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Original Article

Effects of water temperature rise on energy budget allocation in Pacific white shrimp (*Litopenaeus vannamei*)

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Abstract

Shrimp farming is suffering from slow growth and high feed intake due to the rise of water temperature during summer. In this study, physiology and bioenergetics of juvenile *Litopenaeus vannamei* reared for 4 weeks at ambient (29 °C) and excessive (33 °C) temperatures were evaluated. Obtained data of feed intake (C), growth rate (P), apparent heat index (AHI), oxygen consumption (R), fecal loss (F), ammonia excretion (U), and molting (M) were converted to energy equivalents. The results indicated that growth energy for shrimp (R+AHI+F) at 33 °C was 1.8-fold higher than that of shrimp at 29°C. Most energy contents (AHI, R, F, U) reared at 33 °C was significantly higher than that of shrimp at 29°C except M and P. Shrimp reared at 33 °C have lost their weight energy by 14.15 %. This indicated that shrimp reared at excessive temperature suffered from insufficient energy for growth.

Keywords: thermal stress, global warming, energy expenditure, oxygen consumption, growth performance

1. Introduction

Climate changes have caused a wide range of impacts on natural systems all around the world. In Thailand, the average temperature peak in summer (April) was higher than 40 °C and continues to rise each year (Meteorological Development Bureau, 2016). Water temperature is recognized as one of the most influencing factors on behavior and physiology of aquatic ectotherms (Sun, Chen, & Huang, 2006) and causing stresses to aquatic life (Chabot & Guénette, 2013).

Farming of Pacific White shrimp, *Litopenaeus vannamei*, has also suffered a great deal from this global impact. As tropical Penaeid species, *L. vannamei* is quite tolerant to a wide range of temperature (20°C to 32°C). However, above 32 °C, shrimps started to feed more diet but grew less efficiently and mortality rate was high (Wyban, Walsh, & Godin, 1995; Limsuwan *et al.*, 2009). Numerous reports indicated that excessive high temperature beyond tolerant level decreased growth and feed intake, and increased energy expenditure (Atkins, & Benfey, 2008).

Energy budget is a balance between energy income and expenditure. It is channeled between the activities of growth, metabolism, ammonia excretion, feces, and molting (in case of crustacean) (Lemos & Phan, 2001). The energy balance within an organism, as determined by biosynthetic reactions can be measured with the equation C = P + R + F+

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U + AHI + M, where C is the energy obtained from food consumption, P is energy utilized for tissue production, R is the energy used in respiratory metabolism, F is energy lost in feces, U is energy lost through nitrogen excretion, AHI is the energy cost of food digestion and consumption, and M is the energy used for molting (Petrusewicz & Macfadyen, 1970).

Energy budget of shrimps vary depending on varieties of life stage, nutrition, and environmental factors (Maldonado *et al.*, 2009; Su, Ma, &Feng, 2010; Ye *et al.*, 2009). Most of the previous studies focused on the ambient conditions of the tested animals. In this study, we investigated juvenile shrimps of an approximate size of 10 g or higher; a size where most shrimp production loss occurred, mainly during summer. The shrimp for experiment were reared at different temperatures (33 °C) for four weeks. During the experiment, R, AHI, U, F, M, and P of the experimental shrimp were evaluated. Obtained results will be helpful for addressing the low growth rate issues and developing an effective solution for shrimp culture during excessive temperature.

2. Materials and Methods

2.1. Maintenance of experimental animals

Juvenile *L. vannamei* (10.30±0.27 g) from commercial farm were transported to the experimental facility and acclimatized for seven days in 10 m × 10 m × 1.5 m concrete tanks filled with 29 °C, 25 psu seawater, 50% water changes, and fed four times daily with commercial feed pellets (38% crude protein and 4% lipid, Krungthai Food Public co., Ltd). Appropriate water qualities (pH 8-8.3, total NH_3-N < 0.15 mg N/L, nitrite <0.08 mg N/L, nitrate <32 mg N/L, and alkalinity >200 ppm) were maintained. Acclimatized shrimps (n=10) were individually reared in separate experimental chambers. Temperature of each experimental tank was controlled by a thermostat heater at 29 °C or 33 °C (Figure 1A and 1B). The experiment was conducted for seven days.

