

Modeling Effect of Thermal Amplitude and Stocking Density on the Growth of Redtail Shrimp *Penaeus penicillatus* (Alock)

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Sha Miao and Shun-Chi Tu (1993) Modeling effect of thermal amplitude and stocking density on the growth of redbtail shrimp *Penaeus penicillatus* (Alock). *Bull. Inst. Zool., Academia Sinica* 32(4): 253-264. We conducted a 120-day study evaluating the simultaneous effects of thermal amplitude and stocking density on the daily growth rate of redbtail shrimp. The three thermal regimes in our study consisted of one constant temperature (28°C) and two daily thermocycles. Growth rates were measured at the end of sequential 30-day periods.

Our results indicate that growth rates from period to period are a quadratic function of thermal amplitude and stocking density. Cyclic temperature was found to be a limiting factor which consequently produces better or worse growth rates than a constant temperature—depending on the thermal amplitude level. Additionally, mean daily growth rate decreased slowly with increasing stocking densities between 7 and 12 shrimp per 0.18 m², but decreased rapidly with increasing stocking densities between 12 and 17 shrimp per 0.18 m². The optimal thermal amplitude and stocking density changed periodically throughout the 120-day experiment.

Key words: Redtail shrimp, Thermal amplitude, Stocking density, Thermocycle, Quadratic function.

The environmental factor of greatest importance to crustacean harvesters is temperature (Neal and Maris 1985). Laboratory experiments, seasonal changes, and latitudinal gradients have all illustrated the effects of temperature on growth rates (Cobb and Wang 1985). Many laboratory experiments have attested to the relationship between temperature and growth rate (Morrissy 1974 1976, Flint 1975, LaCaze 1976, Momot and Gowing 1977, Tcherkashina 1977, Aiken 1980). Larval development rates

are sensitive to constant and daily cyclic temperatures, and these responses are species-specific (Costlow and Bookhout 1971, Sastry 1976 1980). Temperature change rate and the amplitude of the daily cycle also affect development and survival, and the effects are also species-specific (Sastry 1983).

Another factor of concern to the aquaculturist is crustacean adaptability to unnatural conditions—i.e., overcrowding or water quality variation (Provenzano Jr. 1985a). Smith et al. (1978) stated that

population density and growth rate are inversely related. As population density increases, competition for food (Chapman and Howard 1988) and living space (Goldman 1973, Goyert and Avault 1979, Van Olst et al. 1980) usually intensifies. Metabolic wastes, which are directly proportional to population density, have been implicated as being inhibitory to growth and toxic to crustaceans (Wickins 1976, Delistraty et al. 1977, Armstrong et al. 1978, Provenzano Jr. 1985b). Reduced oxygen level (as a result of high biomass or organic decomposition in ponds, or both) is another commonly encountered problem, and is perhaps the most frequent cause of large-scale mortality in crustacean culture (Provenzano Jr. 1985b). Moreover, at very high densities growth may be affected in ways perhaps not related to food availability or water quality (Provenzano Jr. 1985b). McSweeney (1977) has suggested that social interactions at very high population densities inhibit growth.

The production methods for *Penaeus penicillatus* are quite similar to those of *P. monodon* (black tiger shrimp)—a tropical species with a temperature range of 16 – 35°C (Chen 1990). *P. penicillatus* is a cold-tolerant shrimp (Main and Fulks 1990) which can survive at temperatures as low as 10°C (Chen 1990). However, like *P. monodon*, *P. penicillatus* stops growing at temperatures below 20°C (Chen 1990). Our research was designed to model the effects of thermal amplitude and stocking density on the daily growth rate of *P. penicillatus*.

