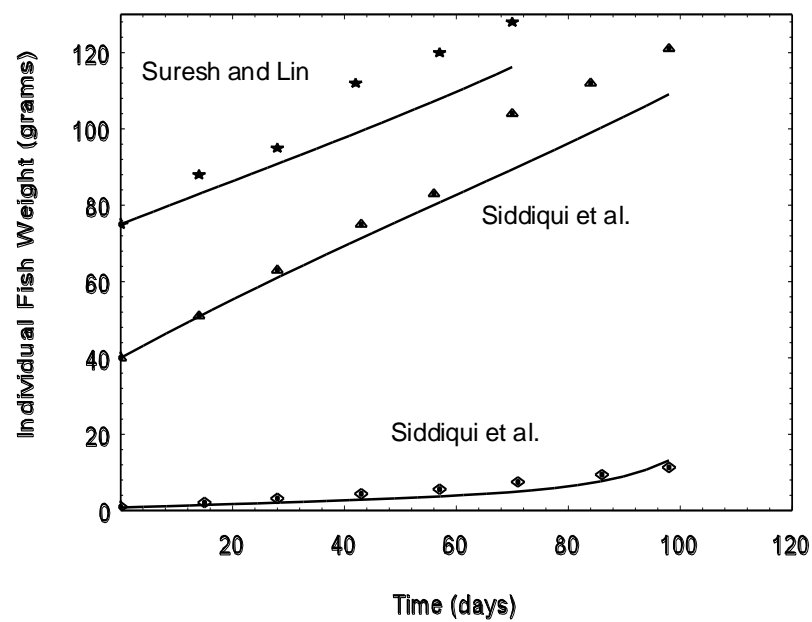


Figure 3. Comparison of Experimental Tilapia Growth Data With Simulated Growth (Solid Lines) Generated by the Bioenergetic Model (data from Siddiqui et al. (1988), Clark et al. (1990), and Suresh and Lin (1992)).

