A Dynamic Simulation Model for Growth of Penaeid shrimps

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ABSTRACT

Bio-energetic dynamic penaeid shrimp growth model was developed from an existing model on tilapia growth. The model was divided into 6 sub modules: (1) Moulting; (2) Feed consumption; (3) Digestion and biosynthesis; (4) Energy metabolism; (5) Oxidation; and (6) Growth; and was parameterized based on the literature. The model was calibrated and validated with an independent data set.

For calibration, the best agreement between observed and simulated value for growth was achieved when it was assumed that 14% of dietary amino acids was converted to glucose and ratio of fat: protein for energy generation was 0.819. Calculated regression equation and R^2 were $Y = 0.868X + 1.384$ and 0.71, respectively, where Y is simulated and X is the observed final shrimp weight. The Average Relative Error (ARE) was 5.64%. For validation comparing experimental and simulated final shrimp weight, we found $Y = 1.091X + 0.116$, $R^2 = 0.97$ with an ARE of 10.22%.

The model can predict general patterns of shrimp growth. The explanatory character of the model allowed prediction of growth under a wide range of conditions. Effect of feed nutritional quality, feeding rate, body composition, and temperature and moulting on shrimp can be predicted well by the model, which will provide insight of interactions among the growth and growth parameters of shrimp.

INTRODUCTION

In the year 1999, total world fish production expanded rapidly, reaching 126 million tonnes with contribution of 26% from aquaculture. The increase in farmed shrimp production was principally due to the culture of penaeid species, which accounted for 96.3% in 1995 of all cultured shrimp and prawns. Penaeid production, notably of giant tiger prawn and unclassified *Penaeus* species, increased from 31% or 54,000 mt and 12% or 21,000 mt in 1984, to 54% or 503,000 t and 18% or 165,000 t in 1995, respectively (www.fao.org).

The sustainability of coastal shrimp aquaculture is increasingly being questioned. Many problems like disease, loss of agricultural land due to salt intrusion, degradation of ground water sources, mangrove destruction, loss of natural spawning grounds, excessive nutrient enrichment, and activation of mineral acidity in acid sulphate soils and eutrophication of

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coastal water were accounted (Mohan, 1998). The collapse of shrimp mariculture in most tropical countries was due to the lack of ecological and biological understanding, and over exploitation of environmental goods and services (Shetty, 1998).

Little is known about the feeding bioenergetics in shrimp. In order to work out the bioenergetics, more information is needed on the effect on the bioenergetics of growth of feeding behaviour, feed utilisation, body composition, developmental stages and environmental factors (temperature, pH, salinity, dissolved oxygen etc.). Improved knowledge on the bioenergetics of growth in shrimp farming will come from experimental work. However, the experimental units are site specific, expensive and the researcher has to decide testing a few treatments with the required number of replications. Furthermore, the effect of maximum 2 or 3 factors can be measured in every experiment. By integrating results from various experiments into a general model, a conceptual framework can be developed that helps us to compare experiments of different duration or with different inputs and which generates better insight into problems related to excessive nutrient enrichment and eutrophication of coastal waters.

In this research, a bioenergetic model developed by Machiels (1987) and subsequently adapted by van Dam & Penning de Vries (1995) has been reviewed and upgraded to predict individual shrimp growth.

MODEL CONCEPTUALISATION AND IMPLIMENTATION

The model was conceptualised on the basis of the information found in the literature. A relational diagram of the model is shown in Figure 1. The considerations for the conceptual model and important equations are given below.

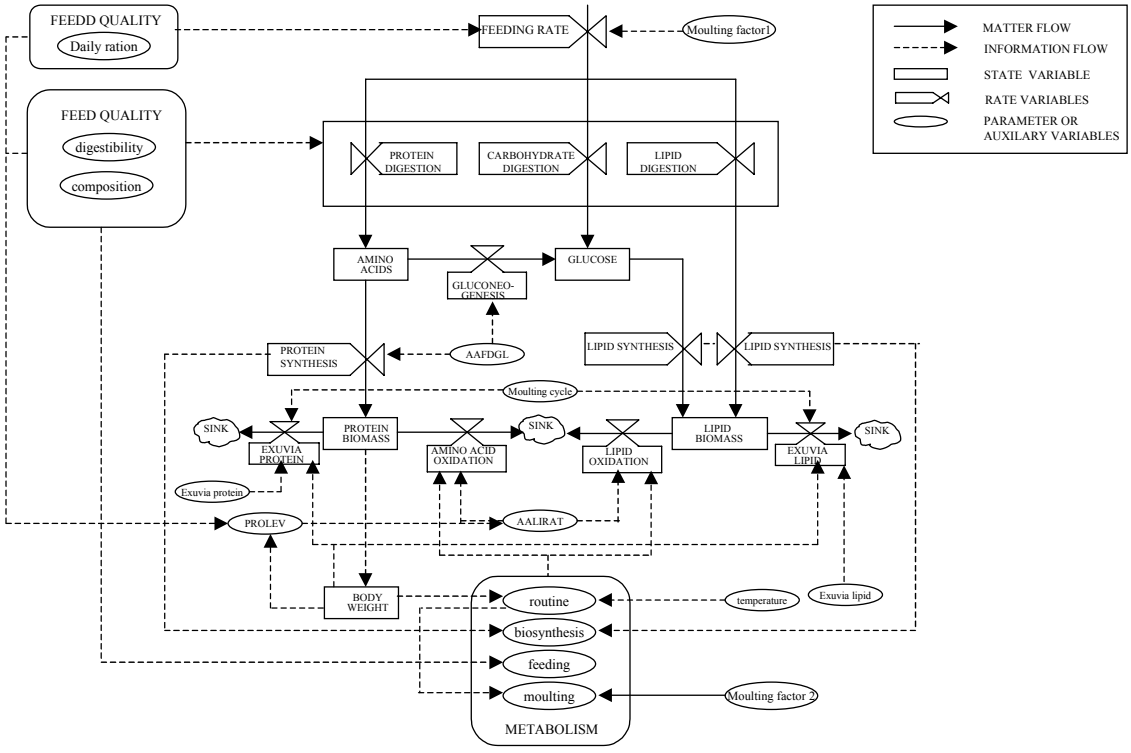

Figure 1: Relational diagram of shrimp growth model. AALIRAT = auxiliary variable determining the ratio of protein to fat oxidation; AAFDGL = parameter determining the proportion of amino acids that is converted to glucose; PROLEV = protein feeding level (in g protein*kg*d^{-1}). For further explanation see text.

