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Development of a growth model for penaeid shrimp

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Abstract

An individual growth model for penaeid shrimp is presented. The main physiological processes simulated were: ingestion, assimilation, faeces production, respiration and female reproduction. The model was used to quantify the most important physiological processes involved in growth and also to examine the effect of food availability and water temperature on shrimp final weight.

The simulation reproduces the typical pattern of growth of penaeid shrimp, characterised by a rapid weight gain during the early life stages and by the achievement of asymptotic length in adults.

The ingestion and respiration rates increased as the animal grew but the weight-specific rates decreased with an increase of shrimp weight.

A sensitivity analysis showed that the model does not produce differences at a 10% change in juvenile food availability. On the other hand, a change of water temperature of the same magnitude had an effect on shrimp final weight.

The model was developed in the visual simulation software Powersim™.

The individual growth model presented in this paper may be integrated into population dynamics models in order to simulate the biomass and density throughout the stages of the shrimp life cycle; such models may be usefully applied both to penaeid aquaculture and to management of wild fisheries.

Keywords: Penaeid; Individual model; Pond culture; Mangroves; Aquaculture; Visual simulation

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1. Introduction

Shrimp growth is a discontinuous process regulated by the moult cycle, which is made up of short moult periods of rapid growth and of longer intermoult periods when no growth occurs. The duration of the moult cycle depends on species and size, and it influences the morphology, physiology and behaviour of these animals (Bureau et al., 2000; Vega-Villasante et al., 2000). Growth depends on sex, stage and environmental factors such as food quantity and quality, water temperature and salinity (Dall et al., 1990).

Due to the economic importance of penaeid shrimp worldwide, particularly in aquaculture, a great effort to understand the growth biology of *Penaeus* spp. has been made in recent years. This includes studies on the influence of environmental factors such as temperature (Wyban et al., 1995; Miao and Tu, 1996; Ye et al., 2003; López-Martínez et al., 2003), salinity (Lemos et al., 2001) and lunar cycles (Griffith and Wigglesworth, 1993) on shrimp growth.

The valuable information presented in those studies may be synthesised and integrated into general models

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in order to simulate the growth of *Penaeus* individuals. These models provide more detailed information concerning physiological processes and their quantification in terms of bioenergetics. The simulation of individual growth can also be used to study the population dynamics through the development of population models that predict population growth and biomass in a given ecosystem. These models are useful for aquaculture planning and management as they provide estimates of growth conditioned by different factors and allow the selection of the conditions that provide a better growth potential.

Despite the great economic importance of these animals and their suitability to aquaculture, only a few models have been developed to simulate individual growth of penaeid shrimp. Growth simulations for penaeid shrimp are based on single-equation models such as the von Bertalanffy (Wang, 1998; Xiao, 1999) and Gompertz growth equations (Jackson and Wang, 1998; Xiao, 1999), bioenergetic models (Mishra et al., 2002) or the Fuzzy Inductive Reasoning (FIR) approach (Carvajal and Nebot, 1998).

The main objectives of the present work are:

(i) To quantify the most important physiological processes involved in growth;
(ii) To analyse the effect of environmental forcing functions on shrimp growth;
(iii) To simulate penaeid shrimp growth by means of an individual growth model;
(iv) To describe how such a model may be integrated into a coupled biogeochemistry–population dynamics model for use in aquaculture management.

