

Full Length Research Paper

Swimming ability and physiological response to swimming fatigue in kuruma shrimp, *Marsupenaeus japonicus*

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The swimming endurance of kuruma shrimp, *Marsupenaeus japonicus* (11.04 ± 2.43 g) at five swimming speeds (23.0, 26.7, 31.0, 34.6 and 38.6 cm s⁻¹) was determined in a circulating flume at 25.7 ± 0.7°C. The plasma glucose and total protein, hepatopancreas and pleopods muscle glycogen concentrations were determined before swimming and immediately after swimming to evaluate physiological effect of swimming. Swimming endurance of *M. japonicus* decreased as swimming speed increased. The relationship between swimming endurance (*t*, s) and swimming speed (*v*, cm s⁻¹) could be described by the logarithmic model as: $t = -6881 \ln(v) + 26090$, $R^2 = 0.97$ ($P < 0.01$). The swimming ability index (SAI), defined as $SAI = \int_0^{9000} v dt$ was found to be 32.43 cm. Metabolic rates of plasma glucose (M_{pg} , μmol ml⁻¹ s⁻¹) and pleopods muscle glycogen (M_{mg} , mg g⁻¹ s⁻¹) during swimming to fatigue increased as swimming speed increased. The relationship between M_{pg} or M_{mg} and swimming speed (*v*, cm s⁻¹) could be described by the exponential model as: $M_{pg} = 3E-06e^{0.140v}$, $R^2 = 0.98$ ($P < 0.01$) or $M_{mg} = 4E-06e^{0.137v}$, $R^2 = 0.95$ ($P < 0.01$), respectively. Swimming to fatigue led to severe loss of plasma glucose and hepatopancreas glycogen concentrations ($P < 0.05$). Plasma glucose and pleopods muscle glycogen might be used as energy source during swimming.

Key words: *Marsupenaeus japonicus*, swimming ability, swimming fatigue, physiological response, glucose, glycogen, total protein.

INTRODUCTION

Swimming ability of aquatic animals may be described by swimming speed and swimming endurance. Swimming ability is important for their survival, potentially affecting their ability to avoid predators and unfavorable conditions, obtain food, reproductive behaviors and control dispersal patterns (He, 2003; Fisher and Wilson, 2004; Wilson, 2005). Knowledge of swimming ability of aquatic animals can be widely used in improving capture efficiency, aquaculture and resource protection (Jing et al., 2005; Rodríguez et al., 2006; Yanase et al., 2007).

Locomotion modes of shrimp include swimming, walking and tail-flip swimming. The pleopods, which are

located under the abdomen, beat in unison when they swim. Locomotion ability is correlated with food capture, migration, predator avoidance and reproduction in shrimp (Arnott et al., 1998; Zhang et al., 2006; Amornpiyakrit and Arimoto, 2008). However, few efforts have been made to study the swimming speed and swimming physiology of penaeid shrimp. Swimming ability and swimming physiology of whiteleg shrimp, *Litopenaeus vannamei* have been investigated in some studies (Solis-Ibarra and Rendon-Rodriguez, 1994; Zhang et al., 2006, 2007). But study on swimming physiology of kuruma shrimp, *Marsupenaeus japonicus* has not been done.

M. japonicus which is widely distributed in the Indo-West Pacific, is one of the most important crustaceans contributing to fisheries and aquaculture (Hamasaki and Kitada, 2006). In order to evaluate the swimming ability and swimming physiology of *M.*

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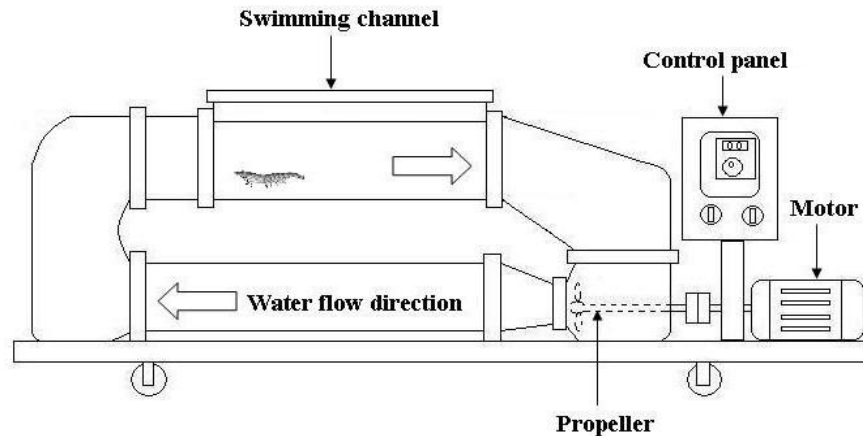