The model was constructed using STELLA II and executed on a personal computer. The basic building blocks in STELLA II are stock, flow, converter, and connector. Stocks represent state variables, which are inter-connected by flows. Flow may carry things into or out of stocks and represent rate constants. Flows are defined and regulated by converters. The converter hold the value of constants, defines external input to the model, calculate algebraic relationship and serves as repository for the graphic functions. The connector is to connect model elements.

EQUATIONS OF THE MODEL

The model is divided into 6 modules. (1) Moulting (2) Feed consumption (3) Digestion and Biosynthesis (4) Energy Metabolism (5) Oxidation and (6) Growth. The equations for the different modules are given below. Some equations of Van Dam & Penning de Vries (1995) were redefined for shrimp.

1. Moulting module

The equations of the moulting metabolism are listed below.

Exuvia composition

The relation between exuvia wet weight and fresh body weight, and the composition of the exuvia (Sarac *et al*., 1994) calculate the amount of the protein and lipid going out from the body. The major equations are given below.

Total protein in exuvia = (crude protein in exuvia _(%)/100)*dry matter of exuvia
Total fat in exuvia = (fat in exuvia (%)/100)*dry matter of exuvia
Dry matter of exuvia = 0.56*wet weight of exuvia
Wet weight of exuvia = (0.057*body weight)-0.08

Moulting factor 1

Moulting factor 1 decides that the shrimp does not eat for three days, two days before and one day after the moulting. The following equations have considered feeding behaviour of *P. monodon* (Choe, 1971).

Feeding rate = IF (moulting_ cycle*0.85 <= MND) and (MND < moulting cycle) THEN 0
ELSE
(IF (time of day >= 6) AND (time of day <18) THEN FDM*(ration/time fed) ELSE 0)
Where, FDM= feed dry matter/100
MND= COUNTER (0, moulting cycle)

Moulting factor 2

Moulting factor 2 determines the increase of oxygen consumption above the routine metabolism at each stage of the moulting. The following logical equation gives a factor for each moulting stage that is multiplied by oxygen consumption of the routine metabolism to calculate the consumption of oxygen for the moulting phenomenon (Figure 3).

Moulting factor 2 = IF MND < moulting_ cycle*0.12 THEN 86.21
ELSE
((IF (moulting cycle*0.12 <= MND) and (MND < moulting cycle*0.4) THEN 0
ELSE
(IF (moulting cycle*0.4 <= MND) and (MND < moulting cycle*0.85) THEN 7.16 ELSE 12.23)))
Where MND = COUNTER (0, moulting cycle)

2. Feed consumption module

The module feed consumption calculates the feeding rate for 12 hrs assuming nocturnal feeding behaviour of the shrimp. The feed given is calculated on the basis of total body weight of total shrimp and feed given (% body weight feed day) and the ration is calculated on the basis of the daily given feed and the total number of shrimp.

Feeding rate (g/12hrs) = ration/time fed
Ration = feed given (g)/number of shrimp

Feed given (g) = body _weight (g)*feed daily (%)
Time fed = 0.5 (the shrimp eat during half of the day)

3. Digestion and biosynthesis module

The principal state and rate variables of this module are the total amino acid for protein synthesis and the total lipid biomass, and the rate protein digestion 1 (for protein synthesis), rate protein digestion 2 (for glucogenesis), rate lipid digestion and rate carbohydrate digestion.

The state variable total amino acid fdr protein synthesis calculates the total amount of protein, which would be available for the growth of the body. The equation considers the fraction of digested protein that is used for protein synthesis (Rate protein digestion 1) and the fraction of the digested protein that is used for amino acid oxidation (Rate amino acid oxidation). The rate of the protein digestion (1) calculates the fraction of protein digested for the growth of the shrimp. The rate considers the feeding rate, protein content of the diet (Feed protein (%), protein digestibility and the fraction of the amino acid not used for gluconeogenesis whereas rate protein digestion (2) calculates the amount of the protein used for the gluconeogenesis (amino acid fraction for gluconeogenesis).

The state variable, total lipid biomass calculates the lipid content of the body. The equation considers the rate of gluconeogenesis, the rate of lipid digestion, the rate of lipid oxidation and the rate of exuvia lipid. The rate of lipid digestion considers feeding rate, lipid content of the feed (Feed lipid (%)) and lipid digestibility.

Rate protein digestion 1 = (feeding rate*(feed protein (%)/100)*protein digestibility*1.18)*(1 - amino acid fraction for gluconeogenesis)

Rate protein digestion 2 = (feeding rate*(feed protein_(%)/100)*protein _digestibility*1.18)* amino acid fraction for gluconeogenesis

Rate lipid digestion = feeding rate*(feed lipid (%)/100)*lipid digestibility*0.96

Rate carbohydrate digestion = feeding rate*(feed carbohydrate (%)/100)*carbohydrate digestibility*1.11

Total amino acid for protein synthesis (t) = total amino acid for protein synthesis (t - dt) + (rate protein - digestion 1 – rate protein synthesis - rate amino acid oxidation) * dt
INITIAL total amino acid for protein synthesis = 0

Total lipid biomass (t) = total lipid biomass (t - dt) + (rate gluconeogenesis + rate lipid synthesis - rate lipid oxidation - rate exuvia fat) * dt
rate gluconeogenesis(o) = total glucose/DT
INITIAL total lipid biomass = (initial body lip (%) /100)*Initial fresh body weight

4. Energy metabolism module

The principal state and rate variables of the module are Total ATP for metabolism, rate ATP for routine metabolism, rate ATP for feeding metabolism, rate ATP biosynthesis and rate ATP for moulting metabolism.

The state variable total ATP for metabolism considers rate ATP for metabolism. The rate ATP for metabolism is the sum of rate ATP for routine metabolism, rate ATP for feeding metabolism, rate ATP biosynthesis and rate ATP for moulting metabolism.

The rate variable rate ATP for routine metabolism calculates the amount of ATP used for routine metabolism. The rate variable considers the redefined equation for routine metabolism (van Dam & Penning de Vries, 1995) on the basis of Dall (1986) and the equation consists of Q_{10}, water temperature, reference temperature, metabolic coefficient, fresh body weight and metabolic exponent.

The rate variable rate ATP for feeding metabolism calculates the ATP required for feeding. The equation considers the feed energy, feeding rate and apparent heat increment (SDA) (%) and ATP factor.

The rate variable rate ATP biosynthesis calculates the energy required for biosynthesis. The equation considers the rate of lipid biosynthesis, rate of gluconeogenesis and rate of protein synthesis.

The rate variable rate ATP for moulting metabolism calculates the ATP used for moulting. The equation considers the routine metabolism and moulting factor 2. Moulting factor 2 determines the increase of oxygen consumption above routine metabolism at each moulting stage.

