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Modelling growth rate of *Penaeus monodon* Fabricius in intensively managed ponds: effects of temperature, pond age and stocking density

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Abstract

Records of shrimp growth and water quality made during 12 crops from each of 48 ponds, over a period of 6.5 years, were provided by a Queensland, Australia, commercial shrimp farm. These data were analysed with a new growth model derived from the Gompertz model. The results indicate that water temperature, mortality and pond age significantly affect growth rates. After 180 days, shrimp reach 34 g at constant 30 °C, but only 15 g after the same amount of time at 20 °C. Mortality, through thinning the density of shrimp in the ponds, increased the growth rate, but the effect is small. With continual production, growth rates at first remained steady, then appeared to decrease for the sixth and seventh crop, after which they have increased steadily with each crop. It appears that conservative pond management, together with a gradual improvement in husbandry techniques, particularly feed management, brought about this change. This has encouraging implications for the long-term sustainability of the farming methods used. The growth model can be used to predict productivity, and hence, profitability, of new aquaculture locations or new production strategies.

Introduction

Until very recently, shrimp farming was a rapidly growing industry in many tropical and subtropical regions: production rose from 177 019 t in 1984 to 875 650 t in 1992 (FAO 1995). In 1993 (the most recent year cited), production dropped to 602 229 t. Another estimate (Anon. 1994) indicates a partial recovery in 1994 to 733 000 t, which comprised about 25% of the total world shrimp production. Although world aquaculture production of shrimp has faltered very recently, long-term growth in cultured shrimp production has the potential to continue because most shrimp-capture fisheries are at or above sustainable exploitation rates. Future increase in demand must be met by aquaculture.

Despite the increasing importance of shrimp aquaculture, many influences on the productivity of shrimp farms are poorly understood. For example, although temperature is known to affect the growth rate of shrimp at various life-history stages (Dall, Hill, Rothlisberg & Staples 1990), few previous studies have quantified this relationship. Maguire & Allan (1992) studied the growth of *Penaeus monodon* Fabricius in aquaria at a range of temperatures and found optimum growth at 27–33 °C. Growth slowed at lower temperatures; at 18 °C, it was only 14% of the optimum rate. However, shrimp in pond culture may react differently to temperature than those in aquaria. Miao & Tu (1993) reported both linear and quadratic relationships between growth rate and temperature for *Penaeus chinensis* (Osbeck), but gave no details of either the methods or the milieu of the study. Teichert-Coddington, Rodriguez & Toyofuku (1994) found that most seasonal variation in yields from Honduran shrimp farms were caused by temperature.

Salinity is also known to influence the growth rate of *P. monodon*, although the precise nature of the relationship is not clear. A range of 15–25‰ is generally accepted as being ideal for farming this species (Boyd 1989), but the effects on growth at more extreme salinities is unknown. Similarly, knowledge about the impact of other important water quality parameters (e.g. dissolved oxygen, pH) on productivity is generally limited to an approximate understanding of the lethal limits.

The growth rates of shrimp, both in culture and in natural systems, are also affected by stocking density. Edwards (1977) found depressed growth rate of *Penaeus vannamei* Boone in coastal lagoons when the density of shrimp was above 2.5 m^{-2}. Others have described density-dependent growth in culture or experimental systems (Caillouet, Norris, Heald & Tabb 1976; Sedgwick 1979; Maguire & Leedow 1983). However, the degree of density-dependence will depend on other aspects of the culture operation, such as water quality, water exchange rates and feeding rates. Under favourable experimental conditions, shrimp densities have been increased to as high as 200 m^{-2} without depression of either growth rate or survival (Sandifer, Hopkins, Stokes & Browdy 1993). Shrimp density at various stages during culture can be affected by the initial stocking density, mortality during the growout, and partial harvest strategies undertaken at the end of the growout. Because of the difficulty of accurately assessing the number of shrimp in a pond, either by direct sampling or by indirect methods such as food demand, growout mortality can only be estimated reliably at harvest time. Therefore the temporal variation in shrimp density is usually unknown.

