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Effects of Temperature and Body Size on the Clearance Rates of a Tidal Flat Bivalve, *Coecella chinensis* (Deshayes)

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ABSTRACT

To know the effects on temperature and body size on the clearance rate (CR) of a small tidal flat bivalve, *Coecella chinensis*, laboratory experiments were performed with 20 individuals of different sizes (ranging from 7 to 25 mm) at 3 different temperatures (10, 15, 20℃). The relationship between body size and CR was determined by an allometric equation. The CR of *C. chinensis* varied greatly ranging from 0.003 to 0.103 L/individual/hr. Both temperature and body size affected significantly on the CR of *C. chinensis*. The CR at 20℃was 1.5 times higher than that at 15℃ and 2.8 times than 10℃. The temperature coefficient (Q_{10}) between 10 and 15℃ was higher than that between 15 and 20℃, which indicates that *C. chinensis* changes its CR more rapidly in lower temperature range. As body size increased, the CR increased more than 10-fold at all temperatures. The CR relative to flesh dry weight (FDW) were fitted well to the power function: $CR = a \times (FDW)^b$. The exponent value (b) of the fitted equation ranged from 0.64 to 0.70, which are similar to those of other bivalves. The weight-specific CR (CR_w) was still affected by body size ($p < 0.05$). This implies that smaller individuals require more energy per unit biomass for growth, and the energy requirement for growth decreases as body size increases.

Keywords: *Coecella chinensis*, Temperature, Body size, Clearance rate.

INTRODUCTION

Coecella chinensis (Deshayes) (class Bivalvia, family Mesodesmatidae) is a small bivalve (ca. 25 mm in shell length) that dominates upper tidal flats containing sandy sediments. Although they are small, the ecological role of *C. chinensis* as a primary consumer cannot be disregarded. To understand its role in the community food web, it is necessary to determine clearance rate (CR) and its dependence on temperature and body size.

There are many studies on the effects of temperature and body size on CR of bivalves (Winter, 1973; Bayne *et al.*, 1976; Werner and Hollibaugh, 1993; Yukihira *et al.*, 1998; Lee *et al.*, 2002a, b; Shin and Lim, 2003). Most studies on feeding of bivalves have dealt with large or commercially important species, such as clam (Shin and Lim, 2003), mussels (Matsuyama *et al.*, 1997; Babarro *et al.*, 2000), oysters (Yukihira *et al.*, 1998; Lassus *et al.*, 1999; Mills, 2000), and scallops (Sicard *et al.*, 1999; Li *et al.*, 2001). There are a few studies with small tidal flat bivalves (Werner and Hollibaugh, 1993; Lee *et al.*, 2002a). Here we established the purpose of this study to know the effects of temperature and body size on the CR of *Coecella chinensis*. This paper will provide information about the feeding physiology of *C. chinensis* and serve as a basis for understanding its ecological role in tidal flat ecosystem.

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MATERIALS AND METHODS

1. Test organisms

Approximately 150 individuals of *Coecella chinensis* were collected at Songjinpo tidal flat in Goeje Island (34°59'50"N, 128°40'51"E), southern coast of Korea. Clams were separated from sediments by sieving with a 5-mm sieve and transported to the laboratory within 1 hr after collection. They were divided randomly into 3 groups. Each group consisted of ca. 50 individuals, which included overall range of body size (shell length from 7 to 25 mm). Each group was rinsed with 1-mm filtered seawater (FSW, salinity: 32 psu), transferred into a 10 L aquarium filled with FSW. Then each aquarium was placed and maintained separately in 3 temperature-controlled incubators with 12L:12D cycle of 5 mE/m^2/sec provided by cool-white fluorescent lights. Temperature of each incubator was set to 10, 15, and 20℃, respectively. Clams were acclimated to the experimental temperatures for 24 hr. They were not fed during acclimation.