MATERIALS AND METHODS

We employed three thermal regimes: one constant temperature and two daily thermocycles. The heaters used for the constant thermal treatment were thermostatically controlled to maintain a 28°C temperature during the study. For the thermocycle treat-

ments we used an apparatus consisting of two timer-controlled thermostats—each connected to a heater. For the 8°C amplitude thermal treatment, one thermostat was set at 32°C and the other at 24°C. The electrical supply was controlled with 12-hour timers which created a thermocycle of increasing aquarium temperature to 32°C from 0700 to 1900 hours daily, then returning the aquarium temperature to 24°C over the following 12-hour cycle. The 16°C amplitude thermal treatment was managed similarly, with floor and ceiling temperatures of 20 and 36°C, respectively. Room temperature was maintained at $17 \pm 1^\circ\text{C}$. The stocking densities used were 7, 12, and 17 redbtail shrimp per 0.18 m² per aquarium. As a result, there were nine treatment combinations of thermal amplitude and stocking density which were randomly assigned to the 45 aquaria; there were five aquaria replicates for each treatment combination. Aquarium dimensions were 60 cm × 30 cm × 36 cm.

A quadratic response-surface model (Gill 1978, Petersen 1985) was used to describe the experimental system as follows:

$$G_p = \beta_{0p} + \beta_{tp} T + \beta_{sp} S + \beta_{tpp} T^2 + \beta_{tsp} TS + \beta_{ssp} S^2,$$

where G_p = daily growth rate (G) at period p;

T = thermal amplitude in degrees centigrade;

S = stocking density;

β_{0p} = intercept on G_p axis; and

β_{tp} , β_{sp} , β_{tpp} , β_{tsp} , and β_{ssp} = regression coefficients for period p.

Variable G in the model represents a daily growth rate equal to $\ln(W_{p+1}/W_p)/t$, where W_p denotes the total weight of redbtail shrimp in a specified aquarium on days 0, 30, 60, and 90 with p = 0, 1, 2, and 3, respectively,

within a duration (t) of 30 days.

Shrimp were provided by Tungkang Marine Laboratory. After a two-week acclimatization period, the experiment commenced and lasted 120 days. The initial redtail shrimp weights ranged from 0.38 to 0.52 g, with a mean of 0.44 g and standard deviation of 0.021 g. A daily ration of 15% body weight was divided into two equal parts and fed to the shrimp at 1000 and 1400 hours. A commercial shrimp pellet diet (manufactured by President Enterprises Corp., Taiwan) was used.

Illumination consisted of four fluorescent light fixtures with two 40-watt bulbs, which were kept on from 0600 to 1800 hours. Each aquarium was screened to prevent the shrimp from jumping out. Filtered sea water from the National Taiwan Ocean University supply system originating from the nearby coast, was used to fill the aquaria. Aquaria were cleaned by replacing one third of the water on a weekly basis; pH, salinity, and dissolved oxygen were measured every other day.

RESULTS

Biomass, growth, and survival statistics for the four 30-day periods are summarized in Table 1. Figs. 1 and 2 indicate that the biomass and growth rate increase and decrease, respectively, as time increases. Individual aquaria survival rates were recorded on a 120-day basis. There were no mortalities until period three, with a peak during the final period. An analysis of variance on survival rate indicated that there was no interaction between thermal amplitude and stocking density (Table 2). However, the main effects of the two studied factors on survival rate were both significant, with $p = 0.0001$ (Table 2). Our analysis of variance on daily growth rate, using a split-plot design, indicated that the three-factor

interaction effect of temperature, stocking density, and time period was not significant (Table 3); neither were the effects of two-

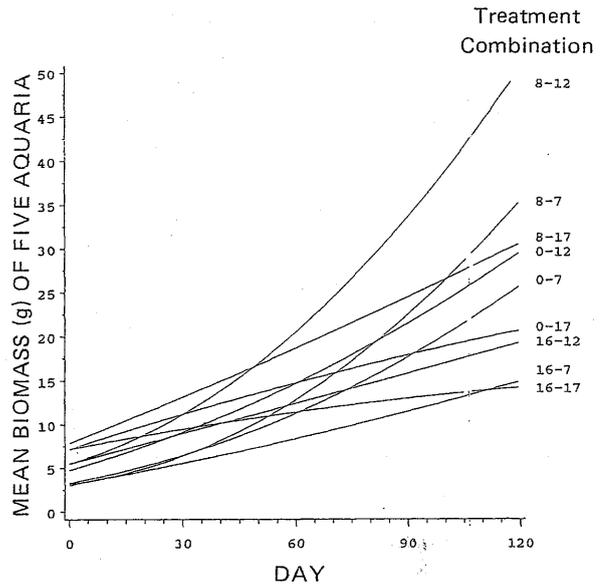


Fig. 1. Mean biomass (g) of five aquaria versus time for each treatment combination (thermal amplitude — stocking density).