2. Materials and methods

2.1. Study site

The model was applied to Maputo Bay (Fig. 1), a large (area: 1200 km^2; volume: 7200×10^6 m^3), shallow (mean depth: 7 m) mesotidal system in southern Mozambique (26° 1′ S, 32° 46′ E), where an important (400 t year^{-1}) shallow-water shrimp fishery exists. The

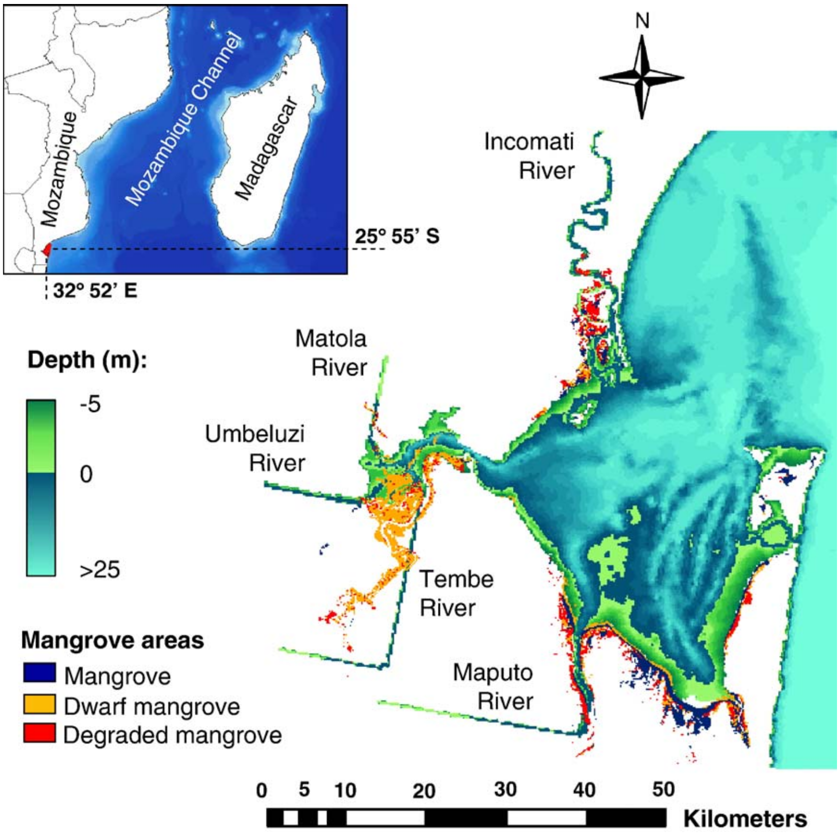

Fig. 1. Location of the study area, showing mangrove areas and bathymetry.

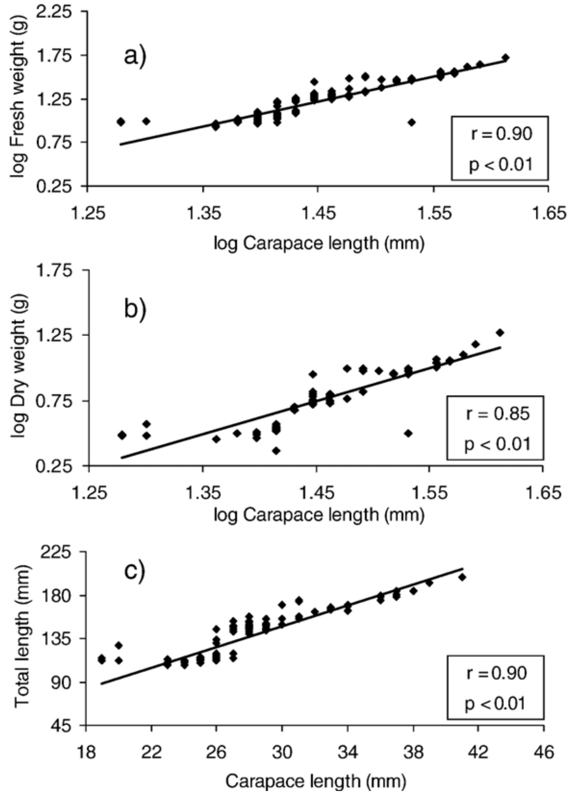

Fig. 2. Morphometric relationships for *P. indicus*: Fresh weight–carapace length (a); Dry weight–carapace length (b) and Total length–carapace length (c).

most abundant species are *Penaeus indicus* and *Metapenaeus monoceros*, which together form 85% of the annual catch in the bay (Palha de Sousa, 1996).

