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Simulation of phosphorus dynamics in an intensive shrimp culture system: effects of feed formulations and feeding strategies

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Abstract

The rapid expansion of shrimp culture has brought concern about potential environmental impacts caused by phosphorus wastes discharged from shrimp farms. This study describes development of a simulation model representing the effect of feed nutritional quality, feed physical characteristics, and feeding strategies on phosphorus dynamics in intensive Pacific white shrimp (*Litopenaeus vannamei*) culture systems, receiving dry feeds in the absence of natural productivity except bacteria. The model represents the addition of phosphorus to the culture system as dry feed, its consumption and metabolism by shrimp, and its loss in uneaten feed, particulate feed, feces, and dissolved in the water. The model was quantified using published information and unpublished research results conducted at the Shrimp Mariculture Research Laboratory of Texas A&M University. The model is multivariate, deterministic, and uses a compartment model structure based on difference equations. Evaluation of the model consisted of simulating two indoor and one outdoor experiments that examined the effect of various feed formulation and feeding parameters on total reactive phosphorus (TRP) concentration in the water. Simulated TRP generally agreed with indoor experimental results, but it was overestimated by 0.13 ppm when compared to the outdoor experiment, probably due to lack of phytoplankton representation in the model. Simulations investigating a range of possible inorganic phosphorus availabilities suggested that when apparent availability is low either animals are using other sources of phosphorus or published values are underestimated and when apparent availability is high either animals are metabolically eliminating excess assimilated phosphorus or published values are overestimated.

Keywords: *Litopenaeus vannamei*; Modeling; Phosphorus dynamics; Shrimp culture

1. Introduction

Shrimp culture is the world's most rapidly expanding warmwater aquaculture sector (Phillips et al., 1993), and this rapid expansion and intensifi-

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cation has caused increased concern regarding the discharge of effluent water rich in inorganic nutrients and organic matter that can lead to eutrophication of receiving bodies of water (Liao, 1992; Phillips et al., 1993; Stanley, 1993). Feed is the major source of nutrients and particulate loads in aquaculture effluent (Avnimelech and Lacher, 1979; Goddard, 1996). Phosphorus pollution from feeds in effluent water was identified as a major problem for commercial operations (Lin, 1995). In general, phosphorus is a limiting nutrient for plant productivity in natural conditions, thus the introduction of trace amounts of phosphorus into water can have profound effects on the structure of aquatic ecosystems (Kadlec and Knight, 1996). Phosphorus overformulation is a common practice because inorganic phosphorus availability from ingredients is not clearly known and feed manufacturers prefer to provide excess phosphorus to avoid growth problems. Reported values of apparent inorganic phosphorus availabilities (AIPA) vary in the literature (Akiyama et al., 1991; Davis et al., 1993) due to the use of different methodologies and error introduced by leaching of phosphorus from the feed and feces. Inorganic phosphorus availability is very difficult to determine but at the same time plays a critical role in determining the amount of phosphorus used by the animals and the amount of phosphorus wastes that enter the environment via effluent water.

This is an effort of Texas A&M University to develop a series of simulation models of nutrient dynamics and shrimp production. In this paper we focus on the development of a simulation model to examine the dynamics of phosphorus in an intensive shrimp culture system with low water exchange and receiving dry feeds in the absence of natural productivity except bacteria. More specifically, the model examines the effects of feed nutritional quality, feed physical characteristics, and feeding strategies on production of phosphorus wastes. After examining the correspondence between model predictions and experimental results, the model is used to identify the range of possible phosphorus availabilities that appear reasonable in terms of generating phosphorus dynamics similar to those observed experimentally.

2. Model description

The model represents the feeding behavior of an average white shrimp, *Litopenaeus vannamei* (Boone), under optimum environmental conditions. Phosphorus is supplemented in the feed in inorganic forms. However, feed ingredients contribute different amounts of organic phosphorus. Organic and inorganic phosphorus forms present different dynamics due to different specific solubilities in water and assimilation by shrimp. Organic phosphorus is tied strongly in organic compounds and therefore its solubility in water is negligible while inorganic forms, except calcium, have high solubility in the water (Windholz, 1983). Organic phosphorus absorption by the animal is generally low, especially from plant products containing phytic acid, which makes inorganic phosphorus less available biologically (Lásztity and Lásztity, 1990). Akiyama et al. (1991) estimated AIPA of 95% for monobasic forms of sodium and calcium phosphate, 45% for dibasic calcium phosphate, and 15% for tribasic calcium phosphate. However, Davis and Arnold (1994) reported lower AIPA values of 68.2% for monobasic sodium phosphate, 46% for monobasic calcium phosphate, 19.1% for dibasic calcium phosphate, and 9.9% for tribasic calcium phosphate.

