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The effects of thermal amplitude on the growth of Chinese shrimp *Fenneropenaeus chinensis* (Osbeck, 1765)

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Abstract

Effects of thermal amplitude of diel fluctuating temperature on the growth, food consumption, food conversion efficiency and apparent digestibility coefficient of Chinese shrimp, *Fenneropenaeus chinensis* (Osbeck), with initial body weight of 0.36 ± 0.04 g were studied at average temperature 25, 28 and 31 °C from May to July, 2000. Among four diel different fluctuation amplitudes of ± 1, ± 2, ± 3 and ± 4°C, the growth rate of shrimp at 25 ± 2, 25 ± 3, 28 ± 2 and 31 ± 1 °C were significantly higher than those at corresponding constant temperatures of 25, 28 and 31 °C, respectively, while growth rate at 31 ± 4 °C was significantly lower than at 31 °C. There is a trend that the optimal thermal amplitude for shrimp growth decreased with the increase of average temperature in the present study. The growth rate of Chinese shrimp was a quadratic function of the thermal amplitude at the same average temperature. Such a growth model may be described by

$$G = \beta_0 + \beta_1(TA) + \beta_2(TA)^2$$

where G represents the specific growth rate on a 33-day basis, TA is thermal amplitude in degree Celsius, β_0 is intercept on G axis, and β_1 and β_2 are the regression coefficients. The optimal thermal amplitude for the growth of shrimp at sizes of this experiment at average temperature of 25, 28 and 31 °C was estimated to be ± 2.0, ± 2.2 and ± 1.4 °C, respectively. The changes of food conversion efficiency were similar to the growth rate, while the trends of food consumption of shrimp between fluctuating temperature and constant temperature were variable at different average temperatures. There was no significant difference in apparent digestibility coefficient between diel fluctuating temperatures and corresponding constant temperatures. Therefore, more food consumption, high food conversion efficiency and more energy partitioned into growth might account for the enhancement in the growth of shrimp at the diel fluctuating temperatures in the present study.

Keywords: Diel fluctuating temperature; Specific growth rate; Food consumption; Food conversion efficiency; *Fenneropenaeus chinensis* (Osbeck)

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1. Introduction

Studies on the influence of temperature on the growth of aquatic animals have been conducted usually under constant temperature regimes. However, temperatures in natural aquatic systems fluctuate diurnally and seasonally. It is desirable, therefore, to determine whether or not accurate predictions of an animal's response to fluctuating temperature regimes can be made from data gained at constant temperatures. Many studies have been conducted to investigate the effects of fluctuating temperatures on a variety of aquatic ectotherms, such as zooplankton (Halbach, 1973; Van As et al., 1980), bivalves (Widdows, 1976; Pilditch and Grant, 1999) and crustaceans (Dame and Vernberg, 1978; Miao and Tu, 1993, 1996), but most have focused on fishes (Biette and Geen, 1980; Cox and Coutant, 1981; Diana, 1984; Konstantinov et al., 1989, 1996; Lyytikäinen and Jobling, 1998, 1999; Sierra et al., 1999; Zdanovich, 1999; Baras et al., 2000). Due to the differences in species and thermal regimes, the results from different studies were quite different from each other.

Chinese shrimp *Fenneropenaeus chinensis* (Osbeck) is a migratory species mainly distributed in the Yellow Sea, which usually migrates for reproduction and overwintering twice yearly among Bohai Sea, Yellow Sea and East China Sea in their natural life cycles (Ge and Wang, 1995; Miao and Tu, 1995). Thus, not only do Chinese shrimp experience temperatures that fluctuate diurnally and seasonally, but they are normally exposed to varying temperatures when they move in water masses, vertically and horizontally, during feeding, swimming or predator avoidance. Until now, although many investigations on the effects of temperature on the growth of Chinese shrimp have been conducted, most of them focus on the effects of constant temperatures (Zhang et al., 1983; Wang et al., 1984; Miao and Tu, 1995; Zhang et al., 1998) and only a few work with the effect of fluctuating temperature on the growth of the shrimp (Miao and Tu, 1996).

This study was designed to compare the growth of Chinese shrimp at constant temperatures and fluctuating thermal regimes and to determine the effects of amplitude of diel thermal fluctuations at different daily average temperatures on the growth of the shrimp. The study will be helpful to elucidate the influence of fluctuating temperature on penaeid shrimp and its mechanism and promote the integration of theory and practice for the bioenergetics of crustacean.