There are five major rivers in the Maputo Bay drainage basin: the Maputo, Incomati, Matola, Umbeluzi and Tembe (Fig. 1). The estuaries of these rivers contain mangrove habitats (Fig. 1), providing important areas for shrimp development (Macia, 1990; Rönnbäck, 1999).

The individual growth model was applied to *P. indicus*, as this species accounts for 60% of the total shrimp catch in the bay (Macia, 1990), but the conceptual framework is applicable to Penaeids in general.

2.2. Laboratory work

Biometric relationships for *P. indicus* were determined for application in the growth model. Commercially frozen individuals were defrosted at room temperature for 12 h, identified, weighed and measured (total length and carapace length). The dry weight was determined by oven-drying at 60 °C for 48 h.

The weight–length (log-transformed) and total length–carapace length relationships were determined by regression analysis, with no sex differentiation due to the low number of males sampled (Fig. 2).

Table 1 shows the weight–length and total length–carapace length relationships obtained for *P. indicus*.

2.3. Growth model

The development of the model for penaeid growth involved the following steps:

1. Conceptualisation based on the main physiological processes that influence growth and parameterisation according to the existing literature regarding penaeid ecology and life cycle;
2. Implementation and testing in a visual modelling platform;
3. Validation of the model results.

2.4. Model conceptualisation and parameterisation

The individual model was developed to simulate the growth of a penaeid shrimp from the juvenile stage to the end of the life cycle. Shrimp larval stages (nauplius, zoe and mysis) have a very short duration (less than 3 weeks) (Haywood et al., 1995), and were not included in the model.

The growth model includes five physiological processes: ingestion, assimilation, elimination, respiration and female reproduction, and is forced by water temperature and food availability (Fig. 3).

2.5. Ingestion

Daily ingestion is simulated after Ivlev (1945) (Eq. (4)). In this equation the quantity of food ingested by shrimp increases with the concentration of food

Table 1
Morphometric relationships obtained for *P. indicus* (*n*: number of individuals sampled, *r*: correlation coefficient)

Relationship	*n*	Equation	*r*	
Weight–length				
Fresh weight (FW) vs. Carapace length (CL)	136	$\log FW = 2.8 \log CL - 2.9$	0.90	(1)
Dry weight (DW) vs. Carapace length (CL)	54	$\log DW = 2.5 \log CL - 2.9$	0.85	(2)
Length–length				
Total length (TL) vs. Carapace length (CL)	128	$TL = 5.4 CL - 14.3$	0.90	(3)

Size-range: 19–41 mmCL.

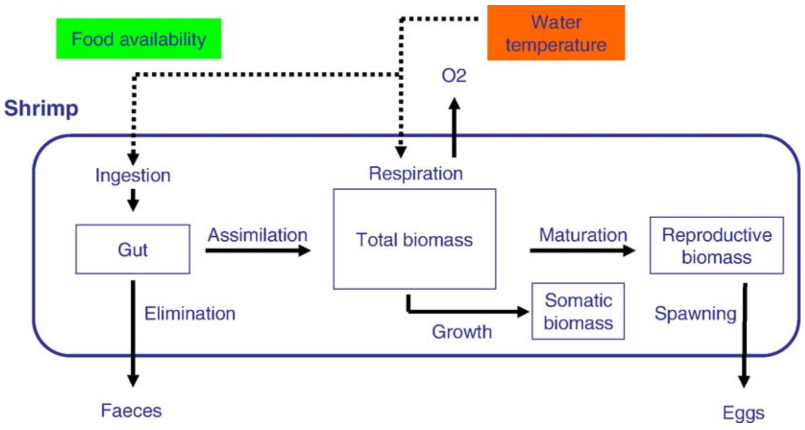

Fig. 3. Conceptual diagram of the individual growth model (dashed arrows correspond to influence of forcing functions on physiological processes).