Figure 1. Diagram of the circulating flume.

japonicus, swimming endurance was determined in a circulating flume. The physiological response to swimming fatigue in hemolymph, hepatopancreas and pleopods muscle was also measured. Results will help better understanding of the swimming ability and swimming physiology of penaeid shrimp and contribute to capture and conservation as well as more efficient culture of the species.

MATERIALS AND METHODS

Experimental animals

M. japonicus (11.04 ± 2.43 g, wet weight, means \pm S.D.) used in the experiment were purchased from local market (cultured, Qingdao, China). Shrimp were acclimated in a 2 m^3 recirculating fiberglass tank for 3 days before experiment. During this acclimation period, shrimp were fed twice daily with commercial pellets (Haima, Fuzhou, China). Filtered seawater in the tank was maintained at temperature of 26.2 ± 0.5 °C, salinity of 32.0 ± 1.0 ‰, and dissolved oxygen (DO) $> 6.0 \text{ mg L}^{-1}$. Shrimp at the intermolt stage were used and fasted for 12 h before experiment. Molt stage was distinguished by the degree of hardness of the exoskeleton (Cheng et al., 2002).

Experimental apparatus

Swimming endurance test was conducted in a circulating flume (Dalian Huixin Co. Ltd., China) with a $100 \times 25 \times 25$ cm (L \times W \times H) swimming channel (Figure 1). The current velocity was determined by a miniature propeller current meter (KENEK, VR-101, Japan). The swimming channel was illuminated by a 22 W fluorescent lamp to ensure uniform illumination. Filtered seawater in the flume was maintained at temperature of 25.7 ± 0.7 °C, salinity of 32.0 ± 1.0 ‰, and DO $> 6.0 \text{ mg L}^{-1}$.

Experimental design

Based on pilot trial, the mean current velocities of 23.0 ± 2.8 , 26.7 ± 2.9 , 31.0 ± 3.6 , 34.6 ± 3.7 and $38.6 \pm 3.3 \text{ cm s}^{-1}$ (means \pm S.D) were chosen for the test. 11 - 18 shrimp were allowed to swim in the

swimming channel at each current velocity. The duration of 9000 s was prescribed as the upper end time for swimming endurance (Zhang et al., 2006). When shrimp maintained a fixed position by swimming against current, the current velocity could be considered to be the swimming speed of shrimp at that time. No feed was given during the experimental period.

Two to four shrimp were used together in each swimming trial. They were trained for 10 min at a low speed to orient them to the current and then accelerated over 1 min to the desired current velocity. When a shrimp showed fatigue, swimming time was recorded. The criterion for swimming fatigue was that a shrimp fell against the downstream screen and would not resume swimming after three shifts to the front of the swimming channel using a small net. The fatigued shrimp was immediately removed from the swimming channel, dried by absorbent paper and weighed to the nearest 0.01 g.

The swimming ability index (SAI), defined as $\text{SAI} = \int_0^{9000} v dt$ was used to evaluate the swimming ability of *M. japonicus*.

Tissues collection

Approximately 200 μl hemolymph was collected from the ventral sinus at the base of the first abdominal segment, using a 1 ml syringe containing 200 μl cooled anticoagulant solution (Vargas-Albores et al., 1993). Hemolymph was centrifuged at 800 rpm for 10 min at 4 °C and plasma was separated and stored at -34 °C for further analyses. Hepatopancreas and pleopods of each shrimp were frozen at -34 °C. 10 individuals of the same size as test shrimp that were not forced to swim in the swimming channel were taken as control group.