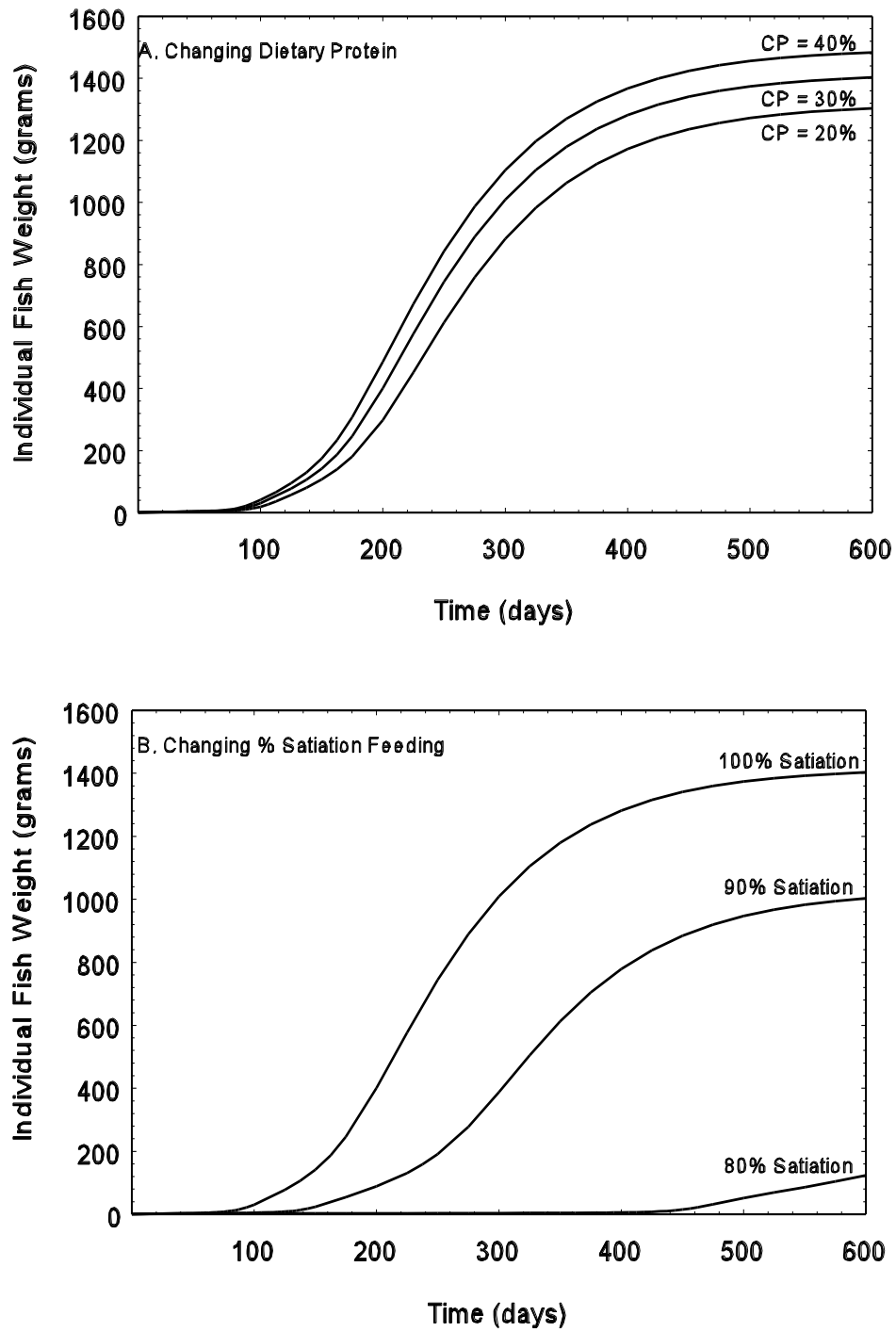


Figure 4. Effects of Dietary Protein Level (Panel A) and Level of Percent Satiation Feeding (Panel B) on Simulated Growth Generated by the Bioenergetic Model.