available (expressed as dry weight: DW), up to a maximum ration, $R_{\max}$.

$$I = R_{\max}(1 - e^{-kF}) \tag{4}$$

where:

I	Ingestion (gDW day^{-1})
$R_{\max}$	Maximum ration (gDW day^{-1})
k	Consumption efficiency (mgDW^{-1} m^{2})
F	Food (mgDW m^{-2})

$R_{\max}$ is a function of both allometry and water temperature (Eq. (5)):

$$R_{\max} = f(B_t)f(T) \tag{5}$$

where:

B_t	Total biomass (gDW)
T	Temperature (°C)

The maximum ration due to allometry was calculated using Eq. (6), obtained for *P. subtilis* (Nunes and Parsons, 2000):

$$f(B_t) = 0.09(\phi B_t)^{0.62} \tag{6}$$

where:

ϕ	Conversion factor from dry weight to fresh weight (dimensionless)

The effect of water temperature on food consumption was simulated as a positive relationship over a given temperature range, followed by a decrease of food intake beyond the optimal temperature (Niu et al., 2003; Wasielesky et al., 2003; Kumlu and Kir, 2005). Wasielesky et al. (2003) found that food consumption increased with temperature but stabilized from 26 °C to 32 °C. Additionally, Hewitt and Duncan (2001) observed that the mean daily consumption of *P. japonicus* was highest at 32 °C (range 28 °C–36 °C). A second order polynomial was used to describe this relationship in the model, based on data from Wyban et al. (1995) and on the assumption that the shrimp ration is maximal at 32 °C. (Eq. (7)).

$$f(T) = \frac{-0.02T^2 + 1.44T - 17.41}{R_{32}} \tag{7}$$

where:

R_{32}	Ration at 32 °C

Several authors refer that larger sizes and faster growth rates are observed in females (Dredge, 1990; Chow and Sandifer, 1991; Buckworth, 1992), therefore the model also takes sexual dimorphism into account. This difference was represented as a lower food intake for males than females (Hansford and Hewitt, 1994). Growth of male animals (expressed as carapace length) was estimated using the von Bertalanffy equation, parameterised from Le Reste and Marcille (1976) (Eq. (8)):

$$L_t = L_\infty\left[1 - e^{-K(t-t_0)}\right] \tag{8}$$

where:

L_t	Carapace length at time t (mm)
L_∞	Asymptotic carapace length (mm)
K	Growth coefficient (day^{-1})
t	Age (day)
t_0	Starting age (day)

The growth curve expressed as carapace length was converted to fresh weight using Eq. (1) and used to parameterise the maximum ration equation for male penaeids by tuning the coefficients given in Eq. (6) to optimally correlate model biomass outputs to the growth curve in Fig. 4 (Eq. (9)):

$$f(B_t) = 0.06(\phi B_t)^{0.68} \tag{9}$$

2.6. Assimilation/faeces production

Part of the food ingested is assimilated in the gut and the remaining fraction is eliminated as faeces. The amount of food assimilated is dependent on the gut content and assimilation efficiency (Eq. (10)).

$$A = GA_{\mathrm{e}} \tag{10}$$

where:

A	Assimilation (gDW day^{-1})
G	Gut content (gDW)
A_{e}	Assimilation efficiency (day^{-1})

2.7. Respiration

Shrimp metabolic losses were assumed to be due to oxygen consumption (respiration) and dependent on the individual biomass and temperature. Respiration was simulated following the equation derived by Dall (1986) for *P. esculentus* (Eq. (11)), which gives the weight-specific respiration rate.

$$M_{\mathrm{w}} = 0.05\mathrm{e}^{0.07T}(\phi B_t)^{-0.185} \tag{11}$$

where

M_{w}	Weight-specific oxygen consumption (day^{-1})

The weight-specific respiration was then multiplied by the dry weight of the animal to give the total respiration, M, expressed as gDW day^{-1}.