2.2 Estimation of the energy budget and rates of physiological process

Energy balances were evaluated using equation:

$$C= P+R+AHI+F+U+M$$

where C is food intake, P is somatic growth, R is oxygen consumption, AHI is apparent heat increment, F is feces, U is ammonium excretion, and M is molting energy (M), (Petrusewicz & Macfadyen, 1970).

2.2.1 Oxygen consumption

Individual shrimp was starved for 24 hrs to reduce the effect of apparent heat increment (AHI) before transferring to a respirometer. The respirometer (clear 800 mL acrylic tube) with a dissolved oxygen probe (Hanna HI 9147, USA) attached at one end was submerged in a temperature controlled water bath. The shrimp in the chamber was placed in the respirometer for 30 min. Dissolved oxygen was measured every 5 min for 30 min. (Figure 1C) Weight-specific oxygen consumption measurements were expressed in (mg O_2/g dry wt/hr) and calculated using the exocaloric coefficient of 3.53 cal/mg O_2 consumed (Elliot & Davison, 1975).

Shrimps from the respirometer were brought back to their experimental chambers, fed normally for 24 hrs then transferred back to the respirometer for AHI measurement. This time, shrimps were fed to satiation 30 min before measurement. R was calculated from the oxygen consumed by the unfed shrimp whereas AHI was calculated from the difference between the oxygen consumed by fed and unfed shrimp (Figure 1C).

2.2.2 Ammonia excretion measurements

Water (250 mL) from the respirometer (Figure 1C) was taken before and after the oxygen consumption experiment and quantified the ammonium concentration using blue indophenol method (Strickland & Passons, 1972). Briefly, sample (10 ml) was mixed with Phenol (0.5 ml), sodium nitroprusside (0.5 ml), and oxidizing agent (1ml). After 1 hr, the absorbance at 640 nm of the mixture was measured using spectrophotometer. Excreted ammonia concentration was converted into energy units using value of 20.5 J/mg N-NH_3 (Elliott & Davison, 1975).

2.2.3 Food consumption, feces, and molting energy measurements

Shrimps subjected to R and AHI measurements were individually kept in separated experimental chambers and further reared for 4 weeks. Excess feed, feces, and molt cascades were measured following a protocol of Vernberg and Piyatiratitivorakul (1998). Briefly, feed leftover was collected by siphoning 30 min after feeding. Feces were collected by siphoning every 1 hr after feeding. Molting was monitored every morning and the molting cascades were collected when present. All collected samples were oven-dried (60 °C) for gross energy content analysis using an Isoperibo Bomb calorimeter (AC-350 Leco Corporation, USA). The resulting calorie values were converted into Joules using the conversion factor of 1 calorie equal to 4.1840 Joules (Gnaiger, 1983). The difference between consumed energy and energy lost in feces was calculated to determine the absorbed energy (Ab). The percentage of absorbed energy to consumed energy was calculated to obtain the absorption efficiency energy (AbE) values (Elliott & Davison, 1975).

2.2.4 Scope for growth energy measurement

The scope for growth (P) was determined as described by Vernberg and Piyatiratitivorakul (1998). Prior to the experiment, the standard growth curve of normal shrimp was constructed under normal laboratory condition (similar to the condition in 2.1). Shrimps at the weight of 9, 10, 11, 12, 13, 14, 15, 16, and 17 g (5 shrimps each) were collected, freeze dried, and ground thoroughly. The energy content of the ground shrimp was analyzed using Isoperibo Bomb calorimeter. The standard curve of shrimp growth was plotted using the obtaining energy content of the shrimps from each weight

$$\text{Energy content (J/g)} = 3603.2 \times \text{dry weight (g)} - (2011.5) \quad (R^2 = 0.99)$$