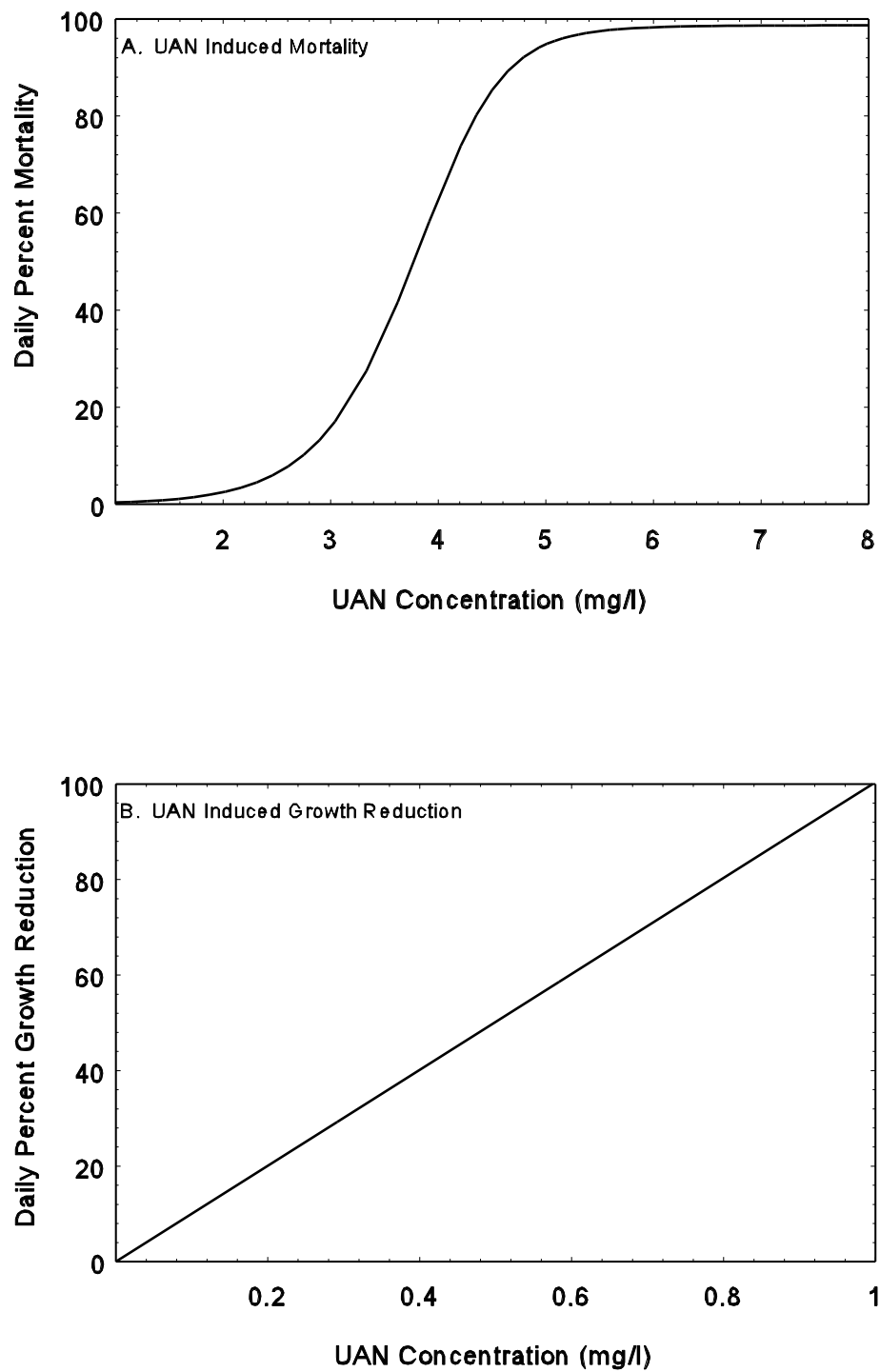


Figure 5. Unionized Ammonia Nitrogen (UAN) Induced Mortality (Panel A) and Growth Reduction (Panel B) Feedback Effects Used in the Bioenergetic Model.

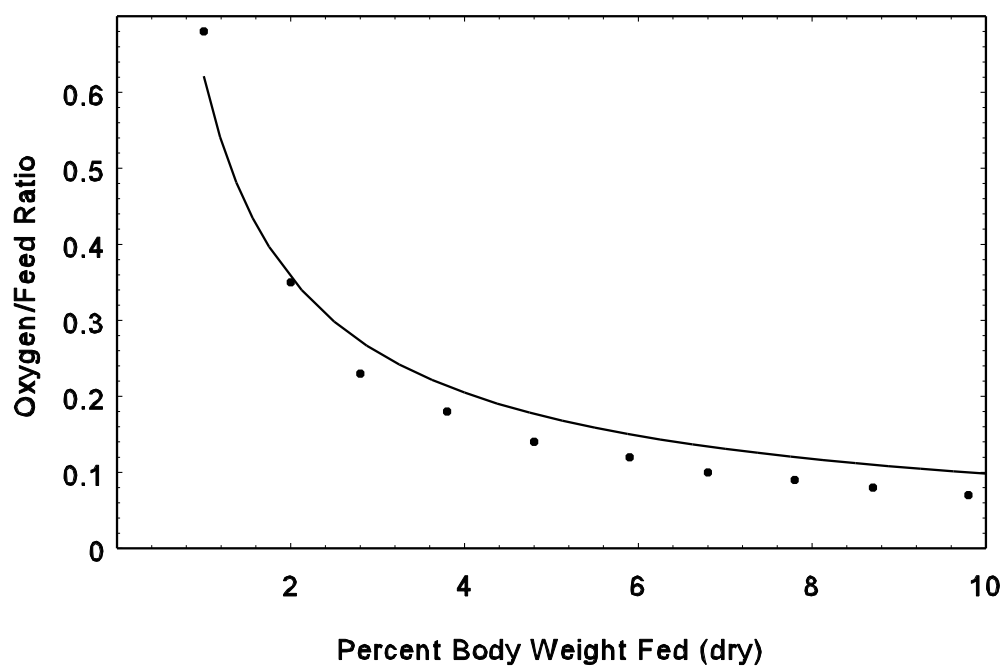


Figure 6. Comparison of Experimentally Derived Oxygen:Feed Conversion Ratios (OFR) With Simulated OFRs (Solid Line) Generated by the Bioenergetic Model With Feedbacks (Data From Colt and Orwicz, 1991).