The model includes two submodels of very similar structure representing organic (Fig. 1) and inorganic (Fig. 2) phosphorus dynamics. In the description that follows, O and I are used as prefixes to indicate that a given variable is represented in organic and inorganic phosphorus submodels, or both. The main difference is that the inorganic phosphorus submodel has an extra state variable representing the dissolved phosphorus in the water (IPW) due to direct leaching rates (DL), which are specific for each inorganic phosphorus form (Fig. 2). More specifically, the model represents the flow of organic and inorganic phosphorus in dry feeds (O&IPF$_i$, where i represents feed freshness categories from 1 to 6 described below), to phosphorus in uneaten feed (O&IUP), phosphorus in particulate feed (O&IPP), phosphorus consumed (O&IPC$_i$), phosphorus in feces (O&IPE$_i$), phosphorus digested (O&IPD), whole-body phosphorus (O&IPB), and inorganic dissolved phosphorus (IPW) (Figs. 1 and 2). The model is formulated as a deterministic compartment model based on difference equations programmed using STELLA® Research v. 5.1© High Performance Systems Inc. (1998), and runs on a personal computer using a 1-h time step. The initial values for all state variables are equal to 0 for all simulations except for inorganic dissolved phosphorus (IPW), which the user determines for each simulation.

The phosphorus added to the culture system as dry feed (o&if) depends on several factors (Fig. 1). Time of feeding (TF) determines the time(s) of day at which feed is added to the system. Feeding rate (Fr) and shrimp biomass (Tb), calculated as number of shrimp (SN) times individual shrimp biomass (IB), determine the total amount of feed provided during a 24-h period. Feeding frequency (FF) determines the number of times that this total daily amount of feed is divided during the 24-h period, and the amount of feed per feeding (AF) determines if these feed portions are equal or not. Dietary phosphorus level (O&IP) determines the amount of phosphorus in each feed portion. The user selects time of feeding, feeding rate, feeding frequency, amount of feed per feeding, and dietary phosphorus level. The feeding rate selected by the user can be a constant or a variable percentage of the shrimp biomass. The user also decides the feeding frequency (from 1 to 24 times per day), the percentage of the total daily amount to feed at each feeding (from 1 to 100%), and the time of day for each feeding. For example, the user might decide to feed a total of 8 kg per day using a feed with 2% of sodium phosphate monobasic and 1% of organic phosphorus, feed four times per day, with 30% of the feed provided at 0800, 20% at 1200, 20% at 1700, and 30% at 2000 h, respectively. We assume that

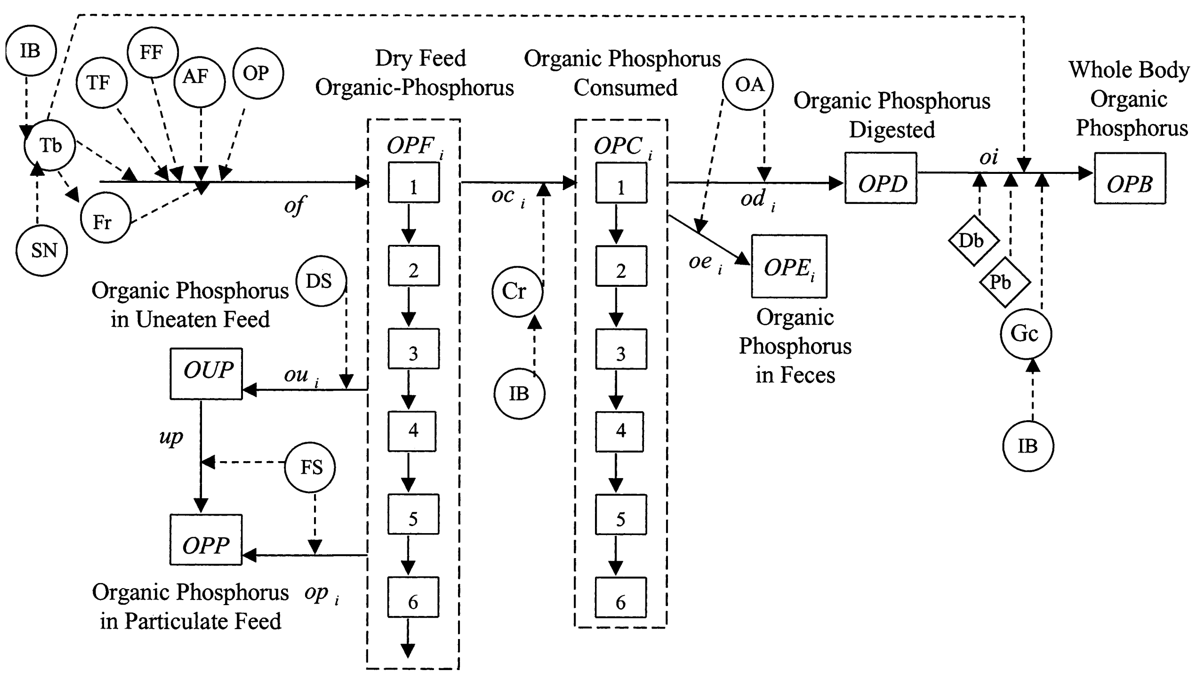

Fig. 1. Conceptual model representing organic phosphorus dynamics in an intensive shrimp culture system. State variables are denoted by three upper-case letters and represented by boxes. Driving variables are denoted by two upper-case letters and represented by circles. Constants are denoted by an upper- followed by a lower-case letter and represented by diamond shapes. Auxiliary variables are denoted by an upper- followed by a lower-case letter and represented by circles. Material transfers are denoted by two lower-case letters and represented by solid arrows. Information transfers are represented by dotted arrows.