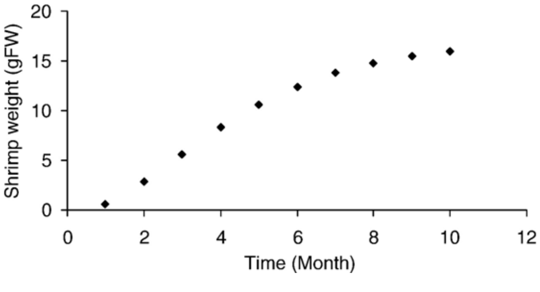

Fig. 4. *P. indicus* male growth curve estimated by the von Bertalanffy equation (Le Reste and Marcille, 1976).

2.8. Gut content and total biomass

The balance between ingestion and assimilation determines the gut content (Eq. (12)):

$$\frac{\mathrm{d}G}{\mathrm{d}t} = R_{\max}\left(1-\mathrm{e}^{-kF}\right)-GA_{\mathrm{e}} \tag{12}$$

Where the first term on the right hand side corresponds to the ingestion and the second to the assimilation. The change in total individual biomass (Eq. (13)) is thus:

$$\frac{\mathrm{d}B_t}{\mathrm{d}t} = GA_{\mathrm{e}}-M-S \tag{13}$$

where:

M	Respiration (gDW day^{-1})
S	Spawning (gDW day^{-1})

2.9. Reproduction and non-somatic biomass

To describe female reproduction two processes were considered: maturation and spawning. The gonadosomatic index was employed to simulate gonad growth as it is widely used to assess the maturation state in these animals (Cha et al., 2002). A constant rate of gonad growth over the maturation period was considered. The non-somatic biomass may be described according to Eq. (14):

$$\frac{\mathrm{d}B_{\mathrm{g}}}{\mathrm{d}t} = B_t G_{\mathrm{SI}} \tag{14}$$

where:

B_{g}	Reproductive (non-somatic) biomass (gDW)
G_{SI}	Gonadosomatic index (day^{-1})

The somatic tissue biomass B_{s} may then be calculated as B_t-B_{g}.

The loss of biomass due to spawning (S) was calculated by multiplying the number of eggs produced (Eq. (15)) by the mean weight of a single egg (Eq. (16)).

$$N = 9.3C_{\mathrm{L}}^{2.8} \tag{15}$$

where:

N	Number of eggs produced (day^{-1})
C_{L}	Carapace length (mm)

$$S = NE_{\mathrm{w}} \tag{16}$$

where:

E_{w}	Single egg weight (gDW)

Where available, ecological parameters determined for *P. indicus* in Maputo Bay were used to parameterise the model. Data from other sites and species were included when necessary (Table 2).

2.10. Model implementation

Due to an ontogenic shift of feeding between the juvenile and adult stages (Rothlisberg, 1998), distinct dietary requirements were considered and this distinction was made as a function of carapace length. Since *P. indicus* juveniles live in mangroves (Macia, 2004) and their diet is mainly composed of primary producers, microphytobenthos biomass was used as a proxy to represent the food supply for this stage. The food supply was simulated as a forcing function by means of a time series for the Maputo Bay mangrove areas. Adults consume the second trophic level, and as they are epibenthic their diet consists of microinvertebrates such as gastropods and polychaetes (Rothlisberg, 1998). Adult diet was not explicitly simulated and was assumed to be non-limiting.

Due to the fact that the different life stages have distinct salinity preferences, this variable was not simulated in the model, based on the assumption that each stage grows in the preferred salinity range.

The simulation period was one and a half years, a typical maximum life span for many tropical penaeids (Dall et al., 1990).

The model was implemented in the visual simulation package Powersim™, running on the Windows™ operating system. A 2-h timestep was used and the model equations were solved using an Eulerian integration scheme.