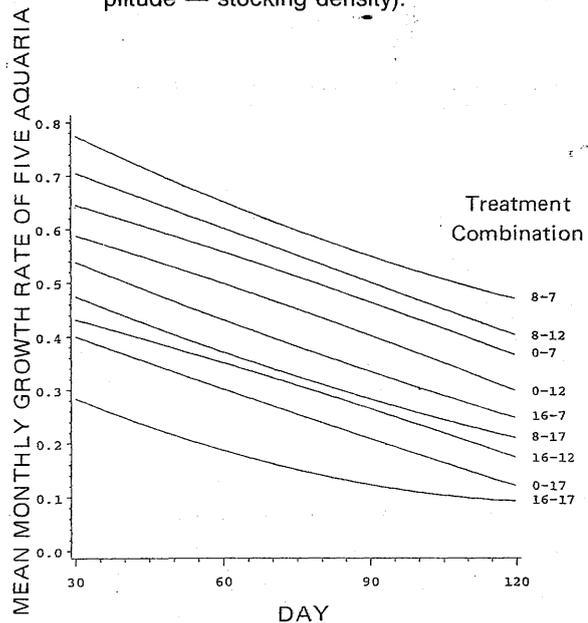


Fig. 2. Mean monthly growth rate of five aquaria versus time for each treatment combination (thermal amplitude — stocking density).

Table 1. Statistics^a for studied variables for any given treatment combination throughout the 120-day period

Treatment combination ^b	Response variable ^c	Day 0	Day 30	Day 60	Day 90	Day 120
0-7	W	3.36 ± 0.504	6.41 ± 0.769	11.19 ± 1.455	17.80 ± 2.492	25.62 ± 2.818
	G		0.022 ± 0.001	0.019 ± 0.001	0.015 ± 0.001	0.012 ± 0.001
	S					0.89 ± 0.120
0-12	W	4.92 ± 0.640	8.85 ± 1.062	14.61 ± 2.045	21.79 ± 2.397	29.34 ± 2.641
	G		0.020 ± 0.001	0.017 ± 0.001	0.013 ± 0.001	0.010 ± 0.002
	S					0.83 ± 0.132
0-17	W	7.31 ± 1.023	10.95 ± 1.423	14.62 ± 1.455	18.23 ± 2.001	20.47 ± 2.456
	G		0.013 ± 0.001	0.010 ± 0.001	0.007 ± 0.001	0.004 ± 0.002
	S					0.65 ± 0.093
8-7	W	3.08 ± 0.400	6.70 ± 0.804	12.73 ± 1.782	22.26 ± 2.449	35.47 ± 3.542
	G		0.026 ± 0.001	0.021 ± 0.001	0.019 ± 0.002	0.016 ± 0.001
	S					0.97 ± 0.064
8-12	W	5.52 ± 0.718	11.15 ± 1.561	20.48 ± 2.253	33.58 ± 4.030	50.28 ± 4.525
	G		0.023 ± 0.002	0.020 ± 0.001	0.016 ± 0.002	0.013 ± 0.001
	S					0.88 ± 0.095
8-17	W	7.99 ± 1.198	12.74 ± 1.529	18.91 ± 2.647	24.50 ± 2.695	30.45 ± 3.957
	G		0.016 ± 0.001	0.013 ± 0.002	0.009 ± 0.001	0.007 ± 0.002
	S					0.66 ± 0.097
16-7	W	3.15 ± 0.441	5.33 ± 0.639	8.52 ± 1.108	11.46 ± 1.375	14.85 ± 1.633
	G		0.018 ± 0.002	0.016 ± 0.002	0.010 ± 0.001	0.009 ± 0.001
	S					0.63 ± 0.163
16-12	W	5.64 ± 0.846	8.64 ± 0.950	12.49 ± 1.374	16.00 ± 1.918	19.12 ± 1.911
	G		0.014 ± 0.001	0.012 ± 0.001	0.008 ± 0.002	0.006 ± 0.002
	S					0.55 ± 0.151
16-17	W	7.14 ± 0.928	9.53 ± 1.143	11.31 ± 1.244	12.99 ± 1.688	14.17 ± 1.983
	G		0.010 ± 0.001	0.006 ± 0.002	0.005 ± 0.002	0.003 ± 0.002
	S					0.36 ± 0.113

a. These statistics for studied variables for five aquaria are in the form of mean ± SD, where SD denotes standard deviation.