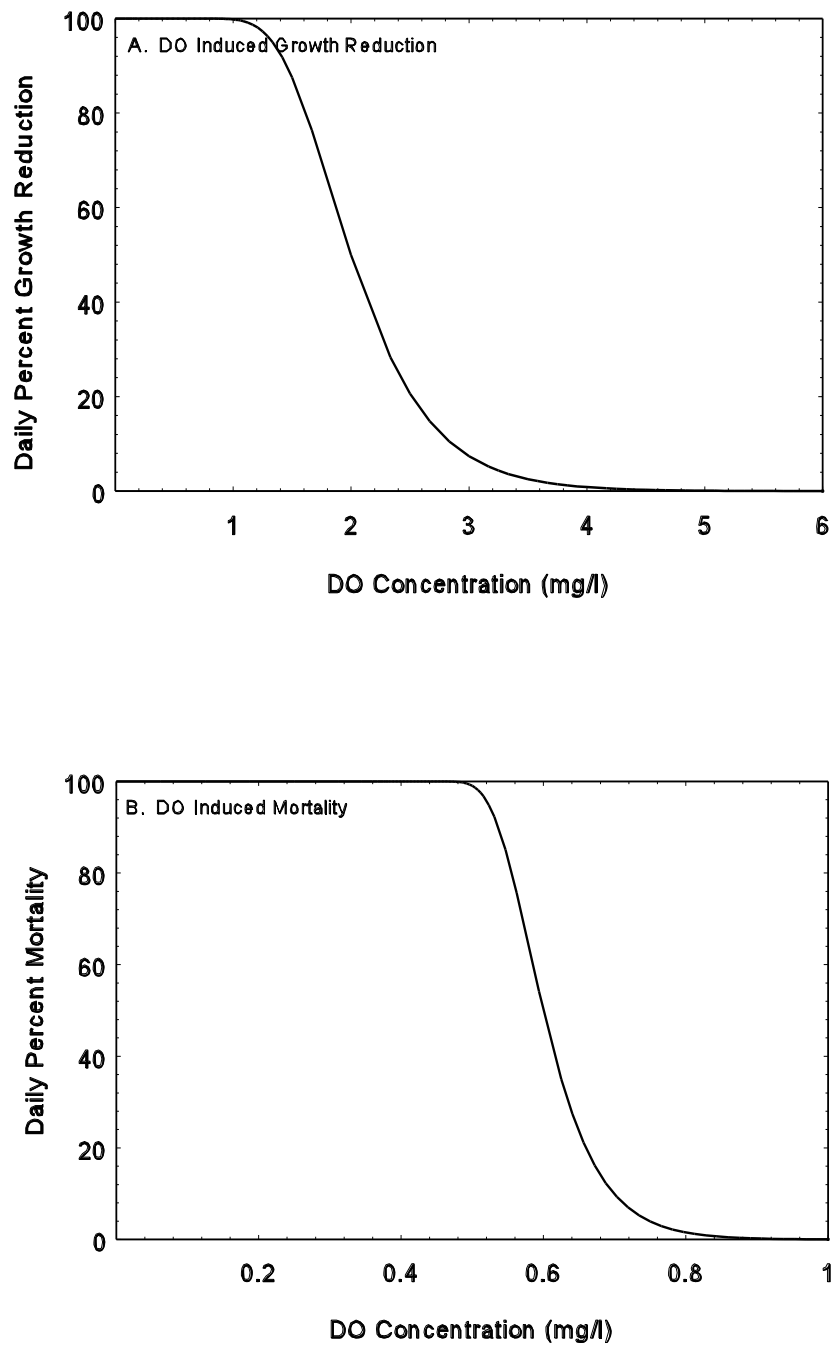


Figure 7. Dissolved Oxygen Growth Reduction (Panel A) and Induced Mortality (Panel B) Feedback Effects Used in the Bioenergetic Model.

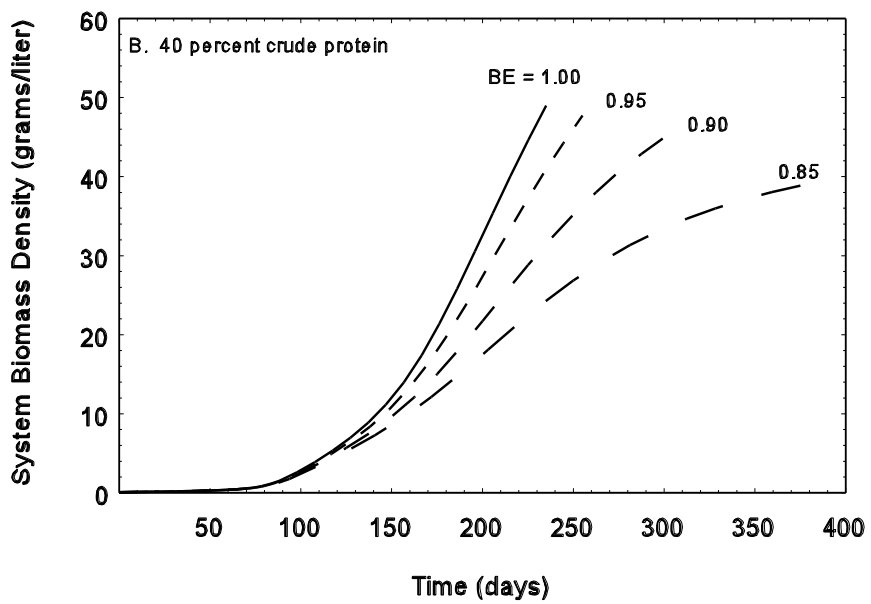
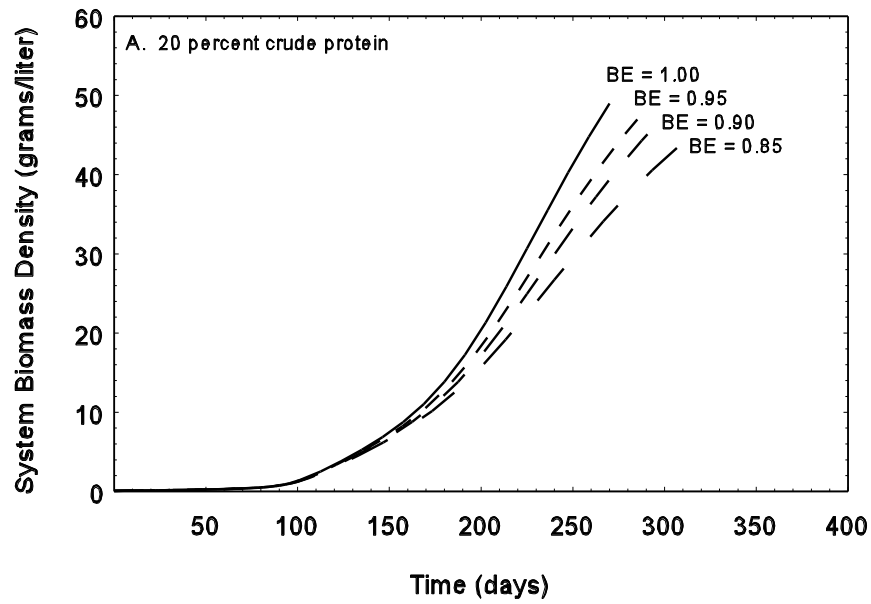