As food for feeding experiments, a dense unialgal culture of *Isochrysis galbana* (Prymnesiophyceae) was prepared. It was grown at 20℃ in a 10 L polycarbonate bottle with enriched f/2 seawater medium (Guillard and Ryther, 1962) without silicate, with continuous illumination of 100 mE/m^2/sec provided by cool-white fluorescent lights. To acclimate to the experimental temperature, the culture was subdivided into 3 bottles, then each bottle was transferred to the incubator 24 hr before the experiments.

2. Feeding experiments

Experiments were designed to determine the CR of *Coecella chinensis* as a function of body size at 3 different temperatures (10, 15, 20℃) when feeding on unialgal diet of *Isochrysis galbana*. Twenty most healthy individuals of C. chinensis, from smallest to largest ones, were evenly chosen for the experiment at each temperature. Either 100-ml or 270-ml polycarbonate bottles (Nalgene) were used as feeding chambers. Each chamber was filled with algal suspension (ca. 1.0 × 10^6 cells/mL) of *I. galbana*, and then each clam was transferred to the chamber. According to the size of each clam, filled volume of algal suspension varied from 25 to 250 ml. The chambers were placed in an incubator with experimental temperature under 5 mE/m^2/sec of cool-white fluorescent lights for 2 hr. To enumerate the concentration of *I. galbana* at the beginning and the end of experiments, 5-ml aliquots were taken from each chamber and fixed with Lugol's solution. Algal concentration was determined by counting (in duplicate) in a Hemocytometer (Neubauer) under a compound microscope (× 400, Olympus). When the experiments were terminated, the shell length (the distance between anterior and posterior ends of the shell) of each clam was measured using an electronic Vernier caliper (Mitutoyo) to the nearest 0.01 mm. To measure the flesh dry weight, soft tissue was separated from the shells, rinsed with deionized water, dried in an oven at 90℃ for 48 hr, and then weighed on an electronic balance (Ohaus) to the nearest 0.001 g.

3. Data analyses

The relationship between shell length (SL, mm) and flesh dry weight (FDW, g) was determined by fitting curves to the power function as follows:

$$\mathrm{FDW} = a \times \mathrm{SL}^{b} \qquad (1)$$

The CR (L/individual/hr) and the weight-specific CR (CR$_w$, L/g/hr) were calculated as follows (Coughlan, 1969):

$$\mathrm{CR} = V \times \ln (C_t/C_0)\ /\ t \qquad (2)$$

$$\mathrm{CR_w} = \mathrm{CR}\ /\ \mathrm{FDW} \qquad (3)$$

where, V is volume of algal suspension (L); C_0 and C_t are the initial and the final concentration (cells/mL) of *Isochrysis galbana*, respectively; t is incubation time (hr).

The relationship between body size and CR was determined by fitting curves to an allometric equation as follows (Bayne *et al.*, 1976):

$$(\mathrm{CR\ or\ CR_w}) = a \times (\mathrm{SL\ or\ FDW})^{b} \qquad (4)$$

To evaluate the effect of temperature on CR across the temperature range, a temperature coefficient (Q_{10}) was calculated as follows (Beiras *et al.*, 1995):

$$Q_{10} = (a2/a1)^{(10/(T2-T1))} \qquad (5)$$

where, *a1* and *a2* are the coefficient values obtained from the relationship between CR and FDW (Eq. 4), and T1 and T2 are two experimental temperatures.

To assess the effects of temperature and body size on CR by statistical analyses, data from each individual were pooled into 4 size classes with a 5 mm interval (Table 1). There were no significant differences (p > 0.05) in shell lengths among individuals at different temperatures for every size classes. Both two-way (model I) and one-way analyses of variance (ANOVA) were performed on SPSS package. Two-way ANOVA on the CR and CR_w data was applied to test for temperature and body size, both as fixed variables. We used Type I sum of squares because it could be assumed that the variables gave little random effects. In case of the interactions between two variables were significant, one-way ANOVA was applied separately to examine the effects of one variable on the CR or CR_w for each treatment of the other variable. Before statistical analyses, CR and CR_w data were tested for normality (Shapiro-Wilk's test) and homogeneity of variance (Bartlett's test). If one of the above ANOVA requirements was not met, the data were $\log_{10}$ transformed, then ANOVA was repeated. If significant F values were observed in any ANOVA tests, multiple comparisons were conducted using Tukey's HSD (Zar,

Table. 1. Shell length of each size class pooled for statistical analyses on the clearance rate of *Coecella chinensis* (C1: 5-10 mm, C2: 10-15 mm, C3: 15-20 mm, C4: 20-25 mm). Numbers in parentheses are the number of pooled individuals for each size class. There are no significant differences (p > 0.05) in shell lengths among individuals at different temperatures for all size classes (ns: no significance).