2. Materials and methods

2.1. Experimental shrimp and acclimation

Chinese shrimp juveniles were obtained from the pond of Hongdao Shrimp Farm, Qingdao, PR China. The shrimp were cultured in aerated fiberglass tanks with seawater and maintained at about 25 °C for least 3 days. Then some of them were transferred into two other tanks to be further acclimated to constant temperature of 28 and 31 °C. The ascending or descending rate was 1.5 °C or so per day. When the final temperature was reached, it was maintained for 3 days to ensure complete thermal adaptation. During acclimation, the shrimp were fed twice daily to satiation with a commercial pellet manufactured by the Mawei Fishery Feed Co. Ltd., Fujian, China (Table 1). A 14 h light : 10 h dark photoperiod was maintained.

2.2. Experimental design and facility

Thermal treatments consisted of 3 constant temperatures, 25, 28 and 31 °C, and 12 diel temperature fluctuations ($t \pm \Delta t$ °C) with daily means of 25, 28 and 31 °C. For treatment of diel fluctuating temperature, temperature fluctuations imitated the natural rhythm of field water temperature at the site of the present experiment (36°1′ N, 120°3′ E) and amplitudes of temperature fluctuations ($\pm \Delta t$ °C) were ± 1, ± 2, ± 3 and ± 4 °C, respectively. The minimum temperature ($t - \Delta t$ °C) was set at 0600 hours and was increased gradually to the maximum one ($t + \Delta t$ °C) at 1400 hours, then was decreased to the minimum once again at 0600 hours the next day (refer to Tian et al., 2004b).

The experiment was conducted in a room whose temperature was controlled at 20 ± 0.5 °C using an air conditioner. Four glass aquaria ($45 \times 25 \times 30$ cm,

Table 1
Proximate composition (%, mean ± S.E.) of the experimental diet

Protein (%)	Lipid (%)	Ash (%)	Energy (kJ/g)	Moisture (%)
43.39 ± 0.22	9.74 ± 0.30	9.91 ± 005	16.88 ± 0.11	8.41 ± 0.06

water volume 35 l) were immersed in one water bath tank (170 × 75 × 30 cm) which controlled the temperature of the aquaria. Each aquarium was covered with 5-mm screen to prevent the shrimp from jumping out. Two circulating pumps (35 W) were applied in each water bath to ensure the even distribution of water temperature in the bath. Two systems were applied to control different water thermal regimes. Constant temperature was achieved by the thermostatic regulation of immersion heaters (WMZK-01). The actual temperature was calibrated daily with a mercury thermal meter to the nearest 0.1 °C. For treatment of temperature fluctuations, the increase, decrease and maintenance of temperature are controlled by a preprogrammed temperature controller, which is specially designed to generate the needed temperature regimes by controlling the heater against the cooling coil.

2.3. Experimental procedure and management

When thermal acclimation was finished, 20 shrimp were chosen randomly from 25 °C thermal acclimation tanks and individually weighed and stocked into four aquaria for corresponding temperature treatment, i.e., constant temperature of 25 °C and diel thermal fluctuations, 25 ± 1, 25 ± 2, 25 ± 3 and 25 ± 4 °C, with each aquarium holding five individuals after 24-h feed deprivation. The same procedure was applied to randomly chosen shrimp, from 28 and 31 °C thermal acclimation tanks, that were stocked into aquaria for the corresponding constant and diel temperature fluctuation treatments, respectively. There were four replicates for each thermal treatment. During the experiment, the shrimp were fed twice to satiation daily (at 0600 and 1800 hours) with the commercial pellet mentioned above. The uneaten feed and feces were separately collected into cups by siphon within 1.5 h after each meal. The collected uneaten feed and feces were settled and then the water above was removed carefully. The molted exuviae (molted exoskeletons) were collected at times. The collected uneaten feed, feces and exuviae were dried at 65 °C and kept for further analysis. Food consumption was estimated from the difference in dry weight between the amount of food applied into the aquarium and food uneaten. At the end of the experiment, all the test shrimp were collected after 24-h starvation and dried at 65 °C for 48 h.