Although few studies have investigated how environmental parameters affect the growth rate of cultured shrimp, such studies have been carried out on fish. Tai, Hatch, Masser, Cacho & Hoffman (1994) developed a growth simulation model for catfish that was primarily concerned with feed quality and feeding strategy, but also incorporated temperature and dissolved oxygen. The extended Gulland & Holt plot (Pauly, Prein & Hopkins 1993) and the extended Bayley plot (Prein & Pauly 1993) have been used to model growth of *Tilapia*. These models extend the classical von Bertalanffy growth model to include environmental influences on both the asymptotic final size of fish and the rate of growth; however, in these models the estimation of parameters requires observational data for both length and weight.

Concern about the sustainability of shrimp farming has become widespread, with major collapses in shrimp aquaculture in Taiwan, the Philippines and China, and severe disease problems in Thailand and the US (Lin 1989; Chua 1993; Primavera 1992). These crises have generally been associated with bacterial and viral diseases exacerbated by high density of farms and increasing intensity of production. It has been suggested that gradually deteriorating pond bottom conditions can contribute to a decrease in productivity (through higher FCR, lower survival and lower growth rates) with each successive crop (NACA 1994; Briggs & Funge-Smith 1994).

In this paper, data from records at a commercial shrimp farm stocked with *Penaeus monodon* are analysed. The Gompertz growth model (Seber & Wild 1989) is further developed to produce a model that accurately predicts the rates of shrimp growth under varying environmental conditions, and partitions the effects of environmental parameters (including pond age) on growth rate. The model is used to quantify the effects of temperature, salinity, pond age and stocking density on the growth rate of shrimp.

Methods

Shrimp growth and environmental data

The data used in this study were collected by farm staff at a *P. monodon* shrimp farm in north-eastern Queensland, Australia, from March 1989 to September 1995. Up to 12 crops were taken from each of the 48 ponds during the study period. The average shrimp weight was assessed weekly by capturing about 200 shrimp from each of four locations in each pond, and weighing the total sample. Water temperature, dissolved oxygen (DO) and pH were recorded twice per day (dawn and midday), while salinity and turbidity (secchi disk depth) were measured once; these daily readings were used to derive the weekly data (minimum dawn temperature, pH and DO; average salinity and secchi depth), which were recorded by the farm staff and used in this study. The staff also used food demand and random sampling to make weekly estimates of shrimp survival, but initial screening of these estimates found they were inconsistent. Instead, mortality was calculated during each crop from the percentage of shrimp surviving at harvest, using the equation: annual mortality $= 365 \times [-\log(\text{percentage survival})/(\text{days of growout})]$. Although the mortality is standardized and expressed in yearly terms for convenience, in fact no crop lasted longer than 245 days.

Growth model

The shrimp growth data were fitted to a model of the form:

$$w_t = w_\infty \left(\frac{w_0}{w_\infty} \right)^{\exp\left(-\int_0^t (\alpha + \beta x) ds\right)} \quad (1)$$

where w_t is weight at time t, w_0 is initial weight, w_∞ is the final asymptotic weight, and α describes the basic growth rate at average environmental conditions. The term βx expands to a series of terms $(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \ldots)$ where $\beta_1, \beta_2, \beta_3 \ldots$ describe the additional effects of the environmental variables $x_1, x_2, x_3 \ldots$ on growth rate. The growth-rate terms are integrated over time, since the values of the environmental variables can vary with time. The growth model used in this study is derived from the Gompertz model (Seber & Wild 1989) and is related to the commonly used von Bertalanffy model (if the environmental conditions are held constant, log(w) then follows the von Bertalanffy growth curve). In the model used herein the asymptotic final weight of shrimp is assumed not to vary under the different environmental conditions, and the parameters of the model can be estimated from only data for weight and the environmental parameters.

Data were analysed with PROC NLIN in the SAS® statistical package. Environmental variables were first transformed by subtracting the overall mean (temperature, 25.0 °C; salinity, 26.3‰; pH, 7.6). In these analyses, no attempt was made to identify any effect of different ponds on growth rate, since the large number of ponds would have decreased the precision of all the other estimates. Different ponds were therefore treated as replicates. Shrimp weighing less than 2.0 g were not analysed, since these weights are relatively imprecise. Initially, the first observed weight was used as the starting weight for each pond and crop to obtain the preliminary parameter estimates. An iterative procedure was then used to obtain the final parameter estimates by updating the estimates of the initial weights based on previous parameter estimates. The iteration was carried out until there was little improvement in the estimates.