Total ATP for metabolism (t) = total ATP for metabolism (t - dt) + (rate ATP for metabolism) * dt
INITIAL total ATP for metabolism = 0
Rate ATP for metabolism = Rate ATP for routine metabolism + Rate ATP for feeding metabolism +Rate ATP for biosynthesis + Rate ATP for moulting metabolism
Rate ATP for_ routine metabolism = (Q10^((water temperature-reference temperature)/10))*metabolic coefficient*(body weight ^ metabolic exponent)
Rate ATP for feeding metabolism = (feed energy * feeding rate*(Apparent heat increment (%)/100))/ATP factor
Rate ATP biosynthesis = rate of lipid biosynthesis rate + rate of gluconeogenesis + rate of protein synthesis
Rate ATP for moulting metabolism = rate ATP for routine metabolism * (moulting factor 2/100)
Apparent heat increment = 6 % of the feed energy
ATP factor = 77.3 kj/ mole ATP
Cost of lipid synthesis = 0.015 mole ATP/g
Cost of gluconeogenesis = -0.095 mole ATP/g
Cost of protein syntheses = 0.075 mole ATP/g
Metabolic coefficient = 0.053019
Metabolic exponent = 0.815
Reference temperature = 25 ^{o}C

5. Oxidation module

This module calculates the amount of amino acid and lipid used for oxidation to generate energy for the metabolism. The main state and rate variables are the amino acid used for oxidation and lipid used for oxidation, amino acid oxidation rate and lipid oxidation rate. The state variable, amino acid used for oxidation, considers the amino acid oxidation rate. The equation of amino acid oxidation rate consists of the rate ATP for metabolism, amino

acid ATP factor and the amino acid switch. The amino acid switch decides the proportion of amino acid for the oxidation on the basis of the body lipid content.

The state variable lipid used for oxidation calculates the amount of lipid used for the oxidation. The equation of the state variable considers the lipid oxidation rate.

Amino acid used for oxidation (t) = Amino acid used in oxidation (t - dt) + (amino acid oxidation rate) * dt
INITIAL Amino acid used in oxidation = 0
Amino acid oxidation rate = amino acid switch *rate ATP for metabolism *Amino acid ATP factor
Amino acid switch = IF (Body lipid>min body lipid) THEN (1-fat proportion 1) ELSE (1)
Lipid used for oxidation (t) = lipid used in oxidation (t - dt) + (lipid oxidation rate) * dt
INITIAL Lipid used in oxidation = 0
Lipid oxidation rate = lipid switch *rate ATP for metabolism *lipid ATP factor
Lipid switch = IF (Body lipid>minimum body_ lipid) THEN (fat proportion 1) ELSE (0)
Fat proportion 1 = IF (moulting cycle*0.85 <= MND) and (MND < moulting cycle) THEN 1
ELSE fat proportion
Amino Acid ATP factor = 4.76
Lipid ATP factor = 1.96
Fat proportion = .819
Minimum body lipid = 1.9%

6. Growth module

This module calculates the fresh body weight of the shrimp. The principal state and rate variables are the fresh body weight and the growth rate. The state variable fresh body weight calculates the fresh body weight of the shrimp. The equation of the state variable considers initial fresh body weight and growth rate. The growth rate was calculated on the basis of the total protein biomass and protein level in body.

Fresh body weight (t) = Initial fresh body weight (t - dt) + (growth rate) * dt
INITIAL Fresh body weight = Initial fresh body weight

Growth rate = (total protein biomass / (protein level in body (%)/100))
Protein level in body=20%

PARAMETER VALUES OF THE MODEL

The parameter values in each module were adjusted based on values reported in the literature, and the effects of changes in parameter values on the overall performance of each module were reviewed. The modules are discussed in detail below.

1. Moulting module

The body protein and lipid loss during each moulting, in the form of the exuvia protein and lipid were calculated on the basis of the relation between the fresh body weight and the fresh exuvia weight (Sarac *et al*., 1994), and chemical composition of the exuvia (Table 1).

Table 1.- Chemical composition (dry matter) of exuvia and whole body of prawn, *P. monodon* (Sarac *et al*., 1994).

Composition	Shrimp body	Exuvia
DM (%)	27.48	55.9
Crude protein (%)	72.82	22.47
Ether extract (%)	5.61	1.32
Ash (%)	15.15	62.77
Gross energy (MJ/kg)	20.08	6.34

2. Feed consumption module

The module considers that the shrimp eat only during the night and the shrimp do not eat, two days before and one day after the moulting (Talbot, 1994; Cuzon *et al*., 1982; Reymond & Lagardere, 1990).

3. Digestion and Biosynthesis module

The value of the parameters protein digestibility, lipid digestibility and carbohydrate digestibility were established. The value for the fraction of amino acid used for the gluconeogenesis was calibrated. Table 2 shows the default parameter value of the digestion and biosynthesis module, which are based on the literature.

Table 2.- Default parameters and values used by the Digestion and Biosynthesis module.

Parameters	Shrimp	Source	*C.gariepinus* (Machiels, 1987)
Protein digestibility	92%	Catacutan, 1991	80%
Lipid digestibility	63%	Smith et al., 1985	80%
Carbohydrate digestibility	40%	Clark et al., 1993	40%
fraction of amino acid for gluconeogenesis	-	-	15%

4. Energy metabolism module

Table 3 shows default parameter value of the energy metabolism module. These values are based on the literature. The equation given by van Dam & Penning de Vries (1995) for the routine metabolism of *Oreochromis niloticus* was redefined for the shrimp on the basis of Dall (1986). The energy spent for moulting was calculated at different stages of the moulting cycle on the basis of increase in oxygen consumption above the routine level (Table 4).

Table 3: Parameter value for the energy metabolism module

Parameters	Modified on the basis of Dall, 1986	*Oreochromis niloticus* (van Dam & Penning de Vries, 1995)
Q_{10}	2.55	2
b (exponent)	0.815	0.8
a (rate constant)	0.053019	0.2595
Ref. temperature	25°C	25°C
Specific Dynamic Action (SDA) (%)	6.5 (Rosas & Sanchez, 1996)	15

Table 4.- Increase in oxygen consumption above the routine level at the different moulting stages

Moulting stages	Moulting/ postmoulting	Intermoulting	Early premoulting	Late premoulting (about to moulting)
% increase of O_2 consumption	86.21	0	7.16	12.23
Nature of energy substrate	Lipid dominant	Protein dominant	Protein dominant	Protein dominant
Duration (% of cycle)	12	28	45	15

5. Oxidation module

Protein and fat supply energy for metabolism and biosynthesis. The protein:fat ratio is not constant for all species of fish and shrimp. van Dam & Penning de Vries (1995) and Machiels (1987) described the ratio for *O. niloticus* and *Clarius gariepinus,* respectively. The protein:fat ratio for shrimp was not found in the literature. The model was calibrated for this protein:fat ratio.