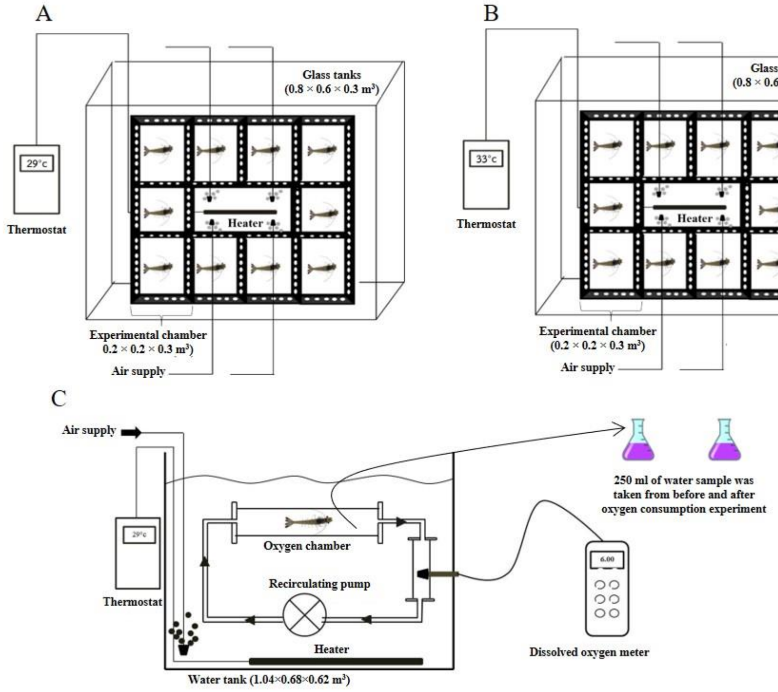

Figure 1. Design of experimental chamber for the juvenile *L. vannamei* reared at 29 (A) 33 °C (B) and respirometer setup for oxygen consumption, apparent heat increment and ammonia excretion measurement (C)

For the experiment, shrimps reared at either 29°C or 33°C were weighted every week (n=5) and then returned to the experimental chambers. The energy contents were then obtained from the equation above. The experiment was carried out for 4 weeks. The difference between the final and initial weights of experimental and standard shrimp weight were used for determining the corresponding somatic growth energy.

2.3 Statistical analysis

Independent samples t-tests were used to examine the mean differences in characteristics measured between the study groups. Results were measured statistically significant at $P<0.05$.

3. Results

3.1 Oxygen consumption

Oxygen consumption of shrimps at 29°C were 20.42 ± 5.08 mg O_2/L/g d.w./day while shrimps at 33°C were 34.83 ± 1.67 mg O_2/L/g d.w./day (Figure 2A) The calculated routine metabolic energy were 301.62 ± 75.03 and 514.43±24.64 J/g d.w./day, respectively (Figure 2B). The oxygen consumption and metabolic energy of shrimps at 33°C were significantly higher than that of shrimps at 29°C ($P<0.05$).

3.2 Apparent heat increment

Energy used for digestion and absorption of the shrimps at 29°C were 359.02 ± 66.66 J/g d.w./day while that of the shrimps at 33°C were 639.94 ± 38.19 J/g d.w./day. (Figure 2C). AHI was calculated by the difference between fed and no fed shrimps. At 29°C, AHI of the shrimps was 57.40 ± 33.66 J/g d.w./day while AHI of the shrimps at 33°C was 125.52 ± 39.33 J/g d.w./day which was significantly higher ($P<0.05$) (Figure 2D). This indicated that shrimps at 33°C lose more than two folds of energy when compared to the shrimps at 29°C.

3.2 Ammonia excretion

The ammonia excretion was measured from the water in the respirometer during the shrimp was tested. The result revealed that ammonia concentration (and calculated energy loss) at 29°C was 4.03 ± 0.48 mg N-NH_3/g d.w./day (40.54 ±6.15J/g d.w./day) while that of 33 °C was 8.68 ± 2.50 mg N-NH_3/g d.w./day (88.93±25.63 J/g d.w./day) which was significantly higher ($P<0.05$) (Figure 2E). This indicated that ammonia excretion of the shrimps at 33°C were significantly higher than that of shrimps at 29°C (Figure 2F).