b. The first column represents thermal amplitude in centigrade, the second column denotes stocking density.

c. W is the total weight in grams of redtail shrimp in each aquarium under a certain treatment combination. Daily growth rate is $G = \ln(W_{p+1}/W_p)/t$, where W_p is total body weight of redtail shrimp in a specific aquarium on days 0, 30, 60 and 90, with $p = 0, 1, 2$ and 3 , respectively. The duration for each time period is denoted by $t = 30$ days. Survival rate is $S = N_{120}/N_0$, where N_{120} and N_0 are the total numbers of redtail shrimp in each aquarium on days 120 and zero, respectively.

Table 2. Analysis of variance in survival rate influenced by thermal amplitude and stocking density throughout 120 days

Source of variation	df	Sum of squares	Mean square	F-ratio	p-value
Total	44	2.01196992			
Thermal amplitude (T)	2	0.91127541	0.45563770	32.81	0.0001
Stocking density (S)	2	0.59317893	0.29658946	21.35	0.0001
Interaction (T-S)	4	0.00751809	0.00187952	0.14	0.9682
Error	36	0.49999749	0.01388882		

Table 3. Analysis of variance in daily growth rate influenced by thermal amplitude and stocking density throughout four 30-day periods

Source of variation	df	Sum of squares	Mean square	F-ratio	p-value
Total	179	0.00825121			
Thermal amplitude (T)	2	0.00178693	0.00089347	73.18 ^a	<0.0001
Stocking density (S)	2	0.00230432	0.00115216	94.36 ^a	<0.0001
Interaction (T-S)	4	0.00011961	0.00002990	2.45 ^a	0.0637
Error one	36	0.00043958	0.00001221		
Period (P)	3	0.00225719	0.00075240	78.37 ^b	<0.0001
Interaction (T-P)	6	0.00007548	0.00001258	1.31 ^b	0.2588
Interaction (S-P)	6	0.00010031	0.00001672	1.74 ^b	0.1183
Interaction (T-S-P)	12	0.00013092	0.00001091	1.14 ^b	0.3390
Error two	108	0.00103687	0.00000960		

a. The divisor of *F* ratios = 0.00001221.

b. The divisor of *F* ratios = 0.00000960.

interaction, including time period with either temperature or stocking density (Table 3). However, the interaction between temperature and stocking density was significant at $p = 0.0637$ (Table 3) and the main effect of time period was also significant at $p < 0.0001$ (Table 3). For this reason, response-surface analyses were conducted for each time period.

For periods one and two, our analysis indicated that a quadratic equation described the daily growth rate as a function of temperature and stocking density (Table 4). Table 5 displays estimated parameters with

their corresponding *t*-tests. However, the lack of fit analysis for period three revealed a significant *F* ratio with $p = 0.0185$, which points out that a higher order equation may be required to describe the experimental system for period three (Table 4); Table 5 also lists the estimated parameters and corresponding *t*-test for fitting the present equation. Results from the last period suggest that the experimental system can be described with a quadratic response-surface model (Tables 4 and 5). Figs. 3 to 6 show the daily growth rate response under the assigned treatment combination

Table 4. Final ANOVA of daily growth rate of redbtail shrimp throughout four 30-day periods