The experiment was conducted from May 30, 2000 to July 2, 2000 and no shrimp died during the experiment. Water exchanges were made to all treatments at the same time and from the same water source. Aeration was provided continuously and one-half to two-thirds of the water volume was changed every other day to ensure suitable water quality. Seawater used in the experiment was filtered by composite sand filter. During the course of the experiment, dissolved oxygen was maintained above 6.0 mg/l, the pH was around 7.8, ammonia was less than 0.24 mg/l, the salinity of seawater was within 28–30 ppt, and a simulated natural photoperiod (14 L : 10 D, light/darkness) was maintained.

2.4. Data calculation and statistical analysis

All indices were calculated as follows:

$$\mathrm{SGR} = 100 \times \frac{\ln W_t - \ln W_0}{T}$$

$$\mathrm{RSGR} = 100 \times \frac{\mathrm{SGR}(t \pm \Delta t) - \mathrm{SGR}t}{\mathrm{SGR}t}$$

$$\mathrm{FCE} = 100 \times \frac{W_t - W_0}{C}$$

$$\mathrm{ADC} = 100 \times \frac{C - F}{C}$$

where SGR is specific growth rate (SGR, %/d), RSGR is relative specific growth, FCE is food conversion efficiency (%), ADC is apparent digestibility coefficient (%), W_t and W_0 are final and initial weights (g), T is the feeding duration (d), C is daily food consumption (g), and F is daily faecal production (g). t is mean temperature, Δt is the amplitude of temperature fluctuations, and $t \pm \Delta t$ means diel fluctuating temperature.

Experimental data were analyzed using SPSS 10.0 (SPSS Inc., Richmond, CA, USA), with possible differences among data being tested by ANOVA. Duncan's multiple range test was used to test the differences between treatments. $P < 0.05$ was accepted as the level of statistical significance. Log transformations were used to homogenize the variance of body weight and length before data analyses. Arc-sine transformations were used for feeding rate, food con-

Table 2
Growth of *F. chinensis* (Osbeck) at different thermal regimes

Treatments	Mean temperature (t, °C)	Fluctuation amplitude (Δt, °C)	Initial weight (g)	Final weight (g)	Duration (d)	Daily increments (mg/d)
CT25	25	0	0.35 ± 0.03	0.86 ± 0.09^{a}	33	15.55 ± 1.85^{a}
F25.1	25	1	0.33 ± 0.05	0.94 ± 0.03^{ab}	33	18.27 ± 1.67^{ab}
F25.2	25	2	0.35 ± 0.06	1.09 ± 0.08^{b}	33	22.42 ± 1.62^{b}
F25.3	25	3	0.34 ± 0.06	1.05 ± 0.05^{b}	33	21.32 ± 2.36^{b}
F25.4	25	4	0.36 ± 0.01	0.82 ± 0.09^{a}	33	15.49 ± 2.41^{a}
CT28	28	0	0.35 ± 0.03	0.96 ± 0.08^{a}	33	18.67 ± 3.23^{ac}
F28.1	28	1	0.34 ± 0.06	1.19 ± 0.16^{ab}	33	25.69 ± 1.93^{ab}
F28.2	28	2	0.34 ± 0.02	1.32 ± 0.07^{b}	33	29.61 ± 1.65^{b}
F28.3	28	3	0.35 ± 0.04	1.17 ± 0.13^{ab}	33	24.70 ± 1.69^{ab}
F28.4	28	4	0.37 ± 0.05	0.88 ± 0.07^{a}	33	15.44 ± 2.02^{c}
CT31	31	0	0.36 ± 0.03	1.07 ± 0.08^{a}	33	21.43 ± 0.70^{b}
F31.1	31	1	0.35 ± 0.01	1.38 ± 0.01^{b}	33	31.07 ± 0.49^{a}
F31.2	31	2	0.35 ± 0.01	1.23 ± 0.06^{ab}	33	26.65 ± 0.54^{a}
F31.3	31	3	0.36 ± 0.03	1.10 ± 0.11^{a}	33	22.63 ± 0.69^{b}
F31.4	31	4	0.35 ± 0.01	0.85 ± 0.01^{a}	33	15.16 ± 0.49^{c}

Means with different letters in the same row were significantly different ($P<0.05$).

version efficiency and apparent digestibility coefficient to normalize the data distribution.