3.3 Food consumption, feces, and molting energy measurements

3.3.1 Food consumption

During the experiment, feed intakes of shrimps at 33°C were slightly increased in week 2 and remained the same levels in week 3 and 4 while it was decreased in shrimp at 29°C in week 2 and no significant change in week 3 and 4. At week 1, there was no significant difference of feed intake between shrimp at 29 and 33°C ($P>0.05$). At week 2 and 3, Feed intake of shrimp reared at 33°C were significantly higher than that of shrimp reared at 29°C ($P<0.05$). At week 4, there

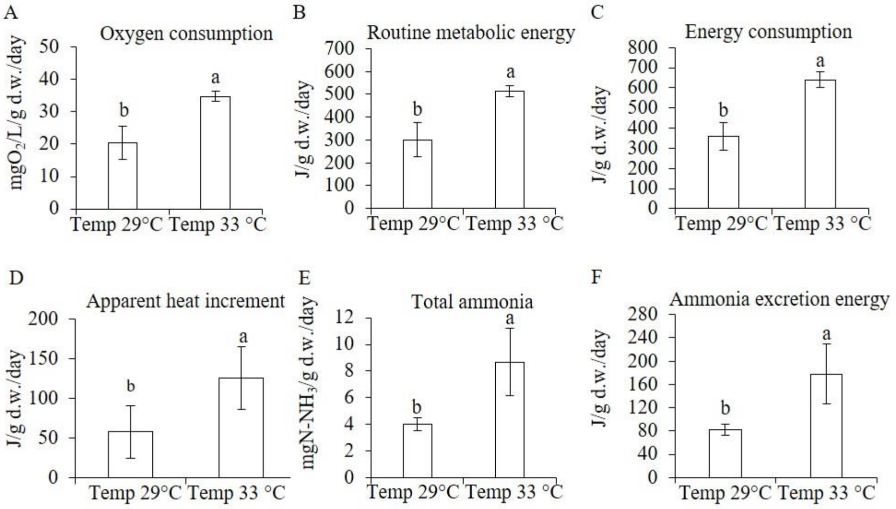

Figure 2. Effect of temperature on oxygen consumption (A), Metabolic energy, conversion of oxygen consumption to joule (B), Energy consumption, conversion of oxygen consumption of fed shrimp to joule (C), Apparent heat increment (D), Ammonia concentration (E) and Ammonia excretion energy (F) of the juvenile *L. vannamei* maintained at 29 and 33°C

was no significant difference between that of shrimp from those 2 treatments (P>0.05) (Figure 3A).

The calculated ingestion energy of shrimps reared at 33 °C (2,705.81 ± 213.09 J/g d.w./day) were significantly higher than that of shrimp reared at 29 °C (1,929.25 ± 319.07 J/g d.w./day) (P<0.05) while there was no significant difference of the absorbed energy between the shrimps reared in both 29 and 33 °C (665.91 ± 67.66 and 718.16 ± 103.28 J/g d.w./day, respectively) (Figure 3B) and the absorption efficiency energy between the shrimp reared in both 29 and 33 °C (35.50 ± 7.89 and 26.90 ± 5.89 %, respectively) (P>0.05) (Figure 3C)

3.3.2 Fecal energy

Calculated fecal energy loss from the shrimp at 33 °C (1,987.64±309.88 J/g d.w. shrimp/day) was significantly higher than that of shrimp at 29 °C (1,263.34±361.66 J/g d.w. shrimp/day) (P<0.05) (Figure 3D).

3.3.3 Molting energy

The molting frequency of shrimp at 33 °C (3.5±0.54 times) were significantly higher than that of shrimp reared at 29 °C (2.45±0.54 times) (P<0.05) (Figure 3E) while there was no significant difference of energy loss between shrimps reared at 29 and 33 °C (73.45±10.05 and 66.10±10.14 J/g d.w. shrimp/day, respectively) (P>0.05) (Figure 3F).

3.4 Somatic growth energy

Average weight of shrimps reared at 29 and 33 °C were shown in Figure 4 A. The average somatic growth energy of the shrimps reared at 29 °C increased by 150.82±32.27 J/g d.w. shrimp/day while that of the shrimps reared at 33 °C decreased by 165.75±57.37 J/g d.w. shrimp/day (P<0.05) (Figure 4B).