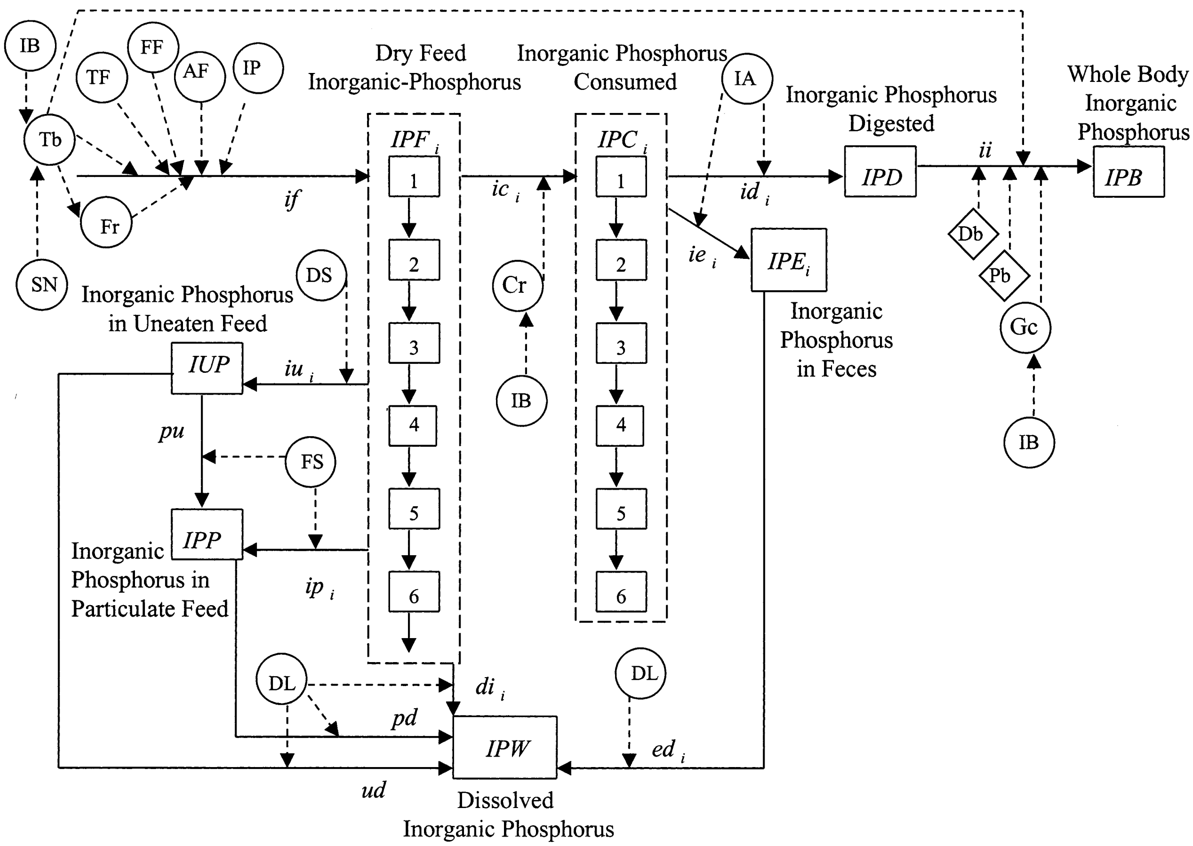

Fig. 2. Conceptual model representing inorganic phosphorus dynamics in an intensive shrimp culture system. Details as explained for Fig. 1.

simulated diets have a calcium:phosphorus ratio of 1:1–1.2 as recommended by Davis et al. (1993). The user forecasts daily individual shrimp biomass (IB) during the simulation period, according to previous experience. Finally, the user can represent shrimp numbers (SN) as a constant or as a curve based on mortality records from a given farm.