Figure 8. Effects of Different Feed Quality on Days-To-Harvest and Maximum System Biomass Density Given Varying Levels of Biological and Mechanical Filter Efficiency.

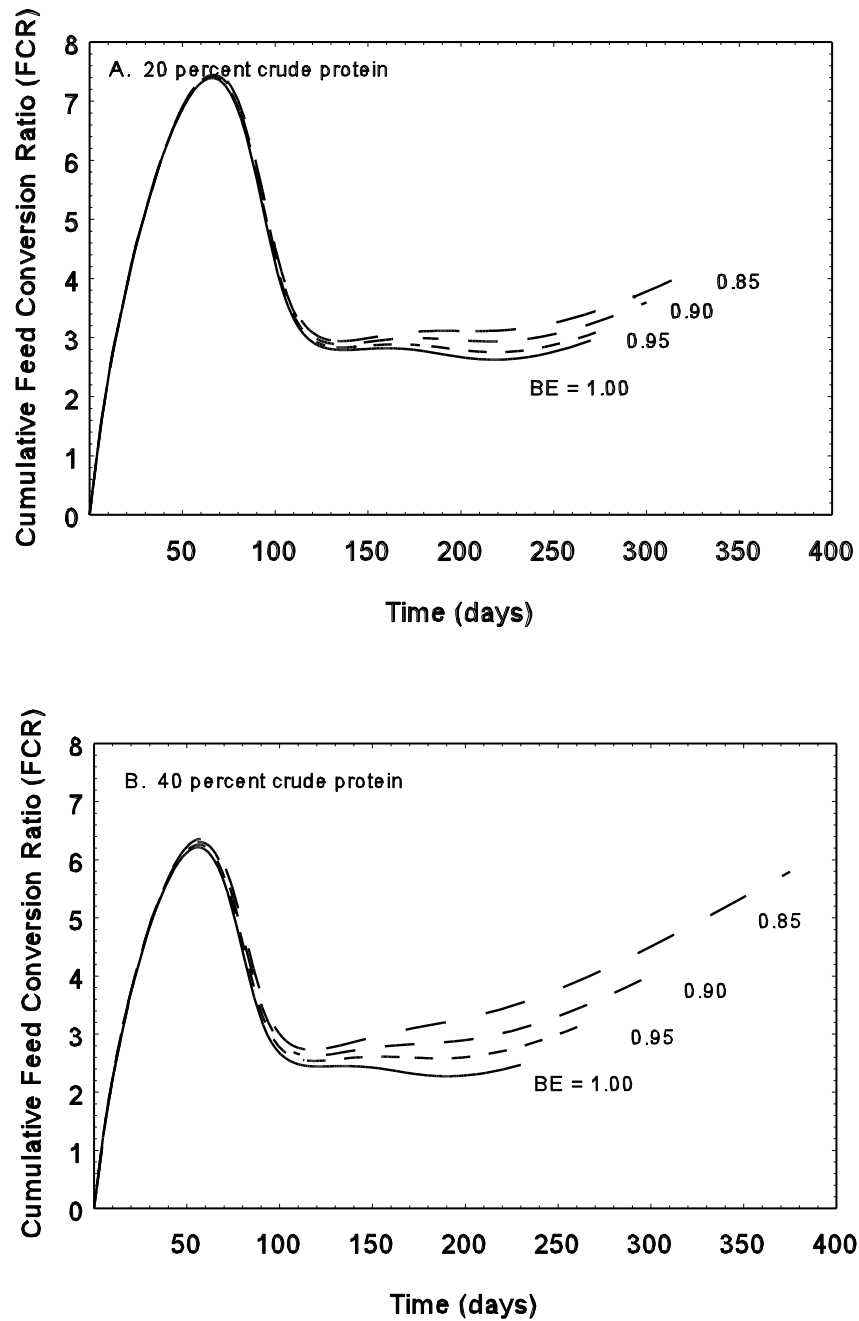


Figure 9. Effects of Different Feed Quality on Days-To-Harvest and Cumulative Feed Conversion Ratios (FCR) Given Varying Levels of Biological and Mechanical Filter Efficiency.