4. Discussion

Oxygen consumption energy of the shrimp reared at 33 °C was significantly higher than that of shrimp reared at 29 °C, indicating that higher temperature led to elevated oxygen consumption. This result was in agreement with other studies in *L. Vannamei* (29 °C: 77.22 and 32 °C: 89.13 mg O_2/kg/h) (González *et al.*, 2010), *Panulirus argus* (20 °C: 15 and 28 °C: 75 mg O_2/kg/h) (Perera, Díaz-Iglesias, Illiana, Carrillo, & Galich, 2007), and *Pandalus borealis* (5 °C: 38 and 8 °C: 48 mg O_2/kg/h) (Daoud, Chabot, Cèline, &, Lambert, 2007). Additionally, increases in oxygen consumption during feeding are attributed to AHI, which takes into the processes of ingestion, digestion, and feed absorption that represent energy conversion steps in metabolism. AHI has been found to be influenced by diet composition, ration level, size, water temperature, and the production and excretion of ammonia (Bhaskar, 2016). In this experiment, shrimp reared at 33 °C displayed significantly higher AHI values than shrimp reared at 29 °C. Energy expenditures associated with increased temperature during feeding are very small compared to those at optimal temperature.

This study demonstrated that raising water temperature stimulated ammonia excretion in *L. vannamei.* Nitrogen waste left over from protein metabolism is excreted through ammonia and ammonium ions and the energy used for removal of ammonia is called ammonia excretion energy (U). The U value for shrimp reared at 33°C was higher than that of shrimp reared at 29 °C (Figure 5A). This indicated that high water temperature led to increased protein degradation in shrimp muscles to compensate the extra energy requirements. Significant effects of elevated temperature on ammonium excretion have also been reported in some commercial crustacean species such as, *Macrobrachium rosenbergii* (Chu & Tau, 1996), *Litopenaeus stylirostris* (Herrera, Re, Sierra, & Díaz-Iglesias 2004) and *L. vannamei* (Jiang, Lawrence, Neil, & Gong, 2000).

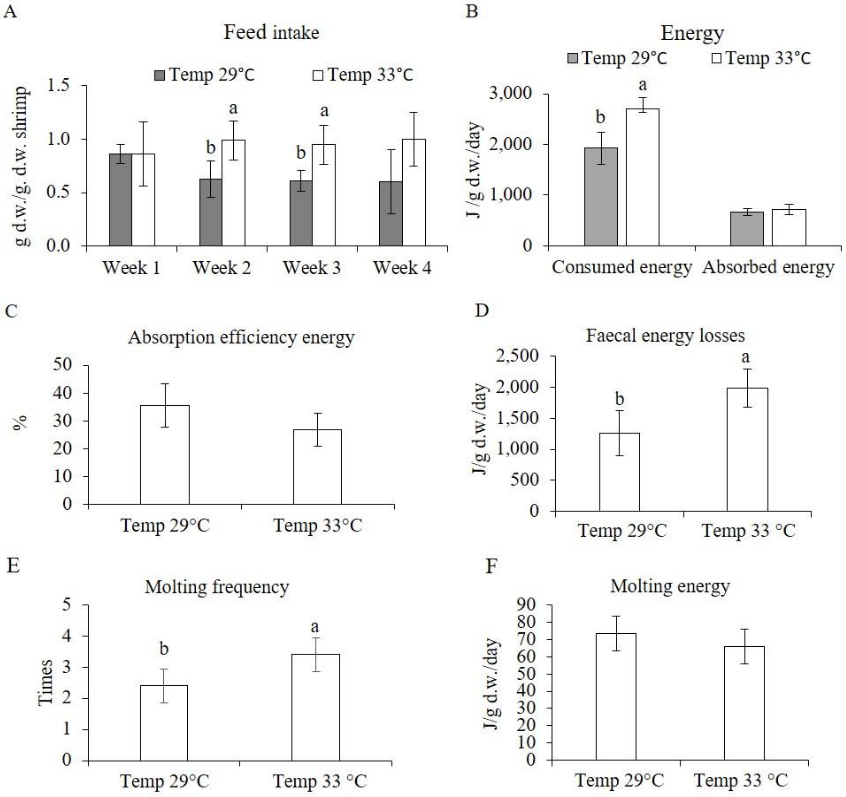

Figure 3. Feed intake (gram of d.w. diet/gram of d.w. shrimp) (A), calculated consumed, and absorbed energy (J/g d.w. shrimp /day) (B), Absorption efficiency energy (C), Fecal (D), Molting frequency (times) (E) and molting energy losses (J/g d.w. shrimp/day) (F) of the juvenile *L. vannamei* reared at 29 and 33 °C for 4 weeks