3. Results

The daily increments in body weight and specific growth rate (SGR) of Chinese shrimp at different thermal regimes were shown in Table 2 and Fig. 1. It can be seen that same thermal amplitude of temperature fluctuations had various influences on the growth of test shrimp at different average temperature. SGR of shrimp at 25 ± 2 and 25 ± 3 °C were significantly higher than those at constant temperature of 25 °C ($P<0.05$), while no significant difference was found among 25 ± 1, 25 ± 4 and 25 °C ($P>0.05$). The shrimp at 28 ± 2 °C grew significantly better than at 28 °C ($P<0.05$). Among four fluctuating temperatures at 28 °C, SGR of shrimp at 28 ± 4 °C was lowest and not significantly different from that at constant temperature of 28 °C ($P>0.05$). SGR of shrimp at 31 ± 1 °C was signif-

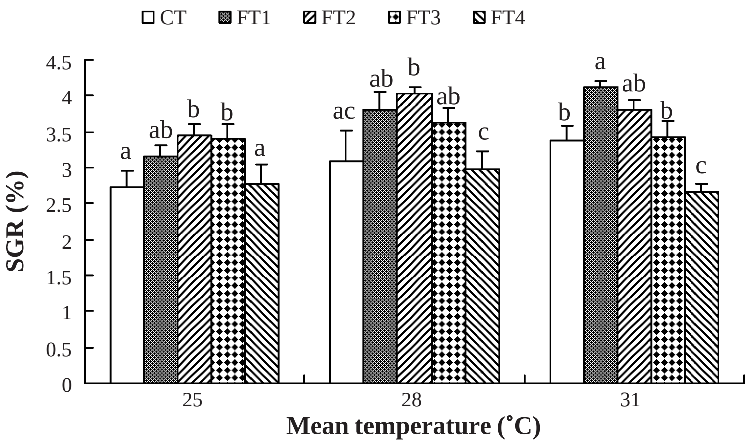

Fig. 1. The specific growth rate (SGR) of juvenile *F. chinensis* (Osbeck) at different thermal regimes CT, shrimp grown at constant temperature; FT1, FT2, FT3 and FT4, shrimp grown at different fluctuating temperatures with fluctuation amplitude of ± 1, ± 2, ± 3 and ± 4. Means with different letters in the same average temperatures are significantly different ($P<0.05$). Error bars represent 1 S.E.

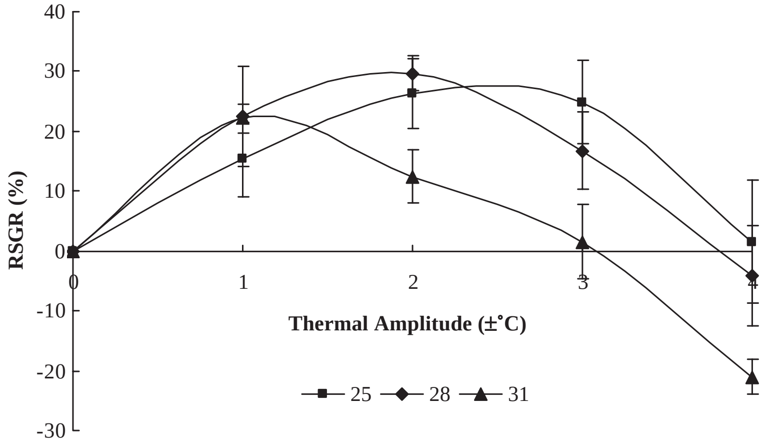

Fig. 2. Relative specific growth rate (RSGR) in body weight [in percent (%), $100\times(\mathrm{SGR}_{(t\pm\Delta t)}-\mathrm{SGR}_t)/\mathrm{SGR}_t$] of juvenile *F. chinensis* (Osbeck) at different thermal regimes. Error bars represent 1 S.E.

icantly higher than those at 31 ± 3, 31 ± 4 and 31 °C ($P<0.05$) but not significantly different from that at 31 ± 2 °C ($P>0.05$). The poorest growth of shrimp occurred at 31 ± 4 °C and the growth rate was significantly lower than at 31 °C ($P<0.05$). The relative specific growth rate of Chinese shrimp at different thermal regime was shown in Fig. 2. It can be seen that there was a trend that the optimum fluctuation amplitude decreased with the increase of average temperatures from 25 to 31 °C.