6. Growth module

Information on the relation between fresh body weight and protein content was not found in the literature. So, the module calculates the fresh body weight on the basis of the average body protein level, i.e. 20% (Sarac *et al.,* 1994).

CALIBRATION AND SENSTIVITY ANALYSIS

1. Calibration

The model was calibrated for protein partitioning i.e. choosing the parameter value for gluconeogenesis, and for the protein: fat ratio for energy generation. The data set used for calibration is summarized in Table 5.

The best agreement between observed and simulated value (Figure 2) for growth was achieved when the value for the protein partitioning parameter was assumed 14% and the ratio of fat to protein 0.819. The calculated regression equation between simulated and observed values and R^2 were then Y=0.87X+1.38 and 0.706, respectively.

Table 5.- Summary of the data set used for calibration

Source	Species	In. Wt.	Fi. wt.	Period	Temp.	FR	Feed composition			
		(g)	(g)	(Days)	°C	%/d	DM %	Pro%	fat%	car%
1	*P. monodon*	3.11	6.92	42	29	2.73	84.9	47.3	7.5	20*
2	Penaedae	0.33	16.3	155	25*	2.8	90*	40	8*	20*
3	P. *merguiensis*	0.29	3.41	56	28	3.5	89.3	50.9	4.1	18.2
4	P. *merguiensis*	0.29	4.86	56	28	3.17	90*	57.2	4.6	20.4
5	P. *vannamei*	1	5	70	26.9	3.35	90*	35	8	20*
6	*P. monodon*	4.89	9.38	62	29	2.45	93	42	12	20*
7	*P. vannamei*	2	15.94	98	31.6	6	90*	25	8*	25*
8	*P. vannamei*	0.37	4.23	42	28.1	5.3	92	32	8	20*
9	*P. monodon*	4.07	7.62	42	27.9	5	95.8	40	7.6	20*

*=Values are assumed

1. Smith (1999), 2. Montoya *et al*. (1999), 3 & 4. Seddgwic (1979b), 5. Lim *et al*. (1997), 6. Bautista & Subosa (1997), 7. Martinez-Cordova *et al*. (1998), 8. Davis & Arnold (2000), 9. Sudaryono *et al*. (1999)

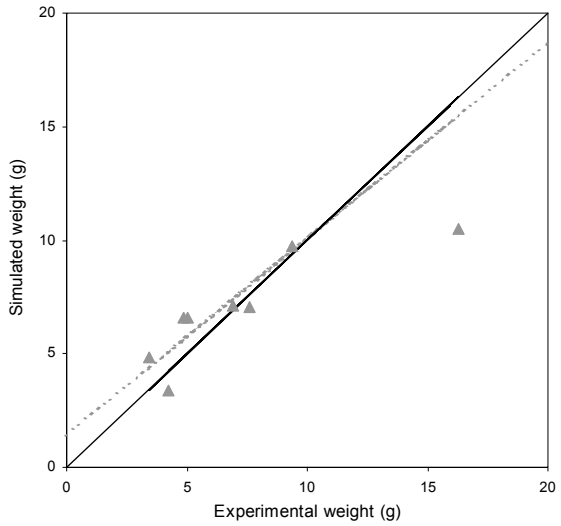

Figure 2: Calibration result for shrimp. The bisector represents perfect agreement between simulated and observed value. The dotted line represents regression line (Y=0.87X+1.38) between simulated and observed weight.

Relative error

The Relative Error (RE) and the Average Relative Error (ARE) were calculated (van Dam, 1995) (Table 6). The equation for the RE is:

$$RE_i = \frac{W_{sim,i} - W_{obs,i}}{\frac{1}{2}(W_{sim,i} + W_{obsi})} * 100$$

Where, RE_i = Relative Error at data point i, $W_{sim,i}$= simulated fish weight at data point i. and $W_{obs,i}$= Observed weight at data point i.

Table 6.- Relative Error (RE) and Average Relative Error (ARE) after the calibration.

Source	RE (%)
1	2.85
2	- 43.19
3	35.06
4	29.92
5	27.14
6	3.76
7	25.22
8	-22.63
9	-7.35
Average Relative Error (ARE)	**5.64**

1. Smith (1999), 2. Montoya *et al*., (1999), 3 & 4. Seddgwic (1979b),
5. Lim *et al*., (1997), 6. Bautista & Subosa (1997),
7. Martinez-Cordova *et al*., (1998), 8. Davis & Arnold (2000),
9. Sudaryono *et al*., (1999)

2. Sensitivity analysis

The sensitivity analysis for different parameters was done using the method described by Piedrahita (1988). The value of different parameters was deviated by ± 10% and the effect on the final weight of the shrimp in terms of deviation in percentage was observed (Table 7).

Table 7.- Sensitivity analysis for default parameters on the final weight of the shrimp

Parameters tested	-10% (%)	+10% (%)
Protein Digestibility	-29.56	67.70
Lipid Digestibility	-0.55	150.55
Carbohydrate Digestibility	0	43.79
moulting cycle (days)	14.05	207.66
Body protein	8.21	-6.57
AA for gluconeogenesis	9.85	28.28
Fat proportion for energy	-68.79	1310.76
Exuvia protein	5.29	-4.93
Exuvia fat	0	0
Q10	0.55	0.55
Metabolic Exponent	30.10	0
Metabolic coefficient	48.90	-10.40
Apparent Heat Increment	1.64	-1.46

GENERAL DESCRIPTION OF MODEL BEHAVIOUR

Shrimp increase their oxygen consumption during moulting. During the intermoulting stage of the moulting cycle, the oxygen consumption remains normal but in the other three stages (premoulting, moulting and postmoulting), the oxygen consumption increases by 7.6%, 12.23% and 86.21%, respectively (Figure 3). Rapidly, after removal of the old cuticle, formation of a new exoskeleton takes place. So, the wet weight of exuvia increases quickly just after the moulting (Figure 4).