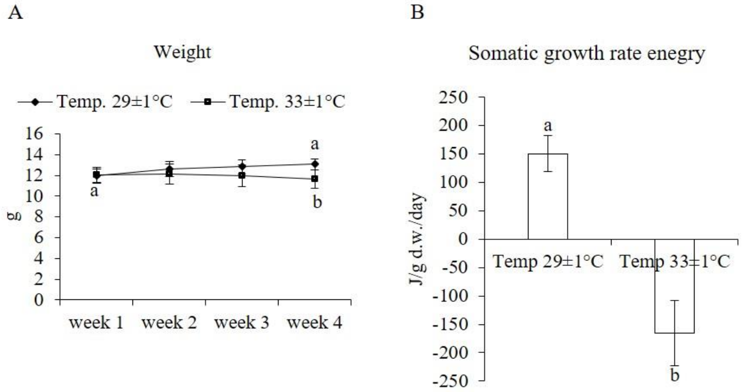

Figure 4. Average weight (A) and somatic growth energy (B) of the juvenile *L. vannamei* reared at 29 and 33 °C for 4 weeks

4.2 Energy allocated from food consumption and digestion processes

Food consumption rates of shrimp varied directly with temperature. Shrimp reared at 33 °C had higher feed intake rate than shrimp at 29 °C (Figure 5A), therefore, the energy consumed during feeding was also higher. However, the absorption efficiency energy (AbE) of shrimp at 33 °C (23.56±5.02%) had lower than shrimp at 29 °C (33.25±7.45%). Thus, shrimp at 33 °C displayed higher food consumption and possessed less absorption energy (Ab) (Figure 5A).

The effect of temperature on shrimp digestive processes, both positive and negative, was found in this study. High temperatures enhanced feed consumption, fecal mass production, and fecal energy loss, but suppressed digestibility, energy absorption, and nutrient assimilation efficiency. Negative effects of high temperature on shrimp digestive processes indicated issues with feed utilization by shrimp reared in these high temperature environments, leading to growth retardation. This was supported by several reports indicating that high temperature led to an increase in feed intake (Wyban *et al.*, 1995), fecal mass production, and stomach evacuation (McGraw & Whiteley, 2012), but

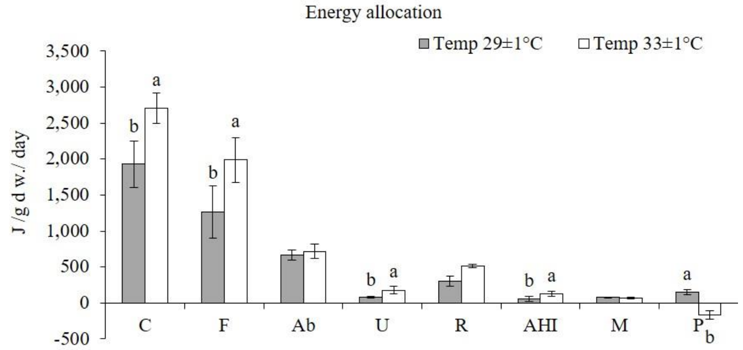

Figure 5. Energy allocations (J/g d.w./day) of the juvenile *L. vannamei* exposed to 29 °C and 33 °C for 4 weeks. C is the energy obtained through food consumption, F is energy lost in feces, Ab is absorbed energy, U is energy lost through nitrogen excretion, R is the energy used for respiration, AHI is energy lost from food digestion and consumption, M is molting energy, and P is energy for tissue production.