Referring to the studies of Miao and Tu (1996), the specific growth rate (SGR) was a quadratic polynomial function of the studied thermal amplitude. Consequently, SGR at corresponding mean temperature can be described by the following equation

$$G=\beta_0+\beta_1(TA)+\beta_2(TA)^2$$

where G represents the specific growth rate on a 33-day basis, TA is thermal amplitude in degree Celsius, β_0 is the intercept on the G axis, and β_1 and β_2 are the regression coefficients, respectively (Table 3). According to the equation, the optimal thermal amplitude to the growth of shrimp at sizes of experiment at mean temperature of 25, 28 and 31 °C was estimated to be ± 2.0, ± 2.2 and ± 1.4 °C, respectively.

The food consumption (FC) of shrimp increased with the increase of average temperature totally. The changes of FC of shrimp were different at various average temperatures. The shrimp at 25 ± 2 and 25 ± 3 °C consumed more food than those shrimp at constant temperature of 25 °C ($P<0.05$). FC for shrimp at fluctuating temperature whose thermal amplitudes were ± 1, ± 2 and ± 3 °C were significantly higher than at constant 28 °C ($P<0.05$). FC of shrimp at fluctuation amplitudes of ± 1 and ± 2 °C were significantly higher than at corresponding constant temperature of 31 °C ($P<0.05$). However, there was no significant difference between FC for shrimp under thermal amplitude of ± 4 °C and those at corresponding constant temperatures ($P>0.05$). (Fig. 3).

Table 3
The regression relation of specific growth rate of *F. chinensis* (Osbeck) to the thermal amplitude at different average temperatures

Mean temperature (°C)	No. samples	$G=\beta_0+\beta_1$ (TA)$+\beta_2$ TA^2							
		β_0	SE	β_1	SE	β_2	SE	R^2	F
25	20	2.686	0.111	0.735	0.132	−0.175	0.032	0.724	15.757*
28	20	3.078	0.136	1.055	0.161	−0.274	0.039	0.845	32.711**
31	20	3.376	0.110	0.745	0.130	−0.264	0.313	0.873	41.265**

G, the specific growth rate on a 33-day basis; TA, thermal amplitude in degree Celsius; β_1, intercept on SGR axis; β_1 and β_2, regression coefficients; and SE, standard error. *$P<0.05$ and **$P<0.01$.

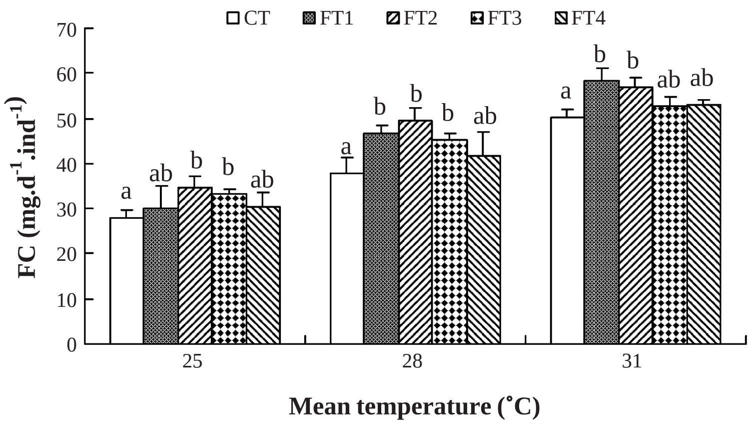

Fig. 3. The food consumption of juvenile *F. chinensis* (Osbeck) at different thermal regimes. For treatment abbreviations, refer to Fig. 1.

There was no significant difference in the apparent digestibility coefficient (ADC) of Chinese shrimp at different thermal regimes (Fig. 4).

The food conversion efficiencies (FCE) of shrimp at 25 ± 2 and 25 ± 3 °C were significantly higher than that at constant 25 °C, while there was no significant difference between 25 ± 1, 25 ± 2 and constant 25 °C. Among four fluctuating thermal regimes at average temperature of 28 °C, FCE of shrimp was highest at 28 ± 2 °C and significantly higher than at constant 28 °C. The lowest FCE revealed in the shrimp at 28 ± 4 °C, which was significantly lower than at constant 28 °C. The shrimp have the highest FCE at 31 ± 1 °C, which is significantly higher than those at 31, 31 ± 3 and 31 ± 4 °C. FCE in shrimp of 31 ± 4 °C was significant lower than at constant temperature of 31 °C. (Fig. 5)

4. Discussion

A temperature fluctuating between 10 and 20 °C does not necessarily have the same effect on organisms as a constant temperature of 15 °C (Odum, 1983). Although results from different investigators were variable, many studies on the effects of fluctuating temperatures on aquatic animals indicated that fluctuating temperatures within the limit of the ecological norms for a species enhanced the growth of aquatic ectotherms (Van As et al., 1980; Miao and Tu,