Results

Pond conditions and management

The farm has 48 ponds of approximately 1 ha each, and the initial stocking density was 32–35 shrimp m^{-2}. Four 2 hp paddlewheel aerators operated continuously in each pond. Weekly maximum temperature (average of all ponds) peaks at 34–35 °C in summer, and during winter the weekly minimum temperature drops to 18–20 °C (Fig. 1). The average difference between weekly minimum and maximum temperature was 4.2 °C. Other water-quality parameters were normally within acceptable limits, except for a small number of low DO readings generally due to aerator failure in midsummer (Fig. 2).

Average harvest weight was 18.1 g (range 5.6–34.6 g) and average crop duration was 157 days (range 63–245 days). The dry-out interval between harvest and subsequent re-stocking varied considerably, according to such factors as rainfall and supply of postlarvae. There was no significant trend in this interval over the course of the study, although it was more variable in 1990, 1991 and 1992 than in other years (Fig. 3).

Preliminary analyses

Two preliminary analyses incorporated different combinations of the environmental parameters into the growth model. The purpose was to identify the subset of environmental parameters with the greatest ability to predict shrimp growth.

The first analysis showed that weekly minimum DO did not have a significant effect on shrimp growth rate, and that the effect of pH, although significant, was very small. These parameters also had the highest proportion of data missing, due to instrument malfunction (pH, 29% missing; DO, 14% missing), so they were excluded from further analysis, increasing the precision of the model.

The second analysis, with minimum DO and pH excluded, showed that water exchange and secchi depth reading did not have a significant effect on growth. Consequently, these parameters were also excluded from the final model.

Final growth model

The final model, which included temperature, salinity, mortality and crop number, explained 99.6% of the total variation in shrimp weight (Table 1).

Parameter estimates, standard errors and 95% confidence limits for the parameters in the model are shown in Table 2. The model predicts a

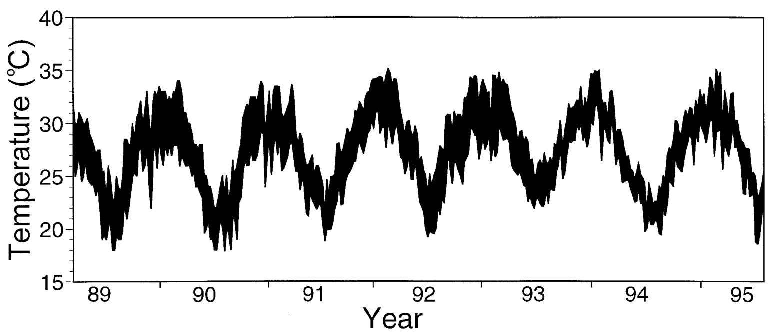

Figure 1 Weekly pond water temperatures, 1989–95. The shaded area represents the range between weekly minimum and weekly maximum temperature (averages for all ponds).