Part of inorganic phosphorus added in the feed leaches into the water (di_i) as a function of direct leaching rates (DL), which are specific for each inorganic phosphorus form (sodium dibasic 80%, sodium monobasic 85%, calcium monobasic 0.1%, calcium dibasic 0%, Divakaran per. comm.). Direct leaching is represented as a percentage, that is, (DL)% of each feed portion becomes dissolved in the water each hour. Shrimp consume (o&ic_i) part of the phosphorus in the feed added to the system as a function of a biomass-specific consumption rate (Cr, Fig. 3a). Part of the phosphorus is lost as feed disintegrates in particles (o&ip_i) as a function of feed stability (FS), which represents the percentage of feed remaining as whole pellets at the end of each hour, that is, (100–FS)% of each feed portion becomes unavailable for shrimp consumption each hour that the feed remains in the water (Figs. 1 and 2). Feed stability in the water is critical because soft, water-soaked pellets are more difficult for shrimp to manipulate and if pellets disintegrate before or during feeding nutrient loss is high (Lim and Destajo, 1979; Meyers, 1991; Lim and Cuzon, 1994; Goddard, 1996). Part of the inorganic phosphorus in particulate feed leaches into the water (pd, Fig. 2) as explained above.

Although shrimp are described as scavengers, shrimp apparently prefer fresh food over food that has been immersed in water for several hours (Hill and Wassenberg, 1985; Lim and Cuzon, 1994), perhaps because nutrient leaching decreases the nutritional quality of the pellets (Cuzon et al., 1982). This behavior is represented in the model by establishing six feed-freshness categories (i), where $i = 1–6$ represents the number of hours that a portion of feed has been in the water (Figs. 1 and 2). Shrimp first consume the freshest food available, then the next freshest, and so on. The number of hours that feed remains 'attractive' and hence available to shrimp varies depending on chemical stimulants that promote continuation of feeding once feeding has begun (Lee and Meyer, 1996). In the model, duration of the feeding stimulant effect (DS) can be specified as 1, 3, or 6 h, after which time any remaining phosphorus becomes unavailable for consumption as uneaten feed (o&iu$_i$), and subsequently as particulate feed (up Fig. 1., pu, Fig. 2) as feed disintegrates due to lack of feed stability (FS), and as inorganic dissolved phosphorus (ud) due to direct leaching rates (DL), as explained above. We assume that shrimp do not consume detritus, although Moriarty (1975) has suggested that it could have nutritional value.

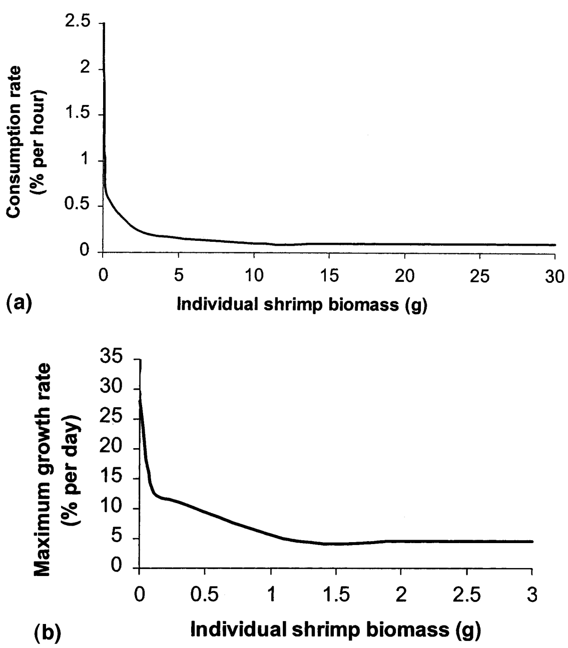

Fig. 3. (a) Consumption rate per hour (Cr) by shrimp and (b) maximum growth rate per day (Gc) of shrimp as a percent of individual shrimp biomass.

Part of the phosphorus consumed is digested (o&id$_i$) and part is excreted in the feces (o&ie$_i$) (Figs. 1 and 2). The phosphorus lost in feces is a function of apparent phosphorus availability (O&IA), which represents the percentage of the phosphorus absorbed by the animal, that is, (100−O&IA)% of each phosphorus portion consumed is excreted in the feces each hour. Part of the inorganic phosphorus in feces (IPE$_i$, Fig. 2) dissolves into the water (ed$_i$, Fig. 2) as a function of the direct leaching rates (DL). Phosphorus leaching from feed, particulate feed, uneaten feed and feces accumulates as dissolved inorganic phosphorus (IPW, Fig. 2), the initial value of which is defined by the user. Any phosphorus not excreted in the feces becomes phosphorus digested (O&IPD). In the model, at the end of each 24-h interval, the amount of phosphorus that has been digested (O&IPD$_t$) during the previous 24 h is incorporated into biomass, provided that this quantity does not exceed a daily limit. The maximum amount of phosphorus that can be incorporated in 1 day is a function of a biomass-specific growth curve (Gc, Fig. 3b), percent dry matter in the shrimp body (DB, 25%, Boyd and Teicher-Coddington, 1995), and percent phosphorus in the shrimp body (PB, 1.2%, Boyd and Teicher-Coddington, 1995):

$$\text{o\&ii} = \min\left[\left(\sum_{t=1}^{t=24} \text{oid}_i\right), ((\text{Gc} \otimes \text{DB} \otimes \text{PB}) \otimes 0.01) \otimes \text{Tb}\right] \quad (1)$$

Phosphorus incorporated each day accumulates as the phosphorus content of shrimp biomass (O&IPB$_t$).