Source of variation	<i>df</i>	Sum of squares	Mean square	<i>F</i> -ratio	<i>p</i> -value
Period One					
Total	44	0.001369075			
Fitted surface	5	0.000963	0.0001926	19.56	<0.0001
Lack of fit	3	0.000052075	0.000017358	1.76	0.1717
Error	36	0.000354	0.000009847		
Period Two					
Total	44	0.001118258			
Fitted surface	5	0.001046	0.0002092	113.39	<0.0001
Lack of fit	3	0.000005850	0.000001950	1.06	0.3793
Error	36	0.000066408	0.000001845		
Period Three					
Total	44	0.000979528			
Fitted surface	5	0.000879	0.0001758	82.81	<0.0001
Lack of fit	3	0.000024114	0.000008038	3.79	0.0185
Error	36	0.000076414	0.000002123		
Period Four					
Total	44	0.000822693			
Fitted surface	5	0.000736	0.0001472	69.27	<0.0001
Lack of fit	3	0.000010185	0.000003395	1.60	0.2070
Error	36	0.000076508	0.000002125		

throughout the four sequential periods. The response-surface model with predicted optimal growth and corresponding thermal amplitude and density coordinates for each time period is summarized in Table 6.

In each aquarium, daily thermal fluctuation showed a sinusoidal pattern. Salinity ranged from 34‰ to 35‰ throughout the study period. Time period had significant effects on pH and dissolved oxygen, both with $p < 0.005$. Additionally, the effects of thermal amplitude and stocking density interaction on pH and dissolved oxygen were significant.

DISCUSSION

Cyclic temperatures are known to im-

prove growth and survival rates in larval forms (Costlow and Bookhout 1971, Christianson and Costlow 1975, Sastry 1975). The mean daily growth rate of redbtail shrimp increased with increasing thermal amplitude between 0° and 8°C, but dropped rapidly between 8° and 16°C at any given density and period (Table 1). Therefore, the effect of cyclic temperatures on growth when compared to that of constant temperature depends on the thermal amplitude levels (Table 1). Sastry (1983) concluded that thermal amplitude and rate of temperature change on a daily basis affect the rate of development of crustaceans differently. The survival and growth rate patterns were similar under the studied thermal controls (Table 1). The highest mean survival rate of 97% was obtained at a thermal amplitude of 8°C and

Table 5. Estimated parameters and corresponding *t*-test of response-surface model^a throughout four 30-day periods

Period	Parameter	df	Parameter estimate	Standard error	<i>t</i> -test for H ₀ : Parameter = 0	<i>p</i> -value
One						
	β_0	1	0.010972	0.005722	1.918	0.0625
	β_t	1	0.001675	0.000343	4.887	<0.0001
	β_s	1	0.001805	0.000998	1.809	0.0781
	β_{tt}	1	-0.000099	0.000015953	6.181	<0.0001
	β_{ts}	1	-0.000024106	0.000018049	- 1.336	0.1894
	β_{ss}	1	-0.000098	0.000040840	- 2.404	0.211
Two						
	β_0	1	0.012975	0.002412	5.378	<0.0001
	β_t	1	0.001137	0.000145	7.871	<0.0001
	β_s	1	0.001452	0.000421	3.452	0.0014
	β_{tt}	1	-0.000081081	0.000006726	-12.056	<0.0001
	β_{ts}	1	-0.000006286	0.000007609	- 0.826	0.4138
	β_{ss}	1	-0.000096	0.000017218	- 5.577	<0.0001
Three						
	β_0	1	0.013357	0.002845	4.694	<0.0001
	β_t	1	0.000696	0.000170	4.086	0.0002
	β_s	1	0.000918	0.000496	1.850	0.0719
	β_{tt}	1	-0.000074352	0.000007933	- 9.373	<0.0001
	β_{ts}	1	0.000017822	0.000008975	1.986	0.0541
	β_{ss}	1	-0.000076656	0.000020308	- 3.775	0.0005
Four						
	β_0	1	0.012005	0.002642	4.543	0.0001
	β_t	1	0.000845	0.000158	5.336	<0.0001
	β_s	1	0.000463	0.000461	1.006	0.3207
	β_{tt}	1	-0.000075739	0.000007367	-10.281	>0.0001
	β_{ts}	1	0.000015929	0.000008335	1.911	0.0634
	β_{ss}	1	-0.000055569	0.000018859	- 2.947	0.0054

a. $G = \beta_0 + \beta_t T + \beta_s S + \beta_{tt} T^2 + \beta_{ts} TS + \beta_{ss} S^2$, where *G* is an estimated daily growth rate of redtail shrimp at various time periods, *T* is thermal amplitude (in centigrade) evenly fluctuated at or around 28°C, *S* is stocking density, β_0 is an intercept of *G* axis, and the other β 's are the coefficients of the equation.

stocking density of 7 shrimp per 0.18 m² (Table 1). Sastry (1976) also reported that larvae of the sublittoral crab *Cancer irroratus* survive better at 10°–20°C and 15°–25°C daily cycles compared to those at a constant 15° or 20°C, revealing that thermal

amplitude in our present study had a maximum and minimum limiting effect on growth and survival.