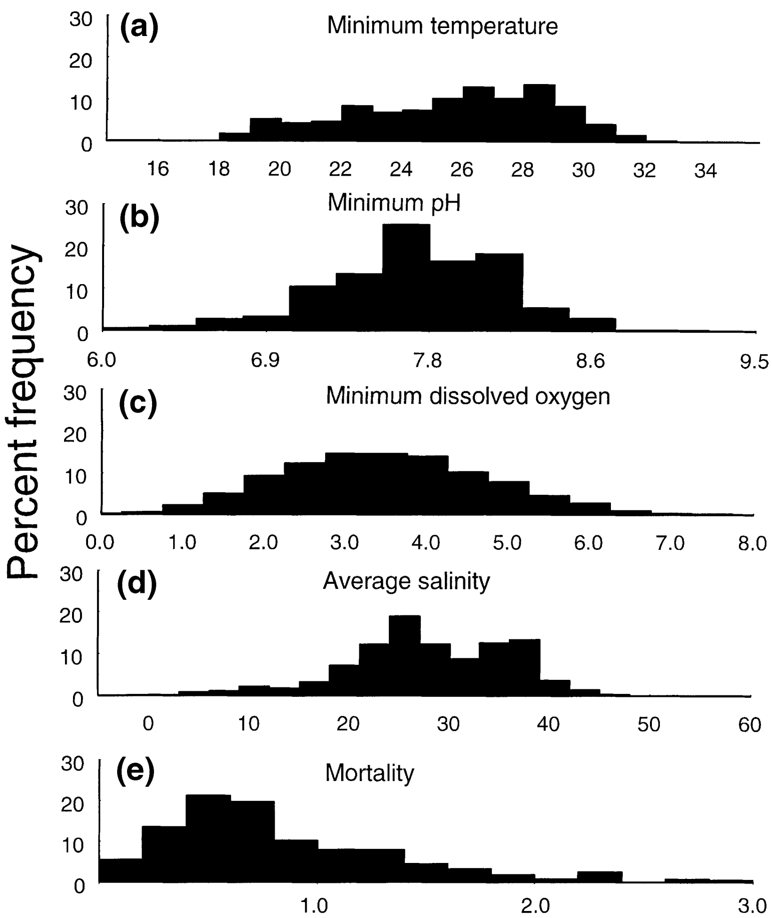

Figure 2 Frequency histograms (percentage) for weekly water quality and other parameters studied in the model. (a) minimum temperature (°C); (b) minimum pH; (c) minimum dawn dissolved oxygen (mg l^{-1}); (d) average salinity (parts per thousand); (e) crop mortality (year^{-1}).

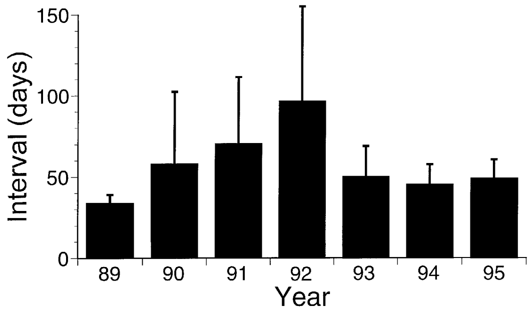

Figure 3 Inter-crop interval (± SE) from 1989 to 1995. The average number of days between harvest and restocking is shown for each year.

Table 1 Non-linear least-squares summary statistics (SS, sum of squares; MS, mean square)

Source	d.f.	SS	MS
Regression	18	38030.64	2112.8134
Residual	7401	151.06	0.0204
Uncorrected total	7419	38181.70	
Corrected total	7418	3212.98	

maximum weight of 54.19 g (w_∞, Table 2). Both linear and quadratic temperature terms were included (T, T^2, Table 2). Although the model indicates salinity has a significant effect on growth, the estimate for salinity (–0.000029, Table 2) is so small that it can be ignored.

The parameter estimates (Table 2) can be used in equation 1 to predict the average weight of a crop of shrimp after one day, given their previous average weight. For example, given a starting weight of 5.0 g, temperature = 28 °C, salinity = 32‰, mortality = 0.1 per year, during crop 2, then the weight after 1 day is:

$$w_1 = 54.193662 \times \left(\frac{5.0}{54.193662} \right)^a$$
$$= 5.114 \text{ g}$$

where $a = \exp\{-[0.013086 + 0.000568 \times (28-25) - 0.000026 \times (28-25)^2 - 0.000029 \times (32-26.3) + 0.0007 \times 0.1 - 0.004932]\}$. (Note that overall means are first subtracted from temperature and salinity.)

A correlation matrix was calculated to investigate potential correlations between the explanatory variables. The only pair of variables with an absolute correlation coefficient greater than 0.5 was minimum dissolved oxygen and minimum temperature (correlation coefficient = –0.5724). This was because of a tendency toward lower morning DO when the water temperature is high, due to the elevated metabolic rates of pond biota (Fig. 4).

Effects of model parameters on growth

Temperature

Both linear and quadratic effects for temperature were significant (Table 2). Growth rate increases steeply with temperature from 18 to 28 °C, and then gradually slows at higher temperatures (Fig. 5a).

The effect of temperature on growth rates can be demonstrated by calculating predicted growth at different temperatures, while holding other modelled parameters constant. At 30 °C prawns reach 34 g after 180 days, whereas at 20 °C the final weight is only about 15 g (Fig. 6a).