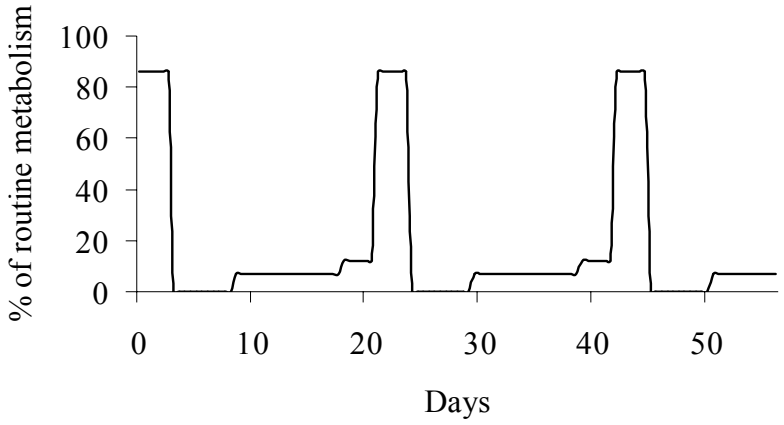

Figure 3.- Simulated increase in oxygen consumption during different stages of moulting

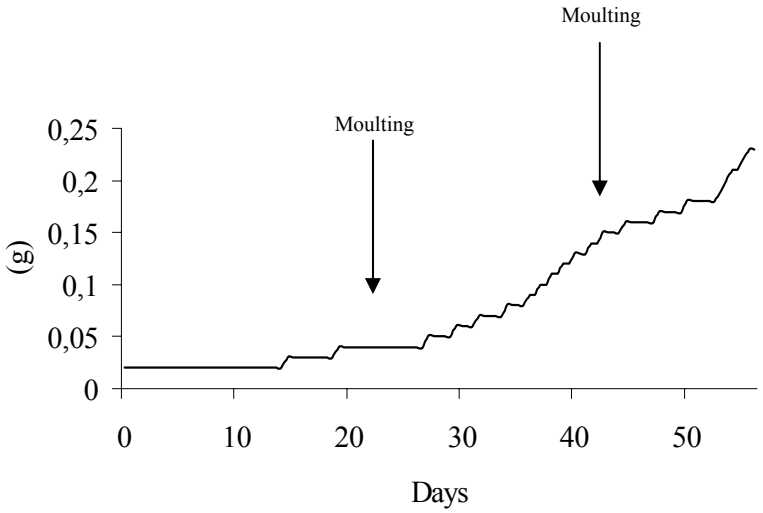

Figure 4.- Simulated wet weight (g) of the exuvia showing rapid increase after moulting

The feeding behaviour of shrimp is different from fish. Most of the cultured species of shrimp are grooved species, which are active at night and burrow in the substrate for a part of the day. In keeping with this natural nocturnal feeding habit of the shrimp, most of the feed in commercial shrimp farms is given in the evening. Shrimp also stop feeding during moulting. The penaeid species stop feeding two days before and one-day after the moulting (Figure 5). The module also calculates the total amount of feed given at any time (Figure 6).

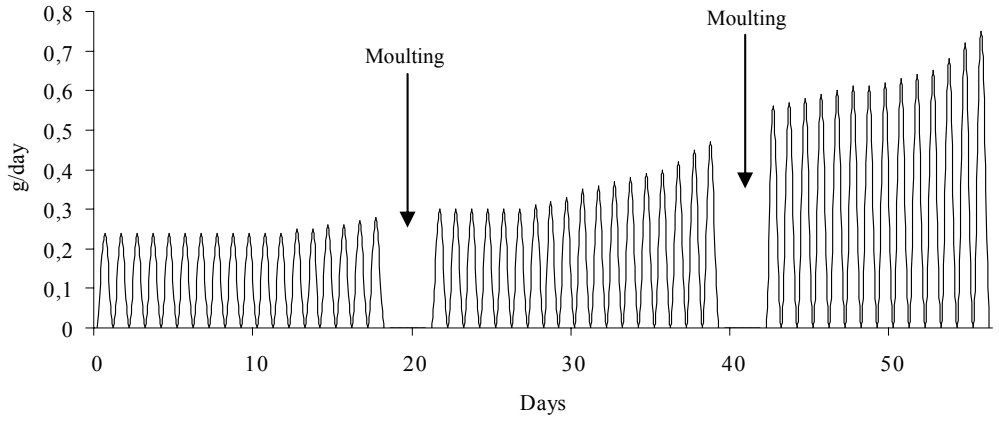

Figure 5.- Simulated feeding rate showing night feeding behaviour and no feeding during moulting

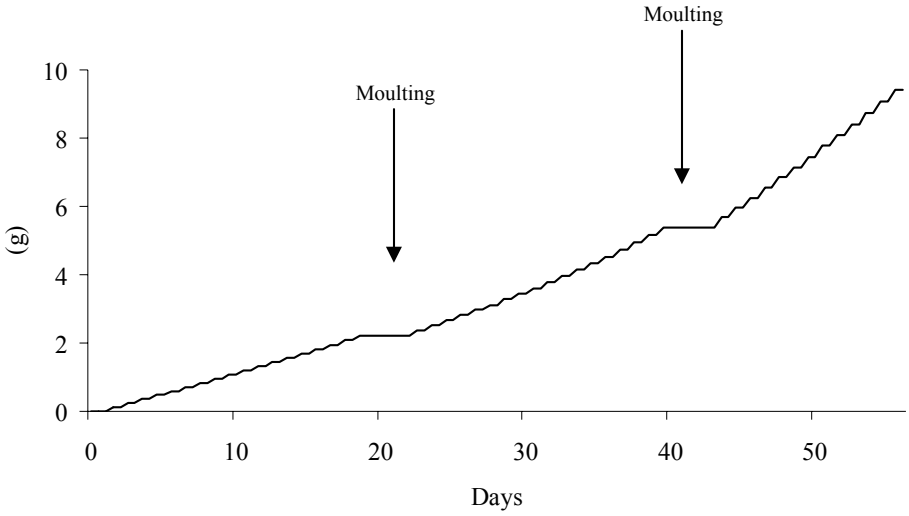

Figure 6.- Cumulative amount of feed given in simulated period

The digestion of feed ingredients (protein, carbohydrate and lipid) leads to amino acid, glucose and fatty acid, respectively. The digested amino acid, glucose and fatty acid are converted through the biosynthesis pathway into body protein and lipid. A fraction of the body protein and lipid is lost during moulting (Figure 7).