Table 1 also indicates that mean daily growth rate decreased slowly with an increase in stocking density from 7 to 12 shrimp

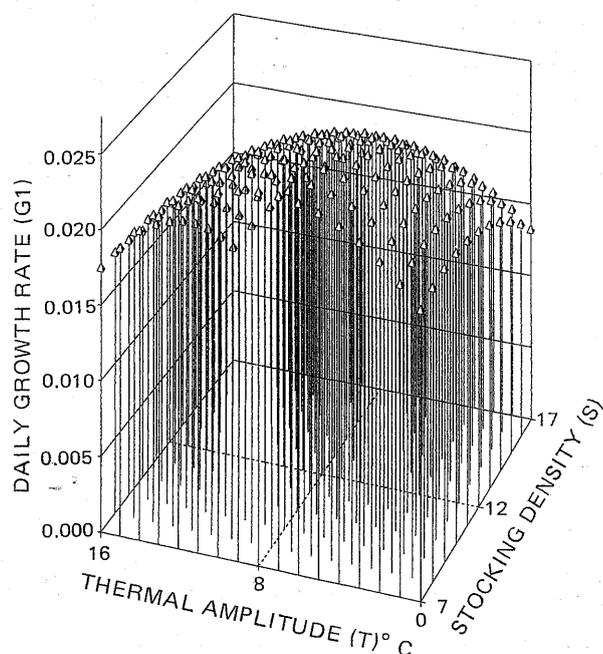


Fig. 3. Estimates of daily growth rate for period one based on $G_1 = 0.010971 + 0.001675 T + 0.001805 S - 0.000099 T^2 - 0.000024108 TS - 0.000098 S^2$.

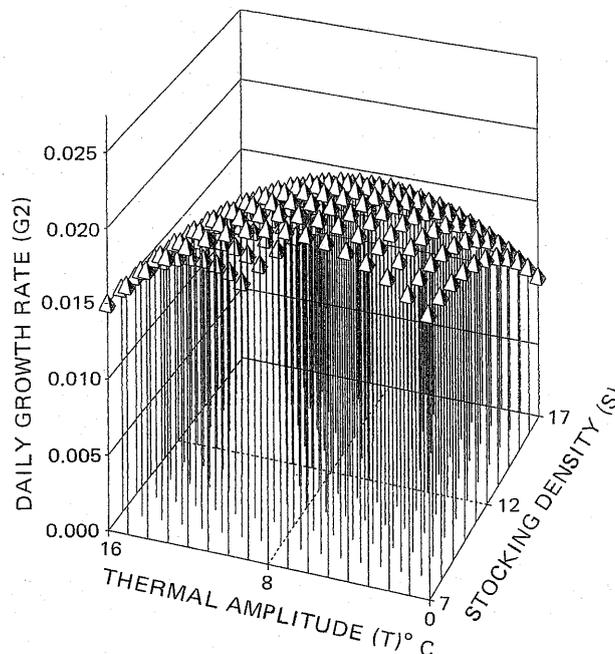


Fig. 4. Estimates of daily growth rate for period two based on $G_2 = 0.012975 + 0.001137 T + 0.001452 S - 0.000081081 T^2 - 0.000006286 TS - 0.000096 S^2$.