Two examples show how the model can accurately predict growth rates of shrimp under different temperature regimes. In the first example, pond temperature dropped steadily, from 30 °C at the beginning of the growout, to 20 °C at the end (broken line, Fig. 7a). Shrimp growth (dots, Fig. 7a) was fairly consistent for the first 100 days but then began to slow, influenced by the reduced temperature. The model accurately predicted shrimp weight throughout the growout (solid line, Fig. 7a). Figure 7b illustrates a different pond and time period (and hence different temperature regime), with the same crop number and comparable mortality. The temperature dropped from 25 °C at the beginning to 20 °C, where it remained from day 60 to about day 100. Then, the temperature increased to almost 30 °C by day 160. Reflecting the lower temperature, the shrimp grew more slowly, reaching only 14 g by 120 days (compared with 18 g in Fig. 7a). However, the rising temperature during the last 20 days increased the growth rate. The model also predicted growth accurately with this temperature regime (solid line, Fig. 7b).

Mortality

Initial shrimp stocking density was consistently between 32 and 35 shrimp m^{-2}. However, variable mortality during a growout affected shrimp density in the pond. If mortality is high, the density of

Table 2 Parameter estimates, their standard errors (SE) and 95% confidence limits (CL). w_∞ estimates maximum asymptotic size, and α estimates basic growth rate (g per day). The other parameters are temperature (*T*) and its quadratic term, salinity, crop mortality (year^{-1}), and the crop number. Crop effects are expressed relative to crop number 12

Parameter	Estimate	SE	95% CL (lower)	95% CL (upper)
w_∞	54.193662	1.440272	51.370268	57.017056
α	0.013086	0.000669	0.011774	0.014397
T	0.000568	0.000012	0.000545	0.000591
T^2	–0.000026	0.000002	–0.000031	–0.000021
Salinity	–0.000029	0.000003	–0.000035	–0.000021
Mortality	0.000700	0.000035	0.000631	0.000769
Crop 1	–0.004460	0.000629	–0.005694	–0.003226
Crop 2	–0.004932	0.000621	–0.006149	–0.003714
Crop 3	–0.004258	0.000636	–0.005506	–0.003011
Crop 4	–0.004182	0.000629	–0.005415	–0.002948
Crop 5	–0.004488	0.000626	–0.005716	–0.003260
Crop 6	–0.005616	0.000644	–0.006878	–0.004354
Crop 7	–0.005521	0.000633	–0.006762	–0.004281
Crop 8	–0.004768	0.000642	–0.006026	–0.003509
Crop 9	–0.004053	0.000632	–0.005292	–0.002814
Crop 10	–0.003732	0.000637	–0.004981	–0.002483
Crop 11	–0.001941	0.000642	–0.003199	–0.000684

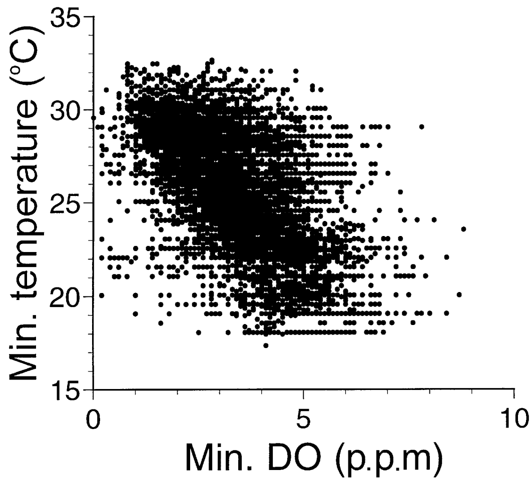

Figure 4 Correlation between minimum weekly dawn dissolved oxygen, and minimum weekly dawn temperature. The data represent 48 ponds over 6 years (1989–95); correlation coefficient = –0.5724.