Biochemical assessment

The plasma glucose metabolic rate (M_{pg} , $\mu\text{mol ml}^{-1} \text{ s}^{-1}$) or pleopods muscle glycogen metabolic rate (M_{mg} , $\text{mg g}^{-1} \text{ s}^{-1}$) of *M. japonicus* during swimming to fatigue was calculated as:

$$M = (C - C')/t$$

Where M was metabolic rate, C was the plasma glucose or pleopods muscle glycogen concentration of control, C' was the plasma glucose or pleopods muscle glycogen concentration after

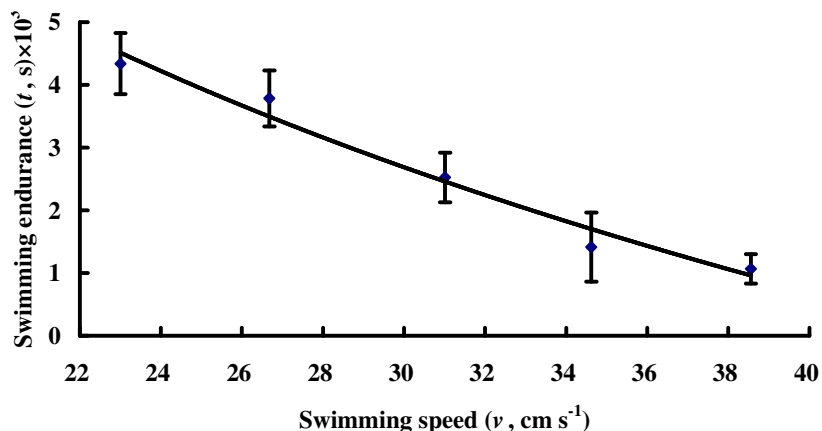


Figure 2. Relationship between swimming endurance (t , s) and swimming speed (v , cm s^{-1}) in *M. japonicus* (means \pm S.E., $n = 11 - 18$).

swimming fatigue and t was the swimming endurance. Commercial kits were used for determining glucose ($\mu\text{mol ml}^{-1}$), glycogen (mg g^{-1}) and total protein (mg ml^{-1}) (Nanjing Jiancheng Bioengineering Institute, China).

Data analysis

Physiological parameters of shrimp before and after swimming fatigue were analyzed using independent sample t-tests. The relationship between swimming speed and swimming endurance, plasma glucose or pleopods muscle glycogen metabolic rate was estimated using curve estimation and the significance of these regressions was tested using ANOVA. Statistical analyses were performed using SPSS 13.0 statistical software and the significance level was $P < 0.05$ for all analyses.

RESULTS

Swimming endurance

Swimming endurance of *M. japonicus* decreased as swimming speed increased. The relationship between swimming endurance (t , s) and swimming speed (v , cm s^{-1}) could be described by the logarithmic model as: $t = -6881 \ln(v) + 26090$, $R^2 = 0.97$ ($P < 0.01$, Figure 2). The relationship between swimming endurance and swimming speed of *M. japonicus* could be also described by the linear model, power model and exponential model (Table 1). SAI of 11.04 ± 2.43 g *M. japonicus* at $25.7 \pm 0.7^\circ\text{C}$ was calculated as $\text{SAI} = \int_0^{9000} v dt = \int_0^{9000} e^{(26090-t)/6881} dt = 32.43$ cm.

Physiological response to swimming fatigue

Physiological responses of *M. japonicus* after swimming fatigue at different speeds are shown in Table 2. After swimming to fatigue at different speeds, the concentration of plasma glucose and hepatopancreas glycogen of *M.*

Table 1. Comparison of four models estimated by Curve Estimation to express the relationship between swimming endurance (t , s) and swimming speed (v , cm s^{-1}) in *M. japonicus*.

Model	Equation	R^2
Logarithmic	$t = -6881 \ln(v) + 26090$	0.97
Linear	$t = -228.65v + 9662.1$	0.97
Power	$t = 4E+07v^{-2.89}$	0.94
Exponential	$t = 45278e^{-0.097v}$	0.97

japonicus was significantly lower than control ($P < 0.05$). Pleopods muscle glycogen concentration decreased and was significantly lower than control at the swimming speed of 23.0, 26.7 and 34.6 cm s^{-1} ($P < 0.05$). No significant change was found for plasma total protein concentration ($P > 0.05$).