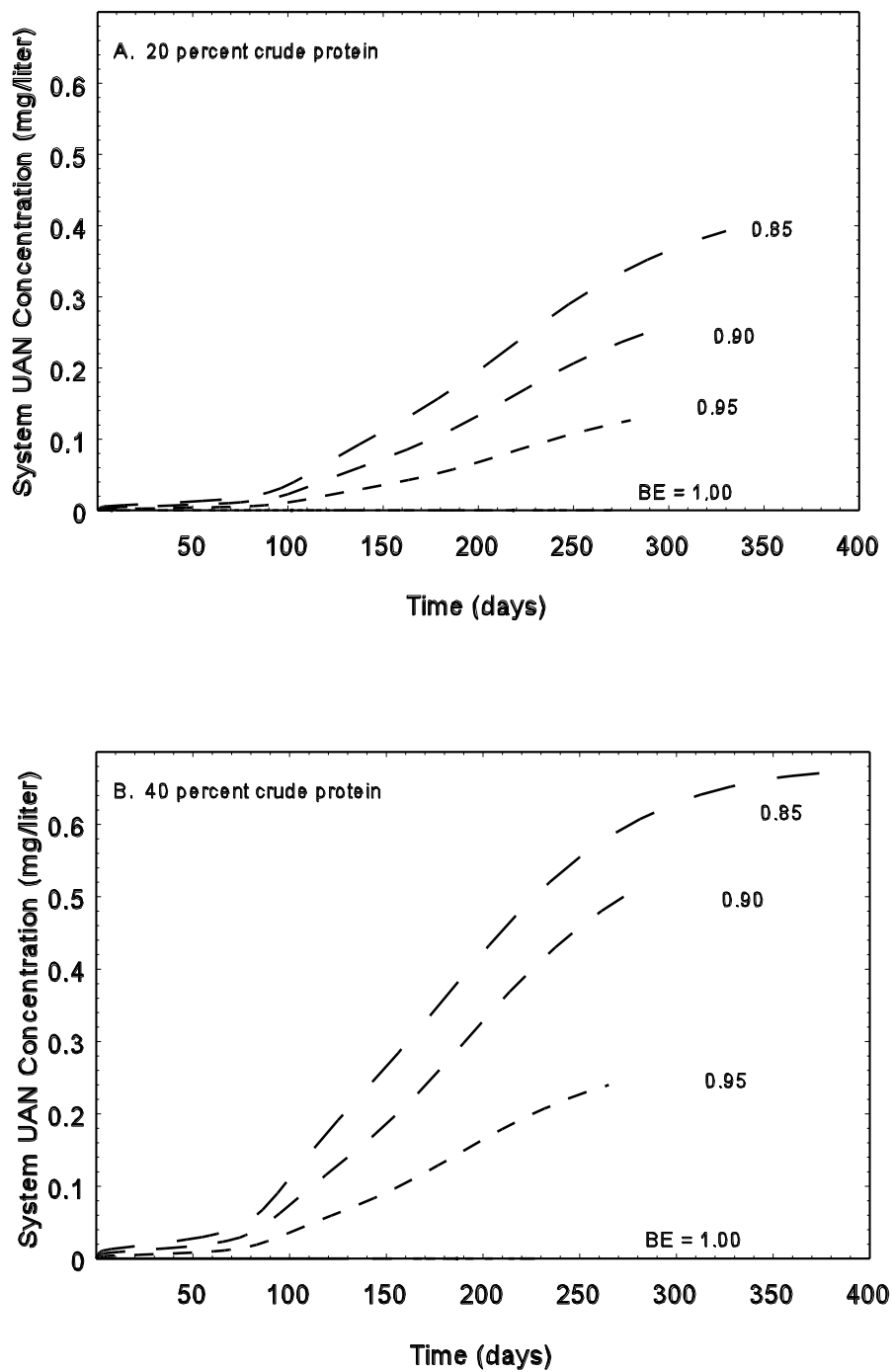


Figure 10. Effects of Different Feed Quality on Days-To-Harvest and System UAN Concentrations Given Varying Levels of Biological and Mechanical Filter Efficiency.