Table 2
Parameters used in the growth model

Parameters	Symbol	Units	Value
Dry weight	DW	g	–
Fresh weight	FW	g	–
Dry weight/fresh weight	Φ	–	5
Food availability	F	mgDW m^{-2}	Time series
Consumption efficiency	k	mgDW^{-1} m^{2}	0.12
Asymptotic length	L_∞	mm	29.9
Growth coefficient	K	day^{-1}	0.013
Hypothetical age at size 0	t_0	day	0.06
Assimilation efficiency	A_e	day^{-1}	0.8
Water temperature	T	°C	26
Gonadosomatic index	GSI	day^{-1}	0.05
Egg weight	E_w	gDW	2×10^{-6}

Parameter values were taken from the literature (e.g. Le Reste and Marcille, 1976; Jorgensen et al., 1991) and tuned to calibrate the model.

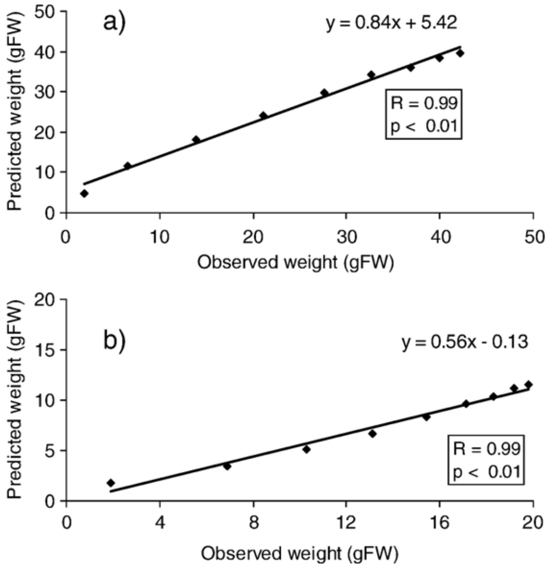

Fig. 5. Correlation between observed (Le Reste, 1978) and simulated weight for females (a) and males (b).

2.11. Sensitivity analysis

A sensitivity analysis of the effect of the juvenile food availability (food is not a limiting factor for later stages) and water temperature on final individual weight was carried out using a 10% change in the values of these forcing functions (Jorgensen and Bendoricchio, 2001).

3. Results and discussion

3.1. Validation

The model was validated with growth data obtained for *P. indicus* in Madagascar by Le Reste (1978) (Fig.

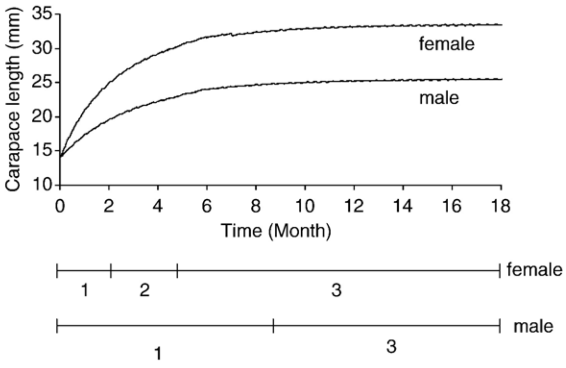

Fig. 6. Model results for shrimp carapace length showing the different life stages based on carapace length (1—juvenile; 2—subadult; 3—adult).

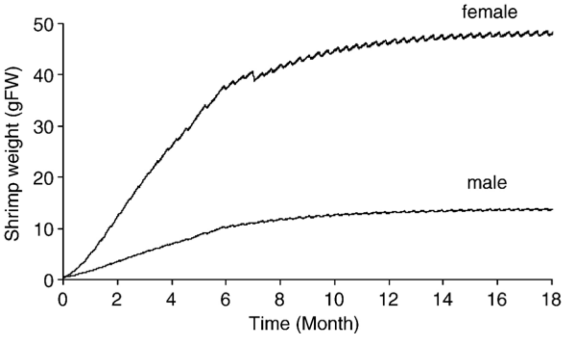

Fig. 7. Model results for shrimp fresh weight over the simulation period.