Size class	Shell length (mm, Mean ± S.E.)			p
	10℃	15℃	20℃	
C1	8.7 ± 1.2 (4)	9.7 ± 0.8 (4)	8.8 ± 0.2 (3)	0.348, ns
C2	13.0 ± 1.1 (6)	13.3 ± 1.5 (5)	13.5 ± 1.6 (7)	0.822, ns
C3	18.2 ± 1.6 (3)	19.0 ± 0.5 (4)	18.3 ± 1.0 (4)	0.487, ns
C4	22.7 ± 1.5 (7)	22.4 ± 0.9 (7)	22.9 ± 1.3 (6)	0.792, ns

Table 2. Comparisons of relationships between the clearance rate and body size in *Coecella chinensis* among different temperatures. Clearance rate was expressed as a function of body size fitted by the allometric equation, $Y = a \times X^b$ (Fig. 2, 3, 4). SL: shell length (mm), FDW: flesh dry weight (g), CR: clearance rate (L/individual/hr), CR_w: weight-specific clearance rate (L/g/hr).

X	Y	Temperature	a	b	R^2
SL	CR	10℃	3.69×10^{-5}	2.083	0.774
		15℃	7.50×10^{-5}	2.069	0.630
		20℃	2.27×10^{-4}	1.880	0.753
FDW	CR	10℃	0.151	0.702	0.804
		15℃	0.287	0.699	0.678
		20℃	0.426	0.639	0.798
FDW	CR_w	10℃	0.151	−0.298	0.425
		15℃	0.287	−0.301	0.280
		20℃	0.426	−0.362	0.559

1984) to determine which means were significantly different from one another. For all analyses, a significance level of $\alpha = 0.05$ was used.

RESULTS AND DISCUSSION

1. Relationship between shell length and flesh dry weight

The relationship between shell length (SL) and flesh dry weight (FDW) of *Coecella chinensis* was fitted well to the power function, FDW = 0.0063 × $SL^{3.012}$ (Fig. 1). All individuals used for the feeding experiments at 3 different temperatures were arranged well along the fitted curve. The exponent value (3.012) was similar to that of *Glauconome chinensis* (Lee *et al.*, 2002a).

2. Relationships between body sizes and clearance rates

In general, the CR of *Coecella chinensis* increased greatly as body size increased. CR ranged from 0.003 to 0.039 L/individual/hr at 10℃, 0.005 to 0.089 L/individual/hr at 15℃, and 0.009 to 0.103 L/individual/hr at 20℃. The maximum CR was more than 10-fold of the minimum at all temperatures. The relationships between SL and CR, and between FDW and CR were fitted well to the power function (Fig. 2, 3). The coefficient values (a) increased as temperature increased in both relationships (Table 2). In the relationship between FDW and CR, there was 1.9-fold difference in a value between 10 and 15℃, and 1.5-fold between 15 and 20℃. The exponent values (b) were higher than 1 in the relationships between SL and CR, while those were lower than 1 in between FDW and CR (Table 2). The b values decreased as temperature increased in both relationships.