During swimming to fatigue at different speeds, the plasma glucose and pleopods muscle glycogen metabolic rates of *M. japonicus* increased as swimming speed increased. The relationship between swimming speed (v , cm s^{-1}) and plasma glucose metabolic rate (M_{pg} , $\mu\text{mol ml}^{-1} \text{s}^{-1}$) or pleopods muscle glycogen metabolic rate (M_{mg} , $\text{mg g}^{-1} \text{s}^{-1}$) could be described by the exponential model as: $M_{\text{pg}} = 3E-06e^{0.140v}$, $R^2 = 0.98$ ($P < 0.01$) or $M_{\text{mg}} = 4E-06e^{0.137v}$, $R^2 = 0.95$ ($P < 0.01$), respectively (Figure 3).

DISCUSSION

Swimming ability

Swimming ability index (SAI) may be considered as a cumulative index of swimming ability that includes not only cruising and burst speed but also the shape of the swimming curve (Tsukamoto et al., 1975). SAI is a good index to quantitatively describe the overall swimming ability and may be used to compare swimming abilities of

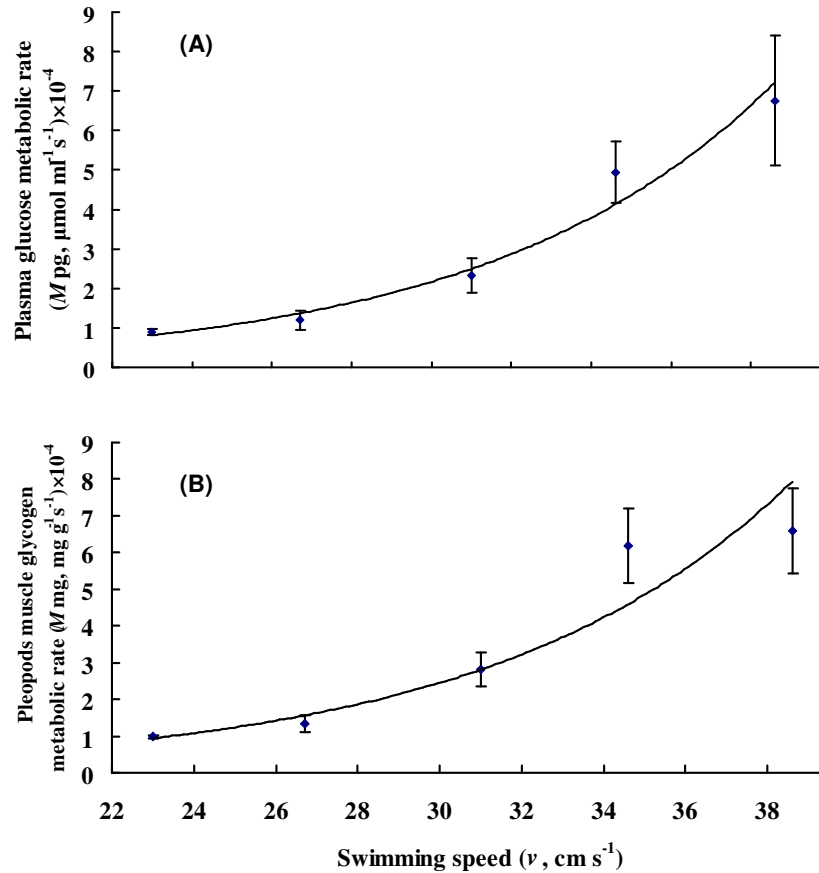


Figure 3. Metabolic rates of plasma glucose (A) and pleopods muscle glycogen (B) in *M. japonicus* during swimming to fatigue at different swimming speeds (means \pm S.E., $n = 10$).

different species of shrimp or different growth stages of the same species (Zhang et al., 2006). Results in the present study showed that SAI of 11.04 g *M. japonicus* at 25.7°C was 32.43 cm. Zhang et al. (2006) reported that SAI of 4.09 g *L. vannamei* at 20°C was 7.28 cm. However, it is not sure the difference in SAI was due to the different species or differences in size, or both. Further study is necessary to investigate the difference in swimming ability among species.