Table 6. Response-surface model^a with predicted optimal response^b and corresponding coordinate^c for four time periods

Period	Intercept and regression coefficients						Optimum		
	β_0	β_t	β_s	β_{tt}	β_{ts}	β_{ss}	G^b	T^c	S^c
1	0.010972	0.001675	0.001805	-0.000099	-0.00024106	-0.000098	0.024710	7.48	8.28
2	0.012975	0.001137	0.001452	-0.000081081	-0.000006286	-0.000096	0.022131	6.73	7.34
3	0.013357	0.000696	0.000918	-0.000074352	0.000017822	-0.000076656	0.018304	5.48	6.62
4	0.012005	0.000845	0.000463	-0.000075739	0.000015929	-0.000055569	0.015753	6.11	5.05

a. Regarding a certain time period (30-day), $G = \beta_0 + \beta_t T + \beta_s S + \beta_{tt} T^2 + \beta_{ts} TS + \beta_{ss} S^2$, where G is the estimated daily growth rate, β_0 is the intercept, and the other β 's are regression coefficients.

b. Maximum daily growth rate.

c. A set of thermal amplitude (T) in centigrade, and stocking density (S) inducing maximum daily growth rate.

per 0.18 m^2 , but decreased rapidly as stocking density increased from 12 to 17 shrimp per 0.18 m^2 for any given thermal treatment and time period. The stocking density effect

on survival was the same as that of growth (Table 1). Communally-reared lobsters exhibit high rates of mortality due to cannibalism, which is associated with the vul-

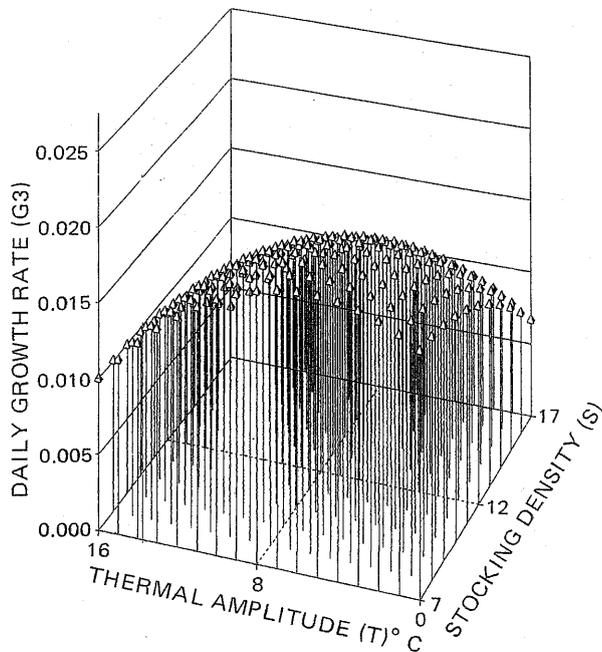


Fig. 5. Estimates of daily growth rate for period three based on $G_3 = 0.013357 + 0.000696 T + 0.000918 S - 0.000074352 T^2 + 0.000017822 TS - 0.000076656 S^2$.

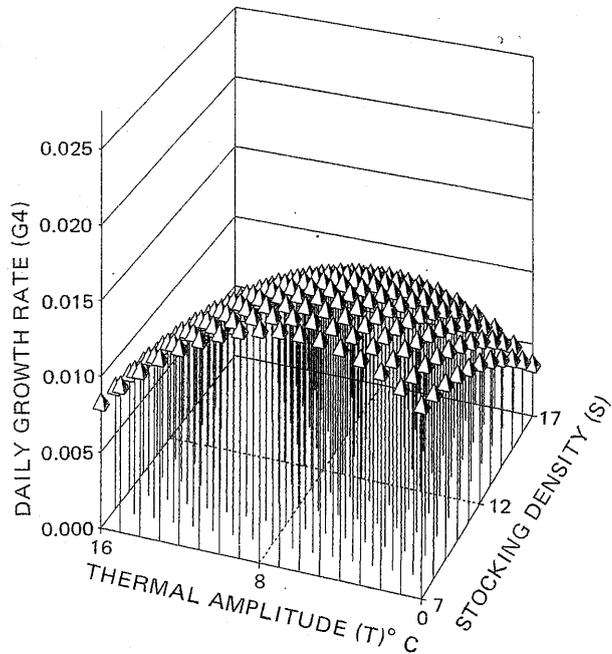


Fig. 6. Estimates of daily growth rate for period four based on $G_4 = 0.012005 + 0.000845 T + 0.000463 S - 0.000075739 T^2 + 0.000015929 TS - 0.000055569 S^2$.