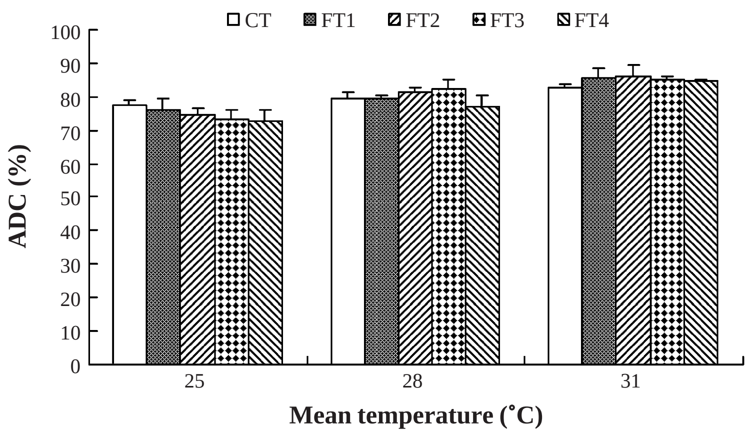

Fig. 4. The apparent digestibility coefficient (ADC) of juvenile *F. chinensis* (Osbeck) at different thermal regimes. For treatment abbreviations, refer to Fig. 1.

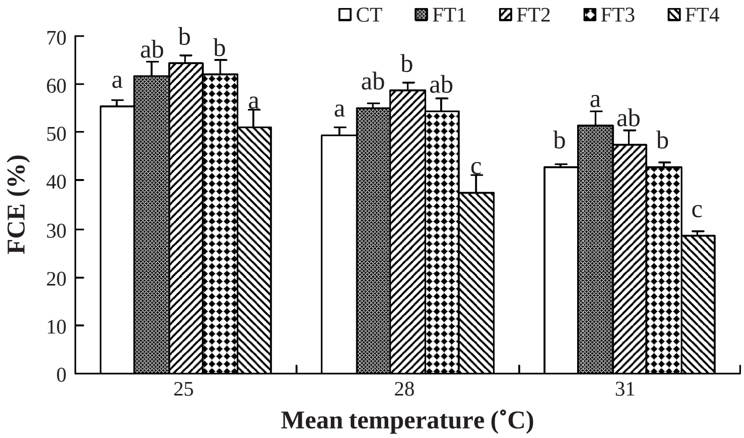

Fig. 5. The food conversion efficiency of juvenile *F. chinensis* (Osbeck) at different thermal regimes. For treatment abbreviations, refer to Fig. 1.

1996; Pilditch and Grant, 1999; Sierra et al., 1999; Zdanovich, 1999; Baras et al., 2000). The positive influence of fluctuating temperatures on the growth of crustaceans has been reported in cladocerans, copepods, crab and penaeid shrimp. The development and growth of *Daphnia pulex*, *Pseudocalanus minutus*, larvae of mud-crab *Rhithropanopeus harrissi*, juvenile Chinese mitten crab *Eriocheir sinensis*, juvenile redtail shrimp *F. penicillatus* and juvenile Chinese shrimp increased at moderate diel fluctuating thermal regimes (Lock and Mclaren, 1970; Costlow and Bookhouk, 1971; Halbach, 1973; Van As, 1980; Miao and Tu, 1993, 1996; Wang, 1999). Results from this study showed that thermal amplitude on a daily basis affected the growth of Chinese shrimp differently. At average temperature of 25 °C, the temperature fluctuation of ± 2 and ± 3 °C produced better growth than constant temperature of 25 °C and shrimp at 28 ± 2 and 31 ± 1 °C exhibited better growth than those at corresponding constant temperature of 28 and 31 °C, respectively. However, the higher fluctuation of ± 4 °C did not show any positive influence on growth of shrimp at three average temperatures. On the contrary, it seemed that high temperature fluctuations reduced the scope for growth. Growth rate of shrimp at 31 ± 4 °C was significantly lower than those at 31 °C. The general conclusion that could be drawn from these data is that temperature fluctuations either produce higher or lower growth rates than that of a constant temperature depending on not only levels of thermal amplitude around that given temperature but also levels of average temperature. There was a trend for the optimal amplitude of fluctuation for growth of Chinese shrimp to decrease with increase of average temperature. According to the previous studies, the optimum constant temperature for Chinese shrimp is 31 °C and temperature beyond 31 °C will inhibit their growth (Miao and Tu, 1995; Tian et al., 2004a). Thus, the upper value of thermal fluctuation at high average temperature will be beyond the limit of the ecological norms and eliminate the advantage in growth provided by optimal fluctuating temperature, which may account for our observation.