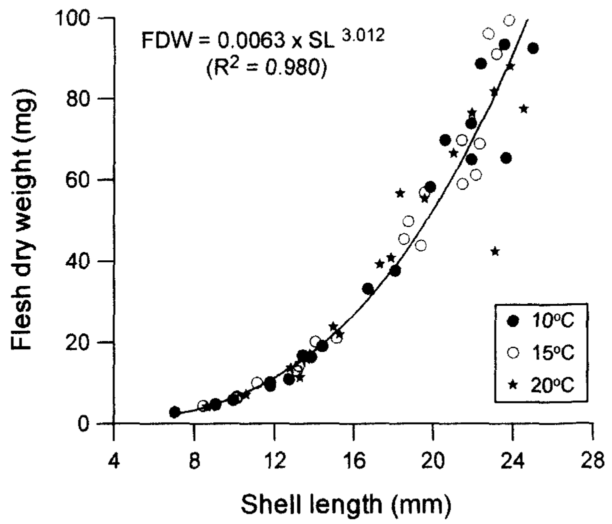

Fig. 1. Relationship between the shell length (SL) and the flesh dry weight (FDW) of *Coecella chinensis* used for the feeding experiments at three different temperatures.

The parameter a determines the absolute magnitude of the CR; it depends on various conditions such as body size, temperature, or algal concentration (Winter, 1973). The a value of *Coecella chinensis* is similar to that for a small bivalve, *Glauconome chinensis*, but is much lower than those for large mussel, clam, oysters, or scallops (Table 3). Parameter b is the slope of the

Table 3. Comparisons of parameters of allometric equation between the clearance rate and flesh dry weight, $CR = a\ (FDW)^b$, among different suspension feeding bivalves.

Species	a	b	Reference
Mytilus edulis	2.41	0.74	Winter (1973)
Crassostrea gigas	10.39	0.27	Walne (1972)
Venus mercenaria	4.53	0.18	Walne (1972)
Pinctada margaritifera	12.34	0.60	Yukihira *et al.* (1998)
Pinctada maxima	10.73	0.62	Yukihira *et al.* (1998)
Placopecten magellanicus	0.94	0.67	MacDonald and Thompson (1986)
Glauconome chinensis	0.43	0.71	Lee *et al.* (2002a)
Coecella chinensis (10℃)	0.15	0.70	This study
Coecella chinensis (15℃)	0.29	0.70	This study
Coecella chinensis (20℃)	0.43	0.64	This study

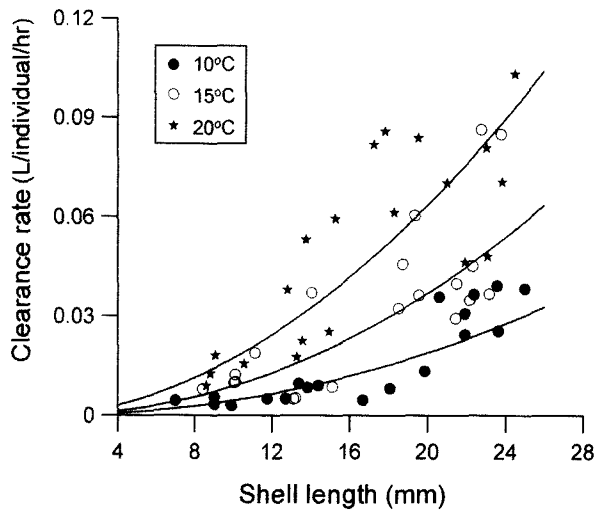

Fig. 2. Clearance rate (CR) of *Coecella chinensis* when feeding on *Isochrysis galbana* as a function of shell length (SL) for each temperature. CR data were fitted by the equation (4). See Table 2 for fitted parameters.

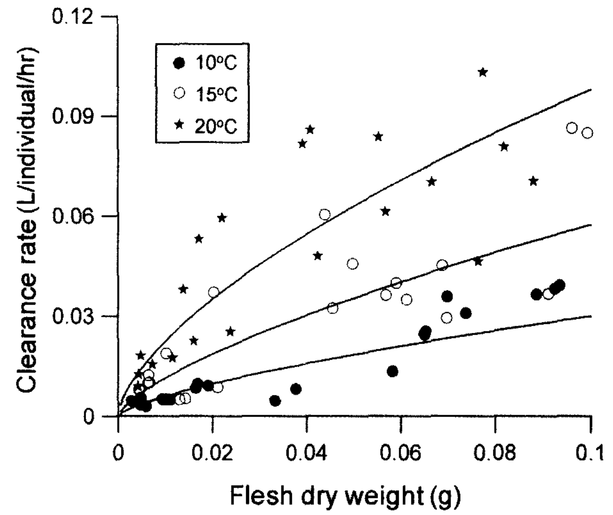

Fig. 3. Clearance rate (CR) of *Coecella chinensis* when feeding on *Isochrysis galbana* as a function of flesh dry weight (FDW) for each temperature. CR data were fitted by the equation (4). See Table 2 for fitted parameters.