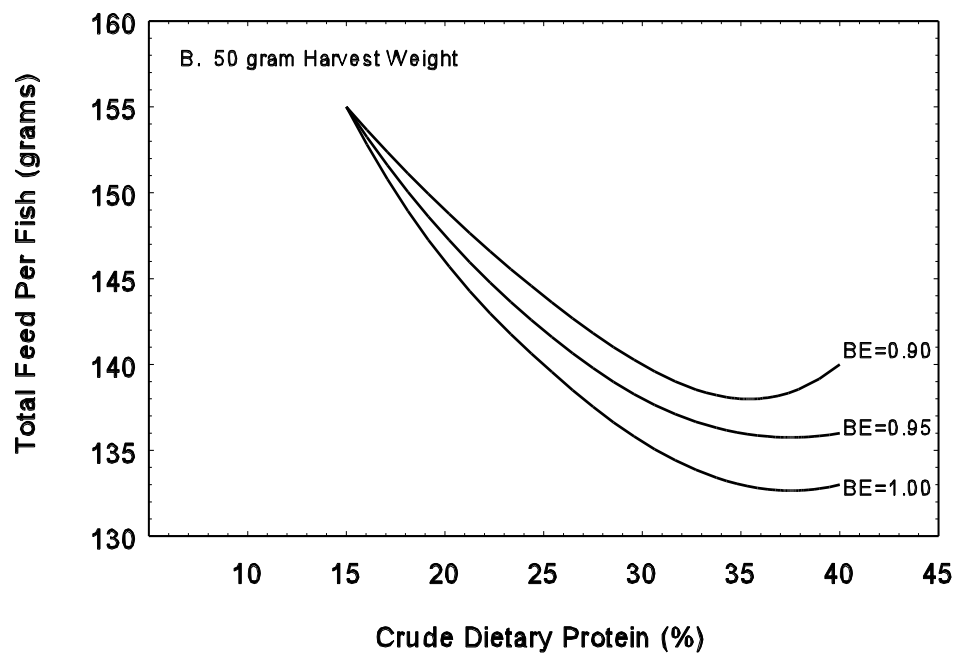
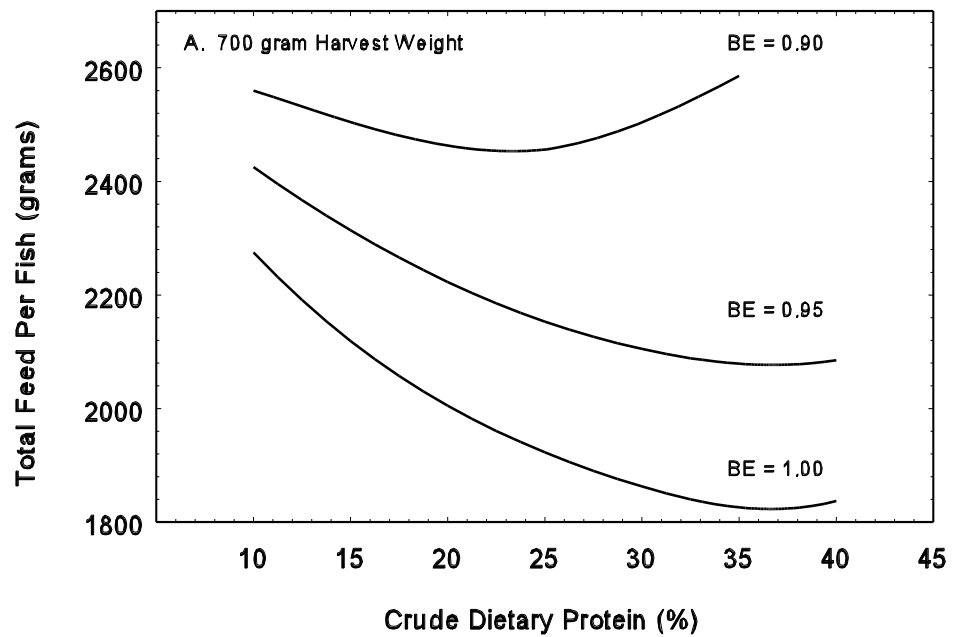


Figure 11. Feed Quantity Versus Dietary Protein Isoquants for 700 gram and 50 gram Tilapia at Varying Levels of Biological and Mechanical Filter Efficiency.