5). This dataset was selected due to the geographic proximity to the study area and the lack of available individual growth data for *P. indicus* in Maputo Bay. The linear regression between the observed data and model results gave a correlation coefficient of 0.99 for both males and females ($p<0.01$ in both cases).

3.2. Simulations

Figs. 6 and 7 show the simulated shrimp growth curve, expressed as carapace length and fresh weight respectively. The juvenile stage in this species has an upper carapace length limit of 25 mm (Benfield et al., 1990); as *P. indicus* females attain sexual maturity for a carapace length range of 30–33 mm (Cristo and Mascarenhas, 1986), the (immature) subadult individuals fall in the 25–30 mm carapace length range; finally, shrimp with a carapace length greater than 30 mm shrimp are considered adults. These stages are indicated in Fig. 6.

The model reproduces the typical pattern of growth of a penaeid shrimp, characterised by a rapid weight gain during the juvenile stage followed by the achievement of asymptotic length of adults (Dall et al., 1990).

The female juvenile stage simulated in the model lasts for about 2 months, which agrees with the time period described for this stage by Dall et al. (1990) and Ehrhardt et al. (2001). For males the upper limit for the juvenile stage must be less than 25 mm as the maximum size is about 30 mm carapace length (Le Reste and Marcille, 1976; Le Reste, 1978). The individual reaches an asymptotic length after 6 to 8 months, which is in accordance with data from Rothlisberg (1998).

The sexual dimorphism is confirmed by a larger size and a faster growth rate of females (0.70% body weight day^{-1}; 0.54% carapace length day^{-1}) than males (0.47% body weight day^{-1}; 0.44% carapace length day^{-1}).

Although different growth curves for the two sexes were obtained, more research is needed in order to test the assumption that food intake is higher in females than males.

Table 3 presents a comparison between the rates of ingestion and respiration for each development stage. The ingestion rate increases as the animal grows but the weight-specific rate decreases. This is observed for many other animals and exploited in shrimp aquaculture, where the relative amount of food supplied decreases with an increase in shrimp weight (Nunes, 2000; Avalle et al., 2003). This may be related to increased assimilation efficiency with growth and with distinct enzymatic activity at the different growth stages (Gamboa-Delgado et al., 2003).

Similarly, the respiration rate is greater for larger animals and lower when considering the relative respiration rate (percentage of biomass), as referred for many penaeid species (Dall et al., 1990).

According to Hill and Wassenberg (1992), *P. esculentus* individuals weighing between 15 and 25 g eat a daily ration that corresponds to 6–9% of their body weight. In the model, for the same weight range, the relative ingestion rate was slightly above this range (12% for females and 11% for males).

The simulation of the moult cycle may constitute an important addition to the model since it has implications on shrimp external growth and influences physiological processes such as feeding and respiration (Hill and Wassenberg, 1992; Rothlisberg, 1998; Molina et al., 2000; Vega-Villasante et al., 2000).

Table 3
Comparison of the average values of ingestion and respiration rates (absolute and relative) for the three size classes

Stage	Ingestion rate		Relative ingestion rate		Respiration rate		Relative respiration rate	
	Female	Male	Female	Male	Female	Male	Female	Male
Juvenile	0.20	0.19	23.74	14.72	0.09	0.13	9.00	8.29
Subadult	0.50	–	11.80	–	0.28	–	6.54	–
Adult	0.78	0.29	8.92	10.98	0.50	0.18	5.69	7.09

Absolute rates are expressed in gDW day^{-1} and relative rates in percentage of dry biomass.

The model results showed that the reproductive processes–maturation and spawning–occur when the individual is at the adult stage at approximately 31 mm carapace length. These results are in accordance with Brinca and Mascarenhas (1986), who refer that female *P. indicus* attain sexual maturity at about 30–33 mm carapace length. The number of eggs released in spawning was close to 124 000, a typical value for penaeid shrimp (50 000–1 300 000) (Garcia and le Reste, 1981; Dall et al., 1990).