The physiological response to swimming fatigue

Frictional drag increases with the square of swimming speed and therefore the metabolic power required for swimming increase with the cube of swimming speed (Schmidt-Neilson, 1984; Vogel, 1994). Metabolic cost of swimming increases with swimming speed in fish and swimming endurance should drop off rapidly as swimming speed increases (Beamish, 1990; Fisher and Bellwood, 2002). In the present study, the plasma glucose and pleopods muscle glycogen metabolic rates of *M. japonicus* during swimming to fatigue increased as

swimming speed increased. Increase of metabolites metabolic rates might result in the reduction of swimming endurance which decreased from 4340 s on average at 23.0 cm s^{-1} to 1067 s on average at 38.6 cm s^{-1} . Swimming endurance of *L. vannamei* was also found to be decreased as swimming speed increased (Zhang et al., 2006).

The concentrations of hemolymph glucose and muscle glycogen were found to decrease in some crustaceans after exercise fatigue (Thorpe et al., 1995; Morris and Adamczewska, 2002; Zhang et al., 2006). In the present study, the similar results were found in *M. japonicus* after swimming fatigue. The decrease in plasma glucose and muscle glycogen might be due to their utilization as energy source during swimming.

Hepatopancreas is considered the main storage organ in shrimp mainly accumulating lipids and glycogen (Adamczewska and Morris, 1994; Verri et al., 2001). Glycogen is regarded as the major metabolic energy reserve in crustaceans and glycogen in the hepatopancreas is a glucose supply (Gade, 1983). The decrease in hepatopancreas glycogen of *M. japonicus* after swimming fatigue indicated that glycogen in the hepato-

Table 2. Physiological response of *M. japonicus* after swimming fatigue at different swimming speeds (means \pm S.E., n = 10).

Physiological parameter	Swimming speed (cm s ⁻¹)					
	Control	23.0 \pm 2.8	26.7 \pm 2.9	31.0 \pm 3.6	34.6 \pm 3.7	38.6 \pm 3.3
Plasma glucose ($\mu\text{mol ml}^{-1}$)	0.80 \pm 0.05	0.36 \pm 0.06**	0.51 \pm 0.06**	0.37 \pm 0.05**	0.42 \pm 0.06**	0.33 \pm 0.04**
Plasma total protein (mg ml ⁻¹)	69.32 \pm 7.43	58.14 \pm 6.09	73.32 \pm 7.09	65.07 \pm 6.77	65.10 \pm 7.24	75.01 \pm 8.42
Hepatopancreas glycogen (mg g ⁻¹)	6.88 \pm 0.64	2.08 \pm 0.28**	2.63 \pm 0.41**	4.42 \pm 0.40**	3.28 \pm 0.43**	4.64 \pm 0.69*
Pleopods muscle glycogen (mg g ⁻¹)	1.21 \pm 0.09	0.68 \pm 0.07**	0.91 \pm 0.09*	1.09 \pm 0.16	0.73 \pm 0.08**	0.91 \pm 0.13

*Indicates a significant difference from control ($P < 0.05$); ** indicates a very significant difference from control ($P < 0.01$).

pancreas might be used as source of plasma glucose which decreased during swimming.

Total protein can serve as a significant source of metabolic energy for crustaceans (Claybrook, 1983). Decrease in total protein in hemolymph has been reported during stressful conditions in shrimp (Chen et al., 1994; Sánchez et al., 2001). In situation of increased energy demands such as stress, protein in hemolymph can be used for energy supply (Racotta and Palacios, 1998). Zhang et al. (2006) reported that after swimming fatigue hemolymph total protein concentration in *L. vannamei* was significantly lower than that of the pre-exercise shrimp. However, no significant change was found for plasma total protein concentration of *M. japonicus* after swimming fatigue in the present study. The disparity might be due to the species difference and the experimental condition. Therefore, further study is needed on the utilization of energy source during swimming in shrimp.

Conclusion

Swimming endurance decreased in *M. japonicus* as swimming speed increased. Metabolic rates of plasma glucose and pleopods muscle glycogen during swimming to fatigue increased as swimming speed increased. Swimming to fatigue

led to severe loss of plasma glucose and hepatopancreas glycogen concentrations. Plasma glucose and pleopods muscle glycogen might be used as energy source during swimming. Results could be helpful in understanding the swimming ability, swimming physiology and the ecological processes of *M. japonicus*.

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