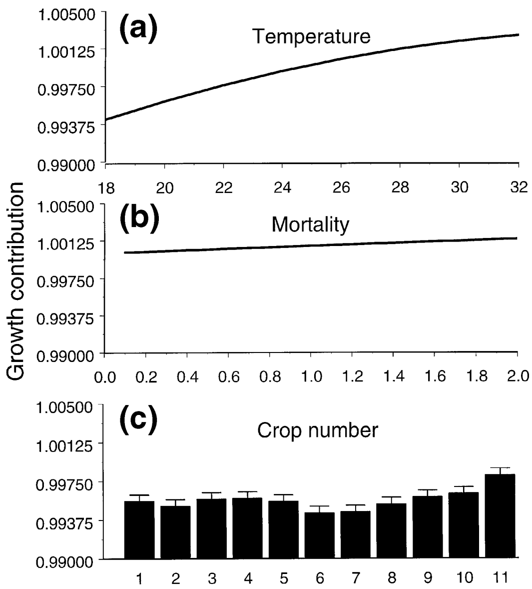

Figure 5 Independent contribution of each parameter to the overall growth model. For each parameter, the value of exp(β*x*) is shown over a range of *x*-values, where β is the estimate of parameter coefficient shown in Table 1, and *x* is the parameter value. (a) temperature, °C (linear and quadratic estimates are combined); (b) mortality, year^{-1}; (c) crop number (bars show standard errors).

shrimp will be reduced. This has a detectable effect on growth rate: at higher mortality (i.e. lower density), growth rates were greater than at low mortality (i.e. higher density) (Fig. 5b). The effect of mortality on growth rate, over the range of mortalities generally evident (0–1 year^{-1}, Fig. 2e) was small: modelled growth at mortality = 0 year^{-1}

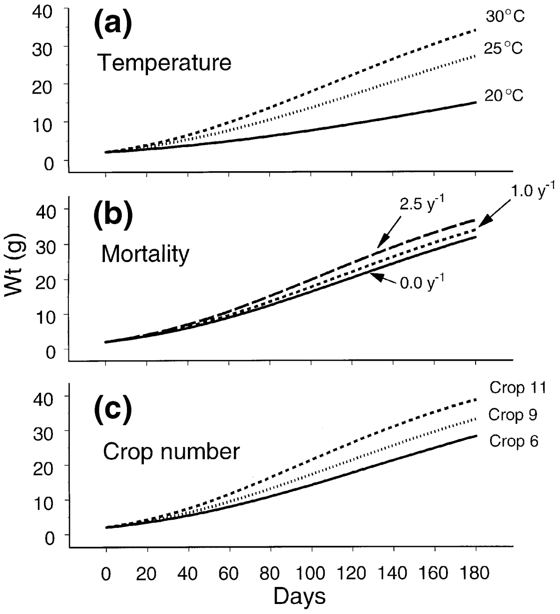

Figure 6 Shrimp growth predicted by the model under different conditions. In each figure, one effect is varied while the other two are held constant. (a) varying temperature (crop = 1, mortality = 0.1 year^{-1}): 20 °C, solid line; 25 °C, dotted line; 30 °C, dashed line. (b) varying mortality (28 °C, crop = 1): mortality = 0.0 year^{-1}, solid line; mortality = 1.0 year^{-1}, short dashed line; mortality = 2.5 year^{-1}, long dashed line. (c) varying crop number (28 °C, mortality = 0.1 year^{-1}): Crop 6, solid line; Crop 9, dotted line; Crop 11, dashed line.

indicated a shrimp weight of 31.6 g after 180 days; at mortality = 1.0 year^{-1} it was 33.7 g (Fig. 6b). However, at a more extreme mortality of 2.5 year^{-1}, corresponding to about 29% survival after a 180 day growout, the increased growth rate is more pronounced, leading to a final weight of 36.6 g (long-dashed line, Fig. 6b).

Actual and modelled growth of shrimp during growouts with different mortality rates is shown in Fig. 7c (M = 0.56 year^{-1}) and Fig. 7d (M = 2.80 year^{-1}). Both figures illustrate crop 6. The growout with the lower mortality reached barely 20 g after 120 days (Fig. 7c), whereas with higher mortality a weight of 24 g was achieved in a shorter time (Fig. 7d). In both examples, the model accurately predicted average shrimp weight. (Although an attempt was made to choose growouts where the temperature regimes are comparable for illustration, the temperature in the lower mortality growout (Fig. 7c) was lower for the first 20 days, which may have increased the difference in growth rate.)