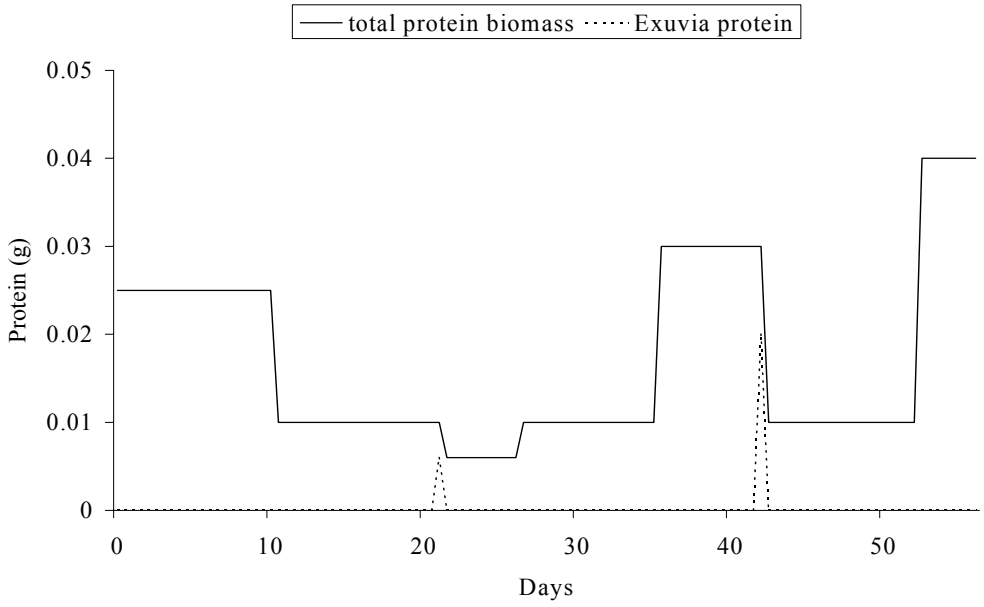

Figure 7.- Simulated total body protein and the protein loss during moulting through exuvia

Figure 8 shows the effect of moulting on the energy required for metabolism. The line of the metabolism ATP and the line of the moulting ATP show an abrupt increase on 21st and

42nd day of the simulation but the line of the routine metabolism does not show any abrupt increase on the said days.

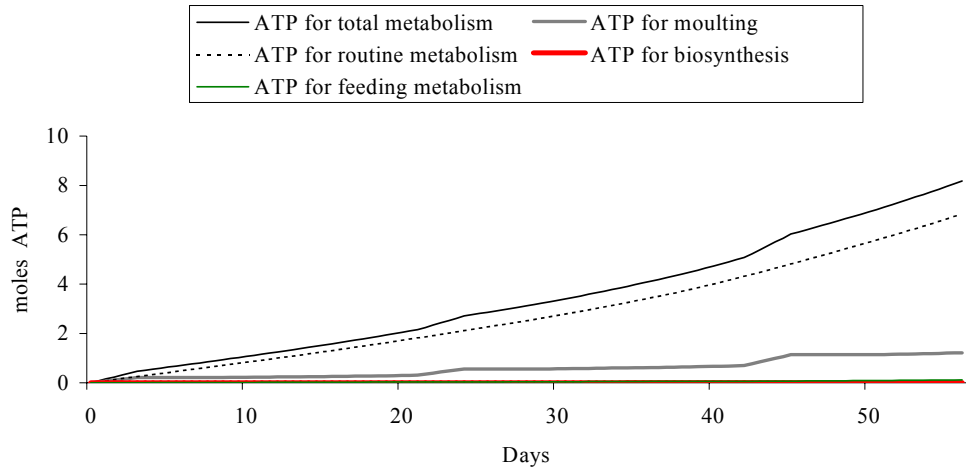

Figure 8.- Simulated ATP required for the total metabolism, moulting, routine metabolism, feeding metabolism and biosynthesis. The amount of ATP for feeding metabolism and biosynthesis is very small, that's why it cannot be seen in graph.

Crustaceans show a typical discontinuous growth pattern due to moulting. At each moulting, water is taken up to expand the new soft skeleton. Paradoxically, almost all real tissue growth or increase in individual biomass takes place during the intermoulting period when water is replaced by tissue. Figure 9 also shows discontinuous weight increase.

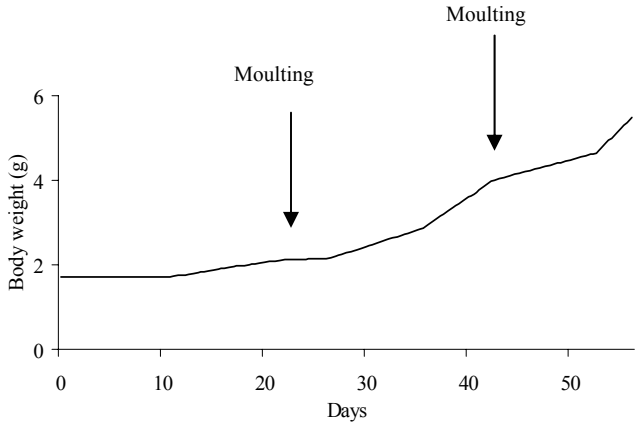

Fig 9.- Simulated body weight showing discontinuous growth

Figure 10 shows the energy breakdown into routine metabolism, feeding metabolism, biosynthesis and moulting metabolism in relation to total metabolism. The routine metabolism was constant, about 75% of the total metabolism, throughout the simulation period and the energy required for moulting was about 50% of the total metabolism

initially, but further it decreased about 15% at the end of the simulation. The fraction of the biosynthesis and the feeding metabolism was small and could not be interpreted.

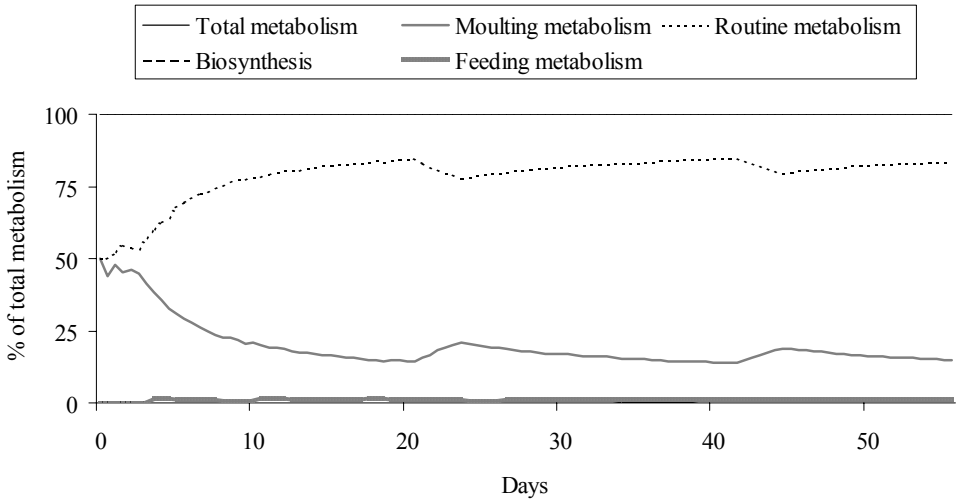

Figure 10.- Breakdown of total metabolism into the routine metabolism, feeding metabolism, biosynthesis and energy needed for moulting. The percentage for biosynthesis and feeding metabolism is so small that can not be seen in graph.