Table 1. Energy partitioning between growth (P), metabolism (R), feces (F), excretion (U) and molting (M) in shrimp species at the different temperature

Shrimp species	Weight (g)	Temperature (°C)	% of ingested energy					References
			P	R	F	U	M	
P.monodon	1.20	28.8 ± 1.8	14.51	66.68	14.54	3.33	0.93	Ye *et al.*, 2009
L.vannamei	5.36	25	14.75	64.42	13.28	6.06	1.43	Zhu *et al.*, 2004
L.vannamei	0.8	30	14.01	69.88	7.88	7.96	0.64	Su *et al.*, 2010
L.vannamei	3.5	25	24.45	49.73	22.9	1.01	2.72	Coelho *et al.*, 2019
L.vannamei	10.30	29	8.08	19.19	64.50	4.40	3.83	Present study
		33	-6.07	23.85	73.10	6.67	2.45	

decreases digestive efficiency (Miegel, Pain, Van Wettere, Howarth, & Stone, 2010).

Fecal energy loss in shrimp at 33°C was higher than that in shrimp at 29°C, indicating the influence of temperature rising (Figure 5A). Generally, most energy expenditure of an organism was channeled to respiration (Ye *et al.*, 2009). In this study, major energy was channeled into fecal energy. This indicated less digestibility rate of the experimental shrimp and also possibly due to the difference of the life stage of the shrimp. There were several studies indicating that shrimp at early life stage tended to spend more energy on respiration than the older shrimp (Lemos & Phan, 2001; Maldonado, *et al.*, 2009).

In this study, molting frequency of shrimp at 33 °C was significantly higher than that of shrimp at 29 °C but no statistical difference was detected between molting energy of shrimp from both temperatures. This result agreed with study indicating that elevated temperature increased molting frequency but decreased caloric values of exuviae (Daoud, Lambert, Cèline, & Chabot, 2010). Molting enhancement by high temperature were also reported in *Macrobrachium borellii* (15°C: 22.2 day and 30°C: 9.9 day) and *Palaemonetes argentines* (15°C: 20.8 day and 30°C: 9.5 day) (Montagna, 2011) and *Eriocheir sinensis* (18°C: 18 day and 30°C: 9 day) (Yuan, Wang, Zhang, Li, & Liu, 2017).

4.2 Somatic growth energy

Values between 14 and 24 % of the total ingested energy have been reported to be channeled for growth in juvenile *Penaeus monodon* and *L. vannamei*; whereas in the present study the growth energy was increased by 8.08 % in shrimp reared at 29 °C while the shrimp reared at 33 °C lost their growth energy by 6.07% (Table 1). Upon prolonged exposure to rising temperatures, mammals, birds, and fish are able to use hepatic lipids as a major energy source (Guderley, Lapointe, Bedard, & Dutil, 2003), whereas shrimp utilize accumulated proteins (Taboada *et al.*, 1998). The weight of shrimps were slightly increased after long term exposure to high water temperature comparing with optimum temperature (29 °C: 2.33 and 33 °C: 1.64 g) as reported in *F. chinensis* (28 °C: 0.61 and 34 °C: 0.33 g) (Tian, Dong, Wang, & Wu, 2006), *Penaeus indicus* (31 °C: 0.2 and 35 °C: 0.056 g) (Vijayan & Diwan, 1995), and *L. vannamei* (29 °C: 8 and 33 °C: 6.2 g) (Limsuwan *et al.*, 2007)

5. Conclusions

Energy budget channeled to respiration, apparent heat increment, ammonia excretion, and feces were increased significantly in shrimp reared in excessive high temperature (33 °C) when compared to shrimp reared at normal temperature (29 °C). Total energy budget of *L. vannamei* reared at 33 °C (728.88 J/g d.w./day) was 1.8-fold higher than that of shrimp reared at 29 °C (399.56 J/g d.w./day). At excessive high temperature, *L.vannamei* juveniles increased energy expenditure through respiration and other routine metabolisms by 4.66%, feces by 8.60% and excretion by 2.27 %. Conversely, the growth energy was lost by 14.15 % due to the compensation for the extra energy needs in heat stressed shrimp, leading to weight loss. Information obtained from this study will be very useful for developing a special formulated diet that provides appropriate sources of energy for shrimp exposing to excessive temperature during summer.

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