Pond age

Pond age, or the number of crops that had previously been grown and harvested in a given pond, has a marked effect on growth rate. Up to about crop 5, growth rate was relatively constant. It was slightly lower during the sixth and seventh crops, and then gradually increased for each crop thereafter (Fig. 5c). The degree of variation in growth rate that can be attributed to crop effects is illustrated by modelling prawn weight with temperature and mortality held constant (28 °C and 0.1 year^{-1}: Fig. 6c). After 180 days, the average weight of a shrimp from crop 6 (the slowest growing crop) was 28 g whereas from crop 11 (the fastest growing crop) it was almost 39 g; and from crop 9 (intermediate growth rate, similar to crops 1, 3, 4, 5 and 10), 33 g.

Actual and predicted shrimp growth rates are illustrated for crops 6 (Fig. 7e) and 10 (Fig. 7f). The mortalities are similar and, while the temperature regimes are different (with rising temperature during crop 10, and dropping temperature during crop 6) the average temperature during the two growouts is similar. The shrimp grew markedly faster in crop 10, reaching 22 g after 115 days, but in crop 6 reached only 18 g. The growth rates predicted by our model were again accurate in both situations.

Discussion

Effect of temperature on growth rate

Because the model used in this study is not based on average temperature, the results must be used cautiously when comparing them with results from other studies or when predicting growth rates under new temperature regimes. The temperature estimates used in this model were generated by measuring temperature at dawn every day, then taking the lowest weekly value of these readings; the average weekly dawn temperature would have been higher. In addition, dawn temperature is typically 2 °C less than afternoon temperature in aerated tropical ponds (C. Jackson, unpublished data). Therefore, the weekly minimum dawn temperature value underestimates the true average water temperature by an unknown amount, possibly as much as 2–3 °C.

The optimum temperature for intensive culture of *P. monodon* is generally considered to be around 30 °C

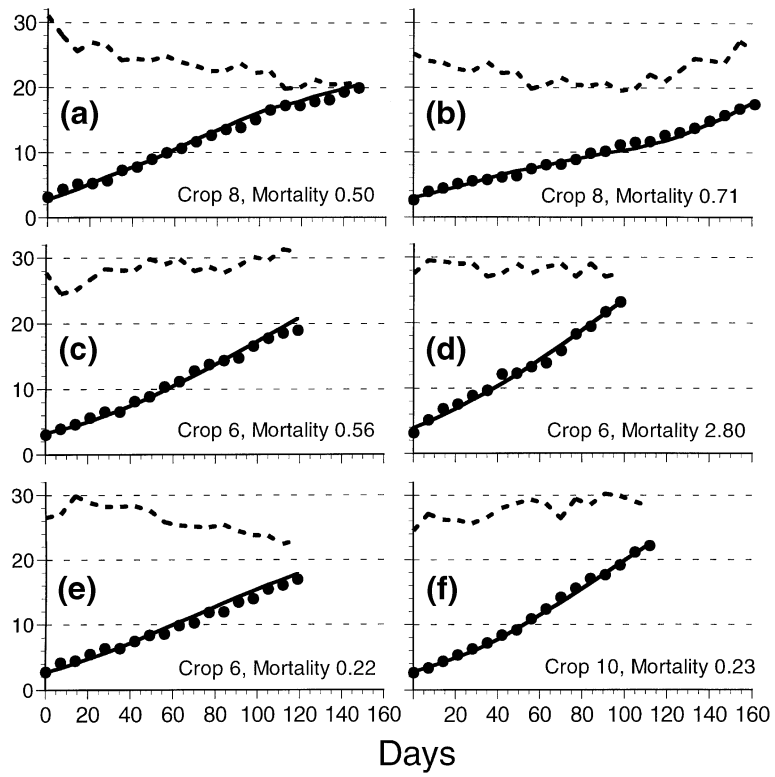

Figure 7 Actual growth rates of prawns (dots) compared with model predictions (solid line), with varying temperature regimes (broken line), crop numbers and mortality rates. *Y*-axis units are both °C and g. (a) Crop 8, mortality = 0.50 year^{-1}; (b) Crop 8, mortality = 0.71 year^{-1}; (c) Crop 6, mortality = 0.56 year^{-1}; (d) Crop 6, mortality = 2.80 year^{-1}; (e) Crop 6, mortality = 0.22 year^{-1}; (f) Crop 10, mortality = 0.23 year^{-1}.