3. Model evaluation

We evaluated the model by simulating two indoor experiments (Velasco et al., 1998) and an outdoor experiment (Hopkins et al., 1995). Because both indoor experiments used semi-purified

Table 1
Feeding rate (Fr), feeding frequencies (FF), time of feeding (TF) and amount of feed per feeding (AF) values used in the simulation of the effect of inorganic phosphorus forms and inorganic phosphorus level on total reactive phosphorus accumulation in the water (experiment 1)

Variable	Value[a]
Feeding rate (Fr)	
Days 1–16	Feed mg $PL^{-1} = 1.555 - 0.116x + 0.086x^2 - 0.003x^3$
Days 17–20	Feed mg $PL^{-1} = -6.427 + 0.805x$
Feeding frequency (FF)	15 times per day
Time of feeding (TF)	01:00, 03:00, 04:00, 05:00, 07:00, 08:00, 13:00, 14:00, 15:00, 17:00, 19:00, 21:00, and 23:00
Amount of feed per feeding (AF)	6.7% each time

[a] Where x is day on growth trial.

diets prepared in the laboratory, feed stability (FS) was assumed to be 90%, and the duration of feeding stimulant effect (DS) was assumed to be consistently high (6 h).

We used modified two-sample t-tests (Steel and Torrie, 1988) at a 95% confidence level to compare experimental total reactive phosphorus (TRP) and simulated values that were computed as (IPW/water volume in the culture system). The whole body organic (OPB, Fig. 1) and inorganic (IPB, Fig. 2) phosphorus were added together to determine total simulated phosphorus content of biomass gain (STP). These values were then compared with the phosphorus content of biomass gain (ETP) for experimental data, which was based on conversion values from Boyd and Teichert-Coddington (1995). Net phosphorus retained (NPR) for simulated (STP) and experimental (ETP) results was computed as (STP or ETP)/(total phosphorus added to the system) × 100. Comparisons of simulated and actual experiments are summarized below.

3.1. Experiment 1: effect of phosphorus form and dietary phosphorus level

This experiment examined the effect of three inorganic phosphorus forms (sodium phosphate monobasic, NaH_2PO_4 and dibasic, Na_2HPO_4, and calcium phosphate dibasic, $CaHPO_4$) and three inorganic phosphorus levels (0.4, 0.8, and 1.2%) on total reactive phosphorus (TRP) accumulation in the water (Velasco et al., 1998). Because organic phosphorus level (OP, 0.34%, Fig. 1) was constant for all treatments, variations in total phosphorus percentage in the feed was due to inorganic phosphorus level (IP, Fig. 2). Postlarvae of 0.92-mg mean initial weight were stocked at 1.5 Pl l^{-1} in 20 l of seawater. The feeding rate, feeding frequency, time of feeding, and amount of feed per feeding are summarized in Table 1. Individual shrimp biomass (IB) was represented by the exponential equation y (mg) $= 0.71 \times 10^{0.11x}$ where x is day of the growth trial. Shrimp number (SN) was represented by the linear equation y (individuals) $= 30.26 - 0.26x$ for all treatments. The simulation period was 21 days and the initial dissolved inorganic phosphorus (IPW) was 1.76 mg (Velasco et al., 1996).

There was no significant difference between simulated and experimental TRP ($P > 0.05$) (Table 2). Total reactive phosphorus increased with increases in inorganic phosphorus levels and showed no difference between monobasic and dibasic sodium forms. Calcium phosphate dibasic resulted in the lowest TRP as indicated by Velasco et al. (1998). Simulated phosphorus content of biomass gain agreed with values calculated from experimental results and remained constant regardless of phosphorus levels or forms. Simulated net phosphorus retained increased with decreasing phosphorus level as reported by Velasco et al. (1996).

3.2. Experiment 2: effect of feeding frequency

This experiment evaluated the effect of feeding frequency on TRP (Velasco et al., 1999). Individuals of 0.5 g mean initial weight were stocked in 20 l of seawater. The feeding rate (Fr) was feed g $= 0.064 + 0.006x$, where x is day of the growth trial. The feeding frequency (FF), time of feeding (TF), and amount of feed per feeding (AF) are summarized in Table 3. Shrimp survival was 100% for all treatments. Individual shrimp biomass (IB) was described by the linear equation y (g) $= 0.47 + 8.41 \times 10^{-2}x$ where x is day of the growth trial. The simulation period was 28 days.