3.3. Sensitivity analysis

The sensitivity analysis (Table 4) showed that the model is not sensitive to a 10% change in juvenile food availability, indicating that, within that range, the available food simulated in the model is abundant enough for shrimp to eat the maximum ration.

On the other hand, a 10% change in water temperature caused a decrease of shrimp final weight for temperatures below and above 26 °C. At 23.4 °C the decrease observed (about 6% for females and 8% for males) was due to a lower consumption of food partly compensated by lower metabolic losses. On the other hand, at 28.6 °C a greater decrease of shrimp weight (close to 29% for females and 39% for males) was verified although a greater food intake occurs at higher temperatures. This decrease occurred since at higher temperatures the metabolic losses also increase and reduce growth. These results suggest that maximum growth occurs at temperatures close to 26 °C, within the optimal range for penaeid growth (26–30 °C) reported by Kutty (1987).

The individual model for penaeid growth calculates the scope for growth (SFG) of both male and female individuals, based on biogeochemical and physical variables and on the shrimp physiology. The SFG may be combined with data on recruitment and population mortality to drive a population dynamics model. In a system such as Maputo Bay, this type of coupled modelling approach allows an integrated description of large-scale circulation, the simulation of key biogeochemical variables relevant to the shrimp food supply, and the detailed simulation of the population dynamics of penaeid juveniles and adults, including the effects of fishing pressure and natural mortality. Details of this approach have been given e.g. in Nunes et al. (2003) and Nobre et al. (2005). The application of this type of integrated model for management of penaeid pond culture is simplified with respect to natural fishery systems as regards: (a) the requirement for detailed description of the hydrodynamics; (b) the stocking and harvesting procedures; and (c) the replacement of natural food sources for artificial feed. This integrated approach for modelling the yield of penaeid ponds, often combined in polyculture with razor clams, is currently being applied to Chinese coastal systems (Ferreira et al., 2005).

Table 4
Results of the sensitivity analysis on shrimp final weight (gFW)

Forcing function	Variation	Shrimp final weight		% Change	
		Female	Male	Female	Male
Food availability	−10%	47.92	13.65	0	0
	+10%	47.92	13.65	0	0
Temperature	−10%	45.23	12.59	−5.70	−7.81
	+10%	34.19	8.28	−28.72	−39.33

4. Conclusions

The model presented in this paper was able to simulate penaeid individual growth at several stages of the life cycle and to estimate the specific growth rates at those different stages. The model quantifies the different physiological processes involved in growth, and these can also be used for aquaculture in terms of feed and waste management. The simulation outputs use biometric conversions to present the results both as (a) total and carapace length, important for management of minimum catch size and of fishery closure periods; and (b) weight, the key variable for harvest yields and market placement.

Since penaeids are important not only for fisheries but also for aquaculture, this model is applicable for the prediction of the duration of the growout period in both natural and cultured environments.

Models which connect physical processes, biogeochemistry and population dynamics offer a great potential for simulating the biomass of commercially important species under natural and cultured conditions, and in particular for determination of optimal carrying capacity. The explicit relationship between individual scope for growth and the abiotic and biotic variables which govern it allows for the analysis of scenarios of different food supply, controlled by environmental (e.g. temperature) and anthropogenic (e.g. effluent discharge) factors. At the population scale, this approach allows for the optimisation of the yield of the marketable cohort/class, fundamental to fisheries management. Models which describe the physics and biogeochemistry of natural coastal systems or rearing ponds may also be directly connected to the recruitment and mortality terms of the population model, allowing the analysis of the effects of dissolved oxygen fluctuations, xenobiotics or disease.

Furthermore, in the case of rearing ponds such models may be used to provide estimates of point-source discharges to adjacent coastal areas, and therefore play a role in licensing procedures with respect to allowable nutrient loading and coastal eutrophication effects.

This model is available free of charge at http://www.ecowin.org/.

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