(e.g. Hirono 1992; 28–30 °C; Maguire & Allan 1992; 27–33 °C). Although the present model predicts maximum growth at 36 °C, most of the observations were in the range 23–30 °C (Fig. 2a) and therefore extrapolation of results of the model much above 30 °C is invalid. The temperature/growth curve predicted by the model does suggest that there is little increase in growth rate above 30 °C (Fig. 5a); assuming average temperature was underestimated by about 2 °C, this would indicate 32–34 °C as the likely optimum average temperature for growth rate, using this farm's practices. However, because survival of shrimp may be lower at high temperatures (Staples & Heales 1991), the optimum temperature for biomass production may be somewhat lower.

Effects of pond age on growth rate

The slight decrease in growth rate during crops 6 and 7 suggests that farm productivity may have begun deteriorating, as has been demonstrated in Thailand (NACA 1994; Briggs & Funge-Smith 1994). However, in the present study, the growth rates have increased during more recent crops. The farm is conservatively managed and has not increased stocking densities. The typical stocking density of 32–35 shrimp m^{-2} implies a maximum feeding rate of about 160 kg ha^{-1} per day (average harvest weight = 18.1 g, applied feed = 2.6% of body weight per day), which is slightly above the maximum 100–150 kg ha^{-1} per day recommended by Boyd (1992). Ponds are also consistently dried for 4–10 weeks between harvest and restocking, although it has been suggested that there is little benefit to be gained from drying pond substrates longer than a few weeks (Boyd & Pippopinyo 1994). Excess deposits in the ponds are removed at the end of the drying period before refilling.

Effect of mortality on growth rate

The relationship between the rates of mortality and growth is complex. It might be expected that conditions causing high mortality would also have a negative impact on growth rate, but this study has shown that, overall, the reverse in fact applies. This is probably because high mortality events are normally of short duration; after the mortality occurs, growth rates improve because the density of shrimp is lower. No reliable data were available for regularly estimating population density throughout the crop, so the estimated relationship between mortality and growth rate must only be approximate. For example, if the mortality occurred very early in the crop, then most of the growout would be influenced by the reduced population density, whereas high mortality just before harvest would not affect the growth rates of the crop.

The negative relationship between the rates of mortality and growth indicates that growth is density-dependent. This explains the relatively low value for w_∞ (54.2 g). The maximum weight achievable by *P. monodon* has been estimated to be as high as 150 g for wild shrimp (Grey, Dall & Baker 1983). The age of shrimp at this size is not known. The much lower estimate derived during the present study is more appropriate for shrimp cultured intensively in ponds. Jong, Kou & Chen (1993) also found pond-grown *P. monodon* reached a much smaller maximum size than wild-caught individuals.

Factors found not significant

No significant effects on shrimp growth rate were detected as a result of water exchange, secchi depth or dissolved oxygen, and the effects of pH and salinity were found to be very small. However, it is likely that some of these parameters do, in fact, have a much more important impact on rates of growth than it was possible to demonstrate in the present study. While the use of existing data from commercial operations can be very cost-effective, such data are primarily collected to meet specific commercial objectives. In the present case, water-quality parameters were only recorded weekly, even though measurements were made at least once every day. In aquaculture ponds, such parameters as secchi depth, pH and dissolved oxygen typically vary widely every day, in response to variation in light levels and stages of phytoplankton succession. Weekly minimum or maximum values of such variables are therefore imprecise estimates, and are likely to be very poor predictors of their effects on growth rate. Studies using more comprehensive data need to be completed before the effects of these variables can be firmly established.

A study is currently being conducted into the changes in management techniques during the period that this farm has been in operation, in an attempt to understand the reasons for recent improvements in productivity. Pond managers have suggested that the most significant change in management is the improved control over the amount of food supplied. Feeding is now matched to demand by careful monitoring of feed trays. The the present results initially suggest that the farming practices of the farm studied, which are similar to those used in other shrimp farms in tropical Australia, can be considered sustainable.

The new growth model described here allows, for the first time, the prediction of the productivity (and hence profitability) of *P. monodon* aquaculture in locations that have not been tried previously, and the evaluation of new production strategies (e.g. varied timing of stocking and harvesting) in existing locations. It has already been used to evaluate the likely commercial success of a different stocking strategy for a local shrimp farm. Further development and widespread adoption of such modelling tools will help reduce the risk profile of aquaculture business enterprises.

Acknowledgments

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