There was no significant difference between simulated and experimental TRP ($P > 0.05$) (Table 4). Feeding frequency did not affect TRP, as reported by Velasco et al. (1999). Simulated phosphorus content of biomass gain also agreed with experimental results.

3.3. Experiment 3: effect of commercial feed in an outdoor system

This experiment evaluated the effect of a commercial feed in shrimp production and water quality (Hopkins et al., 1995). The commercial feed used had a dietary phosphorus level (IP) of 0.5% and contained dicalcium phosphate (Ziegler Bros. Inc. personal communication). Feed stability (FS) and duration of feeding stimulant effect (DS) was assumed to be 80% and 6 h, respectively. Animals of 0.33 g mean initial weight were stocked at 40 animals m^{-2} in a 1000 m^2 pond. Feeding rate (Fr), feeding frequency (FF), time of feeding (TF) and amount of feed per feeding (AF) are summarized in Table 5. Individual biomass increase (IB) was represented by the linear equation y (g) $= 0.23 + 0.10x$ and shrimp number was represented by the linear equation y (individuals) $= 4.0 \times$

Table 2
Comparison of total reactive phosphorus (TRP) concentration in the water and total phosphorus content of biomass gain and net phosphorus retained (NPR) predicted by the model with the results reported by Velasco et al. (1996, 1998) at different total dietary phosphorus levels (TP) (experiment 1)

Source	Experiment						Model		
	TP[a] (%)	TRP (ppm)	S.D.	n	ETP[b] (mg)	NPR[c] (%)	TRP (ppm)	STP[d] (mg)	NPR
NaH_2PO_4	1.2	1.67	0.26	7	10.50	28.3	1.65	10.78	27.5
NaH_2PO_4	0.8	0.94	0.11	7	10.80	42.5	0.93	10.78	41.2
NaH_2PO_4	0.4	0.19	0.05	7	9.30	65.1	0.22	9.53	70.2
Na_2HPO_4	0.8	1.05	0.14	7	10.50	42.5	0.99	10.78	41.2
$CaHPO_4$	0.8	0.54	0.20	7	9.00	42.5	0.68	8.43	41.2

[a] Total phosphorus level (organic level + inorganic level).
[b] Experimental phosphorus content of biomass gain.
[c] Net phosphorus retained.
[d] Simulated phosphorus content of biomass gain.

Table 3
Feeding frequencies (FF), time of feeding (TF) and amount of feed per feeding (AF) values used in the simulation of the effect of feeding frequency on total reactive phosphorus accumulation in the water (experiment 2).

Feeding frequency (FF)	Time of feeding (TF) (h)	Amount of feed per feeding (AF) (%)
Two times per day	08:00 and 20:00	50
Three times per day	08:00, 14:00 and 20:00	33
Four times per day	08:00, 12:00, 16:00 and 20:00	25
Four$^+$ times per day	08:00, 12:00, 16:00 and 20:00	40, 15, 15, 30
Six times per day	08:00, 10:00, 13:00, 16:00, 18:00 and 20:00	16.6
15 times per day	01:00, 03:00, 04:00, 05:00, 07:00, 08:00, 09:00, 11:00, 13:00, 14:00, 15:00, 17:00, 19:00, 21:00, and 23:00	6.7

Table 4
Comparison of total reactive phosphorus (TRP) concentration in the water and phosphorus content of biomass gain predicted by the model (STP) with the experimental results (ETP) reported by Velasco et al. (1999) (experiment 2)

FF	Experiment				Model	
	TRP (ppm)	S.D.	*n*	ETP (mg)	TRP (ppm)	STP (mg)
2	1.41	0.05	6	5.45	1.56	4.80
3	1.37	0.05	6	5.45	1.52	4.85
4	1.38	0.09	6	5.40	1.52	4.81
4^+	1.44	0.07	6	5.43	1.52	4.91
6	1.43	0.11	6	5.28	1.52	4.75
15	1.51	0.12	6	5.50	1.52	5.51

$10^4 - 12.99x$ where x is day of the growth trial. The simulation period was 155 days.

Simulated TRP was 0.13 ppm, significantly higher than the observed value ($P < 0.05$) (Table 6). The overestimation of TRP may be due to lack of representation in the model of phytoplankton uptake of inorganic phosphorus. Simulated phosphorus content of biomass gain and net phosphorus retained were similar to experimental results.

In summary, the model seems capable of predicting TRP and whole-body phosphorus of shrimp under a variety of dietary phosphorus levels and sources, and feeding frequencies.