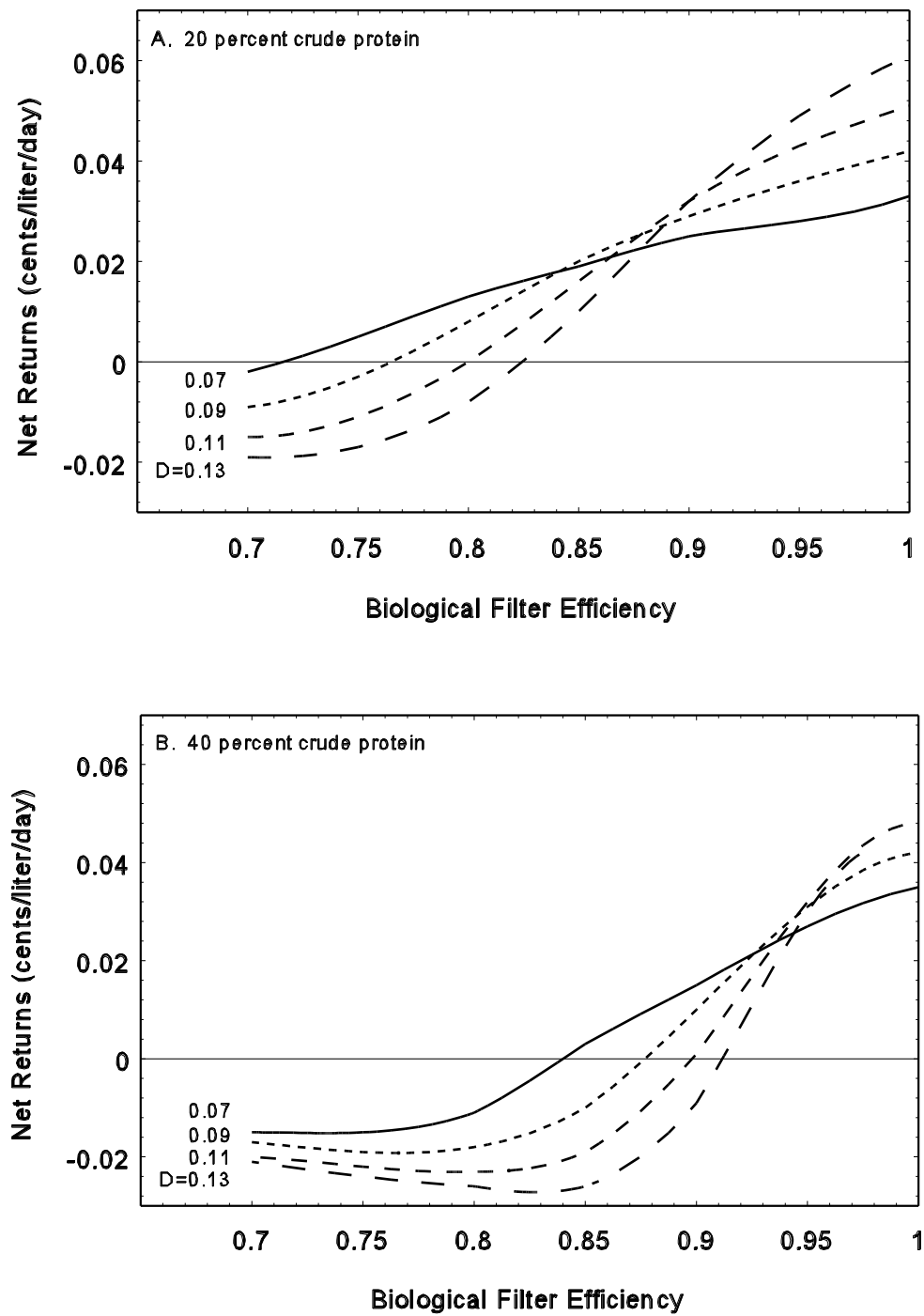


Figure 12. Simulated Daily Returns for Various Initial Stocking Levels (D) and Biological Filter Efficiencies Given a 20 Percent (Panel A) and 40 Percent (Panel B) Dietary Protein Feed.