The effects of thermal amplitude on aquatic animals are species-specific. Studies from fishes revealed that the amplitude of temperature fluctuations that did not go beyond the limit of the ecological norms favor the growth of fishes, whereas fluctuations with very small amplitude do not affect the growth even if their frequency causes sufficiently high rate of temperature changes (Konstantinov et al., 1989). Usually, the optimal thermal amplitude for eurythermic species was greater than those for stenothermic ones. Temperature fluctuations in the range of 8–12 °C ($\pm$4–6 °C) are optimum for the growth of eurythermic fishes such as juvenile common carp, *Cyprinus carpio*, goldfish, *Carassius auratus*, white amur, *Ctenopharyngodon idella*, gudgeon, *Gobio gobio*, goloveshka, *Percottus glehni* and tilapia, *Oreochromis niloticus*, *O. mossambicus*, *O. aureus*, *Ictalurus punctatus*, etc., when its upper value does not cross the ecological limits of the species (Konstantinov et al., 1989, 1996; Gui et al., 1989; Sierra et al., 1999; Baras et al., 2000). In contrast, the range of temperature fluctuations for the stenothermic fishes such as hemigramis *Hemigrammus caudovittatus* is much narrower (3–4 °C, i.e., ±1.5–2 °C) (Konstantinov et al., 1989). Compared to those in fishes, the influences of amplitude on growth of crustaceans have been reported less thoroughly. Most of them focused on larval survival and development of crab (Costlow and Bookhouk, 1971; Sastry, 1975, 1983) and few studies deal with the influence of daily fluctuations amplitude. Miao and Tu (1993, 1996) reported that the amplitude of temperature variation might significantly affect the growth of redtail shrimp *F. penicillatus* and Chinese shrimp as compared to constant temperature at the average value of the fluctuations. The growth rate of Chinese shrimp increased with increasing thermal amplitude from 0 to 4 °C but dropped rapidly from 4 to 8 °C at average temperature of 31 °C (Miao and Tu, 1996). In comparison with fishes, the range of temperature fluctuations favoring growth in penaeid shrimp was much smaller (Miao and Tu, 1993, 1996). In this study, the optimal amplitude of temperature fluctuation for growth of Chinese shrimp was ±1, 2 and 3 °C under three average temperatures, which were much smaller than those in eurythermic fishes and similar to stenothermic ones, although Chinese shrimp is a eurythermic species (Wang and Ma, 1990).

Until now, few investigations have probed into what may contribute to the enhancement in growth of crustaceans although the positive influence of fluctuating temperatures on the development and growth of larvae and juvenile of crab and penaeid shrimp has been reported in some species (Costlow and Bookhouk, 1971; Sastry, 1975; Sastry, 1983; Miao and Tu, 1996; Wang, 1999). Studies from Dame and Vernberg (1978) indicated that diel fluctuating temperature regimes significantly depressed oxygen consumption in the 15–25 °C temperature range in the mud crab *Panopeus herbstii* and the fiddler crab *Uca pugilator* when compared to rates of animals subjected to constant acclimation rates. Since this depression of metabolic rates occurs over that portion of the yearly temperature range within which the animals are most active, it is suggested that these organisms utilize energy more efficiently when subjected to natural cyclic temperature conditions than when subjected to constant temperature environments. Tian et al. (2004b) also found that the oxygen consumption of Chinese shrimp at fluctuating temperatures of 27±3 °C was significantly lower than that at a constant temperature of 27 °C, which could partially explain the increased growth at same fluctuating temperatures (Tian, unpublished data). In the present study, contrary to those at corresponding constant temperature, increased food consumption and better food efficiency were found in shrimp at four fluctuating temperatures that favored the growth of shrimp, whereas there was no difference in apparent digestibility coefficient between diel fluctuating temperature and corresponding constant temperature. Thus, energetic advantage at optimal diel fluctuating temperatures, i.e., high food conversion efficiency, reduced metabolism, as well as more food consumption might account for the enhancement in growth of shrimp in the present study.

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