4. Examination of inorganic phosphorus availability ranges

To identify the range of inorganic phosphorus availability (IA) that predicts reasonable phosphorus dynamics, a sensitivity analysis using three series of simulations using three different sources of phosphorus (sodium phosphate monobasic, sodium phosphate dibasic, and calcium phosphate dibasic) was conducted. Each series consisted of three simulations in which IA (Fig. 2) was set at the higher end (simulation 1), midpoint (simulation 2), and lower end (simulation 3) of the ranges of published values for each phosphorus source as follows:

1. Sodium phosphate monobasic: 95% (Akiyama et al., 1991) to 68.2 (Davis et al., 1993).
2. Sodium phosphate dibasic: 45% (Akiyama et al., 1991) to, 19.1% (Davis et al., 1993).
3. Calcium phosphate dibasic: 45% (Akiyama et al., 1991) to 19.1% (Davis et al., 1993).

All other parameters were set as in experiment 1 described by Velasco et al. (1998). During each simulation, total whole body phosphorus (STP)

Table 5
Summary of the parameters used in the simulation of shrimp production and water quality in an outdoor system (experiment 3)

Variable	Value
Feeding rate (Fr)	8 kg per day
Feeding frequency (FF)	Six times per day
Time of feeding (TF)	08:00, 10:00, 12:00, 14:00, 16:00 and 20:00
Amount of feed per feeding (AF)	16.7% each time

Table 6
Comparison of total reactive phosphorus concentration in the water, phosphorus content of biomass gain, and net phosphorus retained predicted by the model and reported by Hopkins et al. (1995) (experiment 3)

Parameters	Experiment	Model
Total reactive phosphorus (TRP ppm)	0.43 (S.D. 0.17)	0.56
Simulated total body phosphorus (STP g)	–	2200
Experimental total body phosphorus (ETP g)	1848	–
Net phosphorus retained (NPR%)	9	10

Table 7
Effect of sodium phosphate monobasic, sodium phosphate dibasic, and calcium phosphate dibasic availability (IA) on total whole body phosphorus (TP) and total reactive phosphorus (TRP) concentration in the water

Experimental TP (mg)	Simulated TP (mg)				Experimental TRP (ppm)	Simulated TRP (ppm)			
Sodium phosphate monobasic									
	IA:	95	81	68		IA:	95	81	68
10.80		11.10	10.78	9.60	0.94		0.91	0.93	0.95
Sodium phosphate dibasic									
	IA:	45	32	19		IA:	45	32	19
10.80		12.00	10.78	8.60	1.05		0.97	0.99	1.01
Calcium phosphate dibasic									
	IA:	45	32	19		IA:	45	32	19
10.80		14.73	10.78	10.2	0.54		0.50	0.70	0.90

was monitored and compared to experimental phosphorus content in biomass gain (ETP). Because organic phosphorus level (OP, Fig. 1) and organic phosphorus availability (OA, Fig. 2) were constant, the whole body organic phosphorus (OPB, Fig. 1) was constant in all simulations, and therefore, any change in ETP was due to inorganic whole body phosphorus (IPB, Fig. 2). Inorganic dissolved phosphorus (IPW, Fig. 2) also was monitored in terms of TRP and compared to the experimental TRP results.

4.1. Effect of sodium phosphate monobasic availability

At the lowest IA value STP decreased 11% below the estimated value, whereas increasing IA increased STP by 3%. Experimental and simulated TRP were similar regardless of IA values used (Table 7).

4.2. Effect of sodium phosphate dibasic availability

At the lowest IA value STP decreased 20% below the estimated value, whereas increasing IA increased STP by 11%. Experimental and simulated TRP were similar regardless of IA variations (Table 7).

4.3. Effect of calcium phosphate dibasic availability

At the lowest IA value STP decreased 1% below the estimated value, whereas increasing IA increased STP by 36%. At the highest IA value simulated TRP was similar to experimental TRP. However, at middle and lowest IA values simulated TRP was 26 and 67% higher, respectively, than experimental TRP (Table 7).

In summary, when IA was decreased STP tended to be lower than ETP especially when using sodium forms (Table 7). Some authors have suggested that bacteria could be a link between nutrients in organic matter and detritivores, including crustaceans (Moriarty, 1975; Phillips, 1984). Moreover, coprophagy has been identified as a mechanism to obtain nutrients and vital elements used by many marine animals including the shrimp *Litopenaeus setiferus* (Frankenberg and Smith, 1967). Johannes and Satomi (1966) found that fecal material of a marine crustacean, *Palaemonetes pugio*, contained assimilable organic matter and when the feces were consumed and digested the phosphorus content was reduced by 44%. Moreover, even if fecal material is predominantly indigestible material, it may contain bacteria and other microorganisms rich in nutrients available to the animal (Newell, 1965). Also, as indicated by the National Research Council

(1983), shrimp are able to assimilate minerals directly from the aquatic environment. This could explain how the animal meets its phosphorus requirement when reared on diets with low phosphorus availability in waters not depleted of phosphorus.