Effect of protein and feeding rate

The effect of 30, 40, 42 and 45% protein in diet on body weight were simulated. Maximum growth was observed with 45 % protein followed by 42%, 40%. No growth was observed on the 30% protein in diet (Figure 11). Forty two percent protein in the diet showed maximum growth till 25th day of the simulation after that it decreased and 45% protein diet showed higher growth performance than the 42% protein diet.

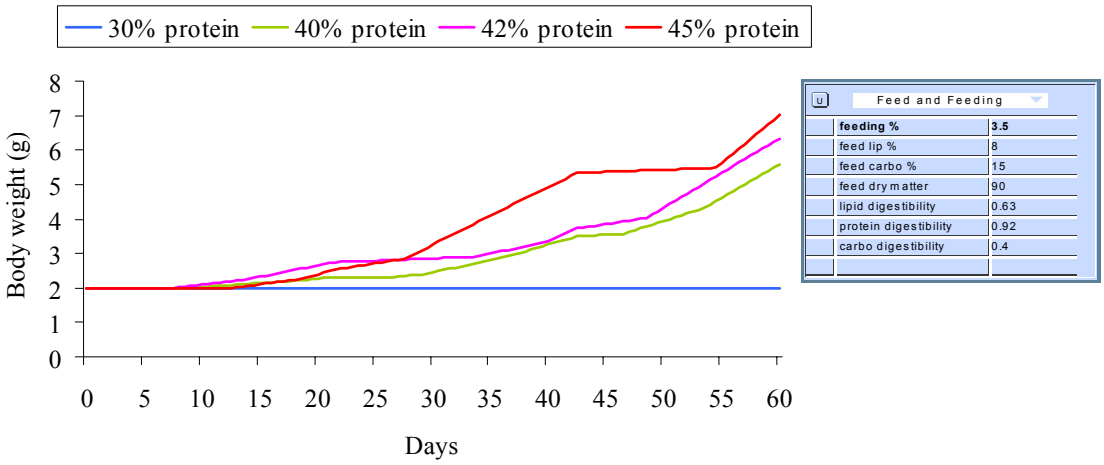

Figure 11.- Simulated effect of diet protein on body weight of shrimp

The effect of different feeding rates (3.2, 3.3, 3.4, 3.5 and 3.6 % body weight feed per day) was simulated. The highest growth was found with the 3.6% body weight feed per day followed by 3.5, 3.4, 3.3 and 3.2% of body weight feed per day (Figure 12).

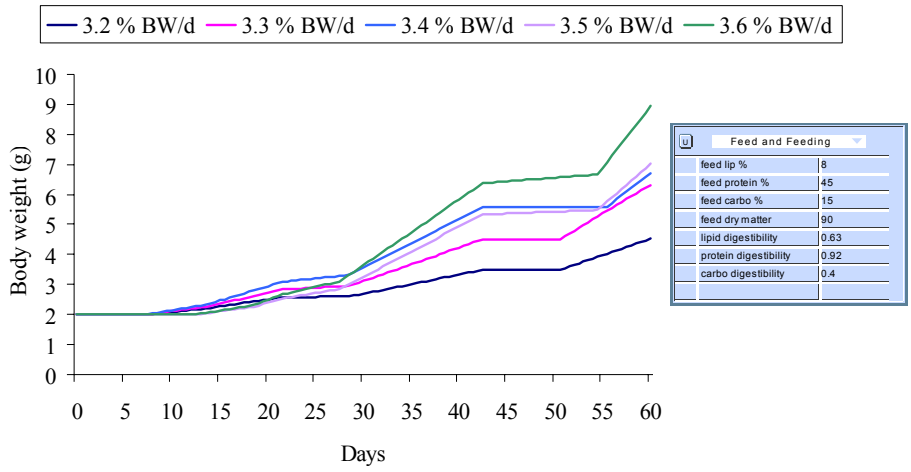

Figure 12.- Simulated effect of feeding rate on body weight of shrimp

VALIDATION OF THE MODEL

After calibration of the model, the model was validated with an independent data set (Table 8). The calculated regression equation between simulated and observed values and R^2 were then Y=1.09X+0.116 (Figure 13) and 0.967, respectively.

Table 8.- Summary of the data set used for validation

Source	Species	In.wt. (g)	Fi. wt. (g)	Period (Days)	Temp. °C	FR %BW/d	Feed composition DM %	Pro%	fat%	car%
1	*P. vannamei*	1.71	4.6	56	25.1	2.5	93.9	42.3	8.8	10*
2	*M. macleayi*	3.18	8.24	49	26.3	4	92	24.1	8*	10*
3	*M. macleayi*	3.16	6.6	56	28	2.7	92	42	8*	15
4	*M. macleayi*	2.95	7.08	56	28	2.8	92	39.1	8*	10*
5	*M. macleayi*	2.99	6.93	56	28	2.8	92	39.1	8*	10*
6	*P. monodon*	0.19	2.91	75	26	3.8	95	37	4.4	16

*=Values are assumed

1. Divakaran & Velasco (1999), 2, 3, 4, 5. Maguire & Leedow (1983), 6. Chen *et al*. (2001)

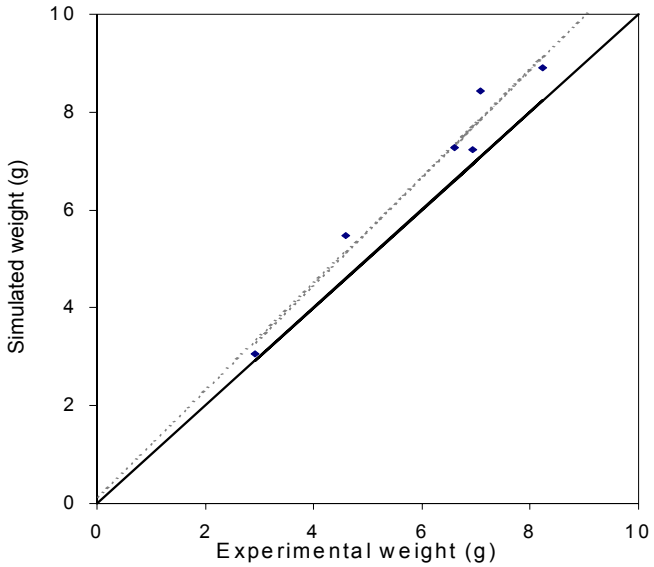

Figure 13.- Validation result for the shrimp growth. The bisector represents perfect agreement between simulated and observed value. The dotted line represents regression line (Y=1.09X+0.116) between simulated and observed weight.