nerability of molting individuals and made worse by inadequate diets (Sastry and Zeitlin-Hale 1977). Even with adequate diets, irregular growth occurs, and some mortality results as dominant individuals defend larger and larger territories (Provenzano Jr. 1985a). During the last two time periods, cannibalism was observed in some aquaria at a stocking density of 12 shrimp per 0.18 m^2 , and cannibalism was frequently noticed in aquaria with a stocking density of 17 shrimp per 0.18 m^2 due to the vulnerability of newly-molted individuals. Moreover, food abundance, water quality, and social behavior are definitely functions of stocking density in any aquatic environment. These results show that the interaction between treatment combination and time on pH and dissolved oxygen are highly significant. Although the lowest dissolved oxygen level was observed

at 4.3 ppm, it was still much higher than the 2.0 ppm critical level suggested by Wickens (1976).

The mean daily growth rate declined chronologically (Table 1); however, the corresponding mean biomass increased at a decreasing rate (Table 1). Many (perhaps most) organisms continue to grow, but at a declining growth rate (Causton 1983); this is further evidenced by the increasing body weight with a decreasing growth rate of *Penaeus penicillatus*, *P. semisulcatus*, and *P. brasiliensis* (Liao and Chao 1987). Figs. 1 and 2 show the patterns of increasing mean biomass and decreasing growth rate for any given treatment combination.

Table 3 shows that thermal amplitude and stocking density interacted significantly ($p = 0.0637$). The interaction effect was evaluated from time period to time period

as a result of the significant effect of time period, with $p < 0.0001$ (Table 3). The response-surface analysis of the present study revealed that most t -tests, for any time period, indicated that the estimated parameters were significantly different from zero. However, a several t -tests suggested that some parameters may have had no significant difference from zero. Consequently, some mathematical terms within a predicted model could be eliminated. For example, Table 5 shows that two values of a t -test in period one were -1.336 and -2.404 , with $p = 0.1894$ and $p = 0.211$, respectively, when testing the parameters of β_{ts} and β_{ss} . A suggested growth model for period one would therefore be:

$$G = 0.010972 + 0.001675 T + 0.001805 S - 0.000099 T^2$$

Such reduced models also appeared for time periods two and four (Table 5). In addition to the reduced models, an interesting phenomenon was noticed from our analysis of lack of fit. The sum of squares due to lack of fit in period three was highly significant at $\alpha = 0.0185$, exposing the inadequacy of the quadratic model in describing the present system (Table 4). A higher-order equation may be required for this specific life stage. In order to maintain the positive energy balance necessary for development, crustaceans may conserve energy by adjusting their metabolic rates to temperature (Sastry 1979). However, metabolic energy expenditure is a major cost factor, and it varies relative to the stage of development and interacting environmental factors (Sastry 1983). Describing this dynamic system, therefore, can not rely on one specific model.

Table 6 summarizes sets of optimal treatment combination intensities for each time period. The optimal stocking densities for periods three and four were below the

designed minimum of 7 shrimp per 0.18 m^2 ; thus, the so-called optimum and its reliability are questionable. Table 6 also displays intercept and regression coefficients of the predicted response-surface model throughout the four periods, suggesting the need for further study of estimated time trend parameters. Data suggest an optimal trade-off between β_s and β_{ss} may be determined in terms of time period. When combining all the parameters, mathematical modeling may help in determining the time period required to maximize culturing productivity.

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溫振幅和放養密度影響紅尾蝦成長之模式

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本文在探討為期120天，溫振幅和放養密度對紅尾蝦單日成長速率之影響。三組溫振幅設計為0°C、8°C和16°C。所謂溫振幅0°C即是將恆溫控制在28°C。至於溫振幅8°C和16°C則是在12小時內將水溫分別從24°C增至32°C以及從20°C增至36°C，而後再在下一個12小時內，將水溫分別降至其起始溫度。密度處理亦有三組，分別是每0.18m²放養7、12和17隻紅尾蝦。每隔30天觀測其成長速率。

結果顯示，在每30天之週期內，成長速率與實驗因子呈二次函數。溫振幅是一抑制因子，因此隨其強度持續增加，將有益成長，或抑制成長。此外，單日成長速率隨放養密度增加而遞減。至於最適宜的溫振幅和放養密度則隨時間週期改變而不同。