In contrast, when IA was increased STP tended to be higher than ETP especially when using dibasic forms of phosphorus (Table 7). This may suggest that IA could be responding to a physiological feedback to balance phosphorus requirement and phosphorus from the diet. Comparison of simulated and experimental results emphasize the need for a holistic approach to better estimate apparent organic and inorganic phosphorus availability. It seems necessary to study availability of organic and inorganic phosphorus sources at different levels concomitantly with phosphorus in the water, feed, feces, and the shrimp body in order to obtain accurate digestibility coefficients.

5. Effect of commercial diets on total reactive phosphorus

Commercial feeds often combine two different forms of inorganic phosphorus. We used the model to examine the effect of two commercial sources of inorganic phosphorus on total reactive phosphorus (TRP) concentration in the water, at six different levels (0.3, 0.6, 0.9, 1.2, 1.5 and 1.8%) of inclusion on the feed. One of the commercial sources of inorganic phosphorus had 66% of calcium phosphate monobasic and 33% of calcium phosphate dibasic, while the other one had 33% of calcium phosphate monobasic and 66% of calcium phosphate dibasic. Feed had an organic phosphorus level (OP) of 0.83% with an availability (OA) of 4%. All other parameters were set to represent a commercial scenario in a one hectare culture system (water volume 10 000 l), juveniles (0.5 g) were stocked at a density of 50 animals m^{-2} during 4 months (2880 h). Individual shrimp biomass (IB) was represented by the linear equation y (g) $= 0.365 + 0.134x$, where x represents day of the growth period. Shrimp number (SN) was represented by the linear equation y (individuals) $= 5.01 \times 10^5 - 1260x$, where x is day of the growth trial. Feeding rate was represented by the logarithmic equation y (%) $= 0.13 - 0.10 \log x$, where x is individual shrimp biomass. Feeding frequency, time of feeding and amount of feed per feeding were three times per day at 08:00, 12:00 and 17:00 h. and 0.33% each time, respectively. Feed stability (FS) was 80% and duration of feeding stimulant effect (DS) was 6 h.

Results showed that TRP increase with increasing calcium phosphate dibasic level (Table 8). The

Table 8
Total reactive phosphorus (TRP) concentration in the water and total phosphorus content of biomass gain predicted by the model using two sources of calcium phosphate at different dietary inorganic phosphorus levels (IP)

IP (%)	Commercial feeds							
	33% monobasic/66% dibasic				66% monobasic/33% dibasic			
	TRPM[a] (ppm)	TRPD[b] (ppm)	STP[c] (kg)	TTP[d] (kg)	TRPM[a] (ppm)	TRPD[b] (ppm)	STP[c] (kg)	TTP[d] (kg)
0.3	0	23 838	62	18	0	11 919	62	18
0.6	0	47 676	62	18	0	23 838	62	18
0.9	0	71 514	62	18	0	35 757	62	18
1.2	0	95 353	62	18	0	49 121	62	18
1.5	0	119 191	62	18	0	59 595	62	18
1.8	0	143 270	62	18	0	71 514	62	18

[a] Total reactive phosphorus from the monobasic form.
[b] Total reactive phosphorus from the dibasic form.
[c] Simulated phosphorus content of biomass gain.
[d] Theoretical phosphorus content of biomass gain.

calcium phosphate monobasic did not contribute to TRP due to its insolubility in the water. The very high TRP predicted by the model probably would never be measured in real situations because the model represents 0% water exchange and did not include other biotic (phytoplankton, algae) and abiotic (soil) factors that could affect TRP in the water. This suggests that the model could be useful to show the potential inorganic phosphorus load from a shrimp production cycle that sometimes is masked in real situations due to continuous water exchange, retention in soil and use by other biota in the culture system.

Phosphorus in total biomass gain (Table 8) was above theoretical values and similar for all treatments. This result suggests that organic phosphorus, in spite of its low availability, may satisfy shrimp phosphorus requirements under the conditions simulated, unless there are unknown interactions among inorganic and organic phosphorus sources that further affect its availability. It would be interesting to investigate how shrimp regulate this ‘excess’ in dietary phosphorus and what other biotic components in the system also are using inorganic phosphorus, thus affecting the TRP concentration in the water (phytoplankton, algae, etc.).

6. Conclusions

The present model representing marine shrimp (*L. vannamei*) culture can predict general patterns of phosphorus dynamics in intensive systems receiving dry feed in the absence of natural productivity except bacteria. Effects of feed nutritional quality, feed physical characteristics, and feeding strategies on whole-body phosphorus, and organic and inorganic phosphorus dynamics were predicted well by the model, which provided insight into effects of interactions among the feed and feeding parameters evaluated. Differences between observed and simulated TRP in the outdoor experiment may be due to the lack of a phytoplankton component in the model.

The model can be used to examine the relative importance of each parameter on phosphorus dynamics. Identification of these processes through simulation can provide valuable information for implementation of research programs and management schemes to control phosphorus wastes in the culture system. The model could be improved by including better estimates of inorganic phosphorus leaching rates, apparent availability coefficients for each phosphorus form, and a phytoplankton component.

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