Relative error

The Relative Error (RE) and the Average Relative Error (ARE) were calculated (Table 9) as described by van Dam, 1995.

Table 9.- Relative Error (RE) and Average Relative Error (ARE) for validation

Source	Rel. Error (%)
1	17.46
2	7.70
3	9.66
4	17.41
5	4.37
6	4.69
Average Relative Error (ARE)	**10.22**

1. Divakaran & Velasco (1999), 2, 3, 4, 5. Maguire & Leedow (1983),
6. Chen *et al*. (2001)

DISCUSSION

Moulting

Duration of the moulting cycle depends on the species and age of the shrimp. In the developmental stages of the shrimp, moulting occurs frequently. Dall (1986) reported the moulting cycle of *P. monodon* of about 21 days. The model is sensitive for the duration of the moulting cycle (Table 7). In this model we have assumed a constant duration of the moulting cycle i.e. 21 days (Table 4). But this assumption could lead into a wrong way to understand the insight of the moulting phenomenon. The length of the different stages of the moulting cycle could be different for the different shrimp species and could also be different at different stages of the life. So, assuming a constant value for the moulting cycle duration could be a major drawback of the model. A relation between size or weight and duration of the moulting cycle could increase the applicability of the model.

It is assumed that the increase in oxygen consumption above the metabolic level due to moulting at the different stages of the moulting cycle is constant (Table 4); insufficient information was found in the literature for different species, or on the age groups. The relation between oxygen consumption and routine metabolism during moulting for different age groups or species should be worked out further.

The loss of body constituents (protein, lipid and carbohydrates) due to moulting in the form of exuvia plays an important role in shrimp bioenergetics (Dall, 1986). The module considered the composition of the exuvia (Table 1) to calculate the out-going fat and protein from body. The ash content of the exuvia is quite high (62.77% on DM basis) (Table 1) and it constitutes mainly chitin and minerals (Travis, 1960; Welinder, 1975). The minerals are absorbed from the outside water just after the moulting (Chang, 1992). We have assumed that the formation of the new cuticle takes place slowly during the intermoulting period and does not have any effect on the rate of the biosynthesis of the body constituents.

Feed consumption

In the FGS (Fish Growth Simulation) model for *O. niloticus,* Van Dam & Penning de Vries (1995) reported that the fish eat only during the day. In the case of shrimp, it is not true. The shrimp eat part of the day. In this model we have assumed that shrimp does not eat during the day and also stop feeding for three days during moulting (two days before and one day after the moulting). But all shrimp species do not follow the same feeding behaviour. Talbot (1994) reported that *P. japonicus* gives better growth result when feed is administered at night at three hours time interval. This diurnal feeding habit of shrimp is subjected to change with species and age. An experimental study also showed that the timing of feeding for *P. vannamei* had no effect on growth (Roberston *et al.,* 1993). More detailed studies on time of feeding of shrimp in ponds are necessary.

Information on the fraction of feed consumed by shrimp was not available in the literature. So, we have also assumed that the feed given to the animals was totally consumed. This could also be a major drawback of the model and the model could over estimate the growth. This also, is an important topic for further research.

In order to increase the accuracy of the model, adequate information on the feeding behaviour of the species and a relation between the body weight and fraction of the feed eaten should be established.

Digestion and biosynthesis

The digestibility of the feed ingredients (protein, lipid and carbohydrate) has been reported in the literature (Akiyama *et al*., 1988; Sunderyono *et. al*., 1996; Forster & Gabbot, 1971; Fenucci *et al*., 1982; Lee & Lawrence, 1985; Smith *et al*., 1985; Catacutan, 1991; Lim *et al*., 1997; Condrey *et al*., 1972; Clark *et al*., 1993). The digestibility of the feed ingredients (protein, lipid and carbohydrate) depends on size, species and previous meals eaten by the shrimp.

For the model, we have considered the digestibility value of the protein from *P. monodon,* and carbohydrate and lipid from *P. vannamei*. This variation of the species could be one of the reasons for deviation of the simulated values from the experimental values.

Energy metabolism

The routine metabolism for *O. niloticus* was well described by Van Dam & Penning de Vries (1995). They found the Q_{10} value, the weight exponent and the rate constant (a) for *O. niloticus* 2, 0.8 and 0.2595, respectively. The equation for the routine metabolism used by Van Dam & Penning de Vries (1995) was redefined on the basis of Dall (1986) for *P. monodon*. We found Q_{10} value, the weight exponent and the rate constant (a) for *P. monodon* 2.55, 0.815 and 0.053019, respectively. The value of the Q_{10} for *P. monodon* is higher than for *O. niloticus* (Van Dam & Penning de Vries, 1995) and for *C. gariepinus* (Machiels, 1987).

The feeding metabolism is calculated on the basis of the SDA value for the species. Van Dam & Penning de Vries (1995) reported SDA value for *O. niloticus* 15% of the feed energy. The shrimp have lower energy requirement for the feeding. Rosas & Sanchez (1996) reported SDA value of 6.5% of the feed energy for the *P .monodon.*

Growth

In this study a discontinuous growth pattern of the shrimp was observed. A similar growth pattern was observed by Sunderyono (1996) & Lime *et al*. (1997). The growth pattern also concurs with the result of Griffiths & Wigglesworth (1993). They found that the growth in *P. vannamei* was cyclical. In the same study in Ecuador, growth peaked at new and full moon; in Columbia growth was also cyclical but it was not lunar.

The protein content of the body depends on the species and age of the fish or shrimp. The relation between protein and body weight for *O. niloticus* (van Dam & Penning de Vries, 1995) and *C. gariepinus* (Machiels, 1987) was well described, but such a relation was not found for the shrimp in the literature. The growth was calculated as a function of the protein gain. It was assumed that protein gain represents a fixed 20% of total fresh weight (growth=protein gain/0.2). Assuming a constant body protein level, could be a reason for the deviation of the simulated values from the experimental values.

Effect of the different dietary protein on growth

The simulated effect of the dietary protein levels on the growth of the shrimp showed highest performance with the 45% protein in the diet followed by 42, 40 and 30% protein in the diet. The results of the simulation concur with the results of Sedgwic (1979a). They reported optimum protein level for the growth of the *P. merguensis* from 34 to 42% of diet. Akiyama *et al*. (1988) reported optimum protein level for different shrimp species like *P. monodon* (45-50%), *P. japonicus* (52-57%) and *P. indicus* (43%). They have also given a general range of dietary protein from 30-57% for optimum growth for all species. The lower limit of the general dietary protein range supports to our study. We have also found no growth on the 30% dietary protein simulation (Figure 11).

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