regression line resulting from the data being plotted on a double logarithmic scale; it indicates the relative increase in the CR with body size. The b value for *Coecella chinensis* obtained in this study is in good accordance with that for *Mytilus edulis* (Winter, 1973), *Pinctada margaritifera, P. maxima* (Yukihira *et al.*, 1998), *Placopecten magellanicus* (MacDonald and Thompson, 1986), or *Glauconome chinensis* (Lee *et al.*, 2002a); it is higher than *Crassostrea gigas* or *Venus mercenaria* (Walne, 1972). According to Thompson and Bayne (1972), our values represent "routine" metabolism, which is intermediate between the

Table 4. Comparisons of shell length (SL), flesh dry weight (FDW) and the weight-specific clearance rate (CR_w) among different suspension feeding bivalves.

Species	SL (mm)	FDW (g)	CR_w (L/g/hr)	Reference
Mytilus edulis	8.5 − 56.5	0.003 − 1.2	1.1 − 11.3	Winter (1973)
Mytilus edulis	25 − 30	0.04 − 0.1	18	Clausen and Riisgård (1996)
Mytilus edulis	14.8	9.6	2.7 − 26.6	Björk and Gilek (1997)
Mytilus edulis	77 − 82	1.8 − 3	0.12 − 2.11	Cranford and Hill (1999)
Potamocorbula amurensis	10 − 20	0.009 − 0.072	5.0 − 17.8	Werner and Hollibaugh (1993)
Crassostrea virginica	−	−	2.5 − 3.0	Strychar and MacDonald (1999)
Argopecten ventricosus−circularis	11.8	0.014	8.7 − 17.8	Sicard *et al.* (1999)
Placopecten magellanicus	91 − 97	6.1 − 9.3	0.06 − 1.05	Cranford and Hill (1999)
Brachidontes pharaonis	30	−	0.8 − 3.0	Sarà *et al.* (2000)
Pinctada maxima (spat)	4.3	0.011	17 − 54	Mills (2000)
Glauconome chinensis	4 − 16	0.001 − 0.025	1.0 − 3.1	Lee *et al.* (2002a)
Saxidomus purpuratus (juvenile)	5 − 6	0.001 − 0.002	0.5 − 13.7	Lee *et al.* (2002b)
Coecella chinensis	7 − 25	0.003 − 0.099	0.1 − 3.9	This study

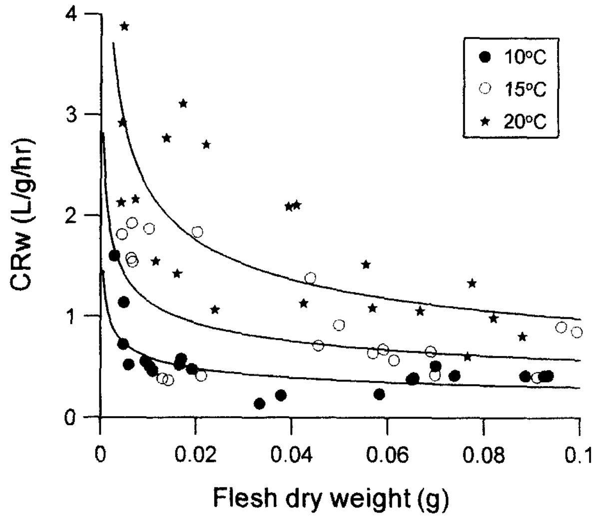

Fig. 4. Weight-specific clearance rate (CR_w) of *Coecella chinensis* when feeding on *Isochrysis galbana* as a function of flesh dry weight (FDW) for each temperature. CR_w data were fitted by the equation (4). See Table 2 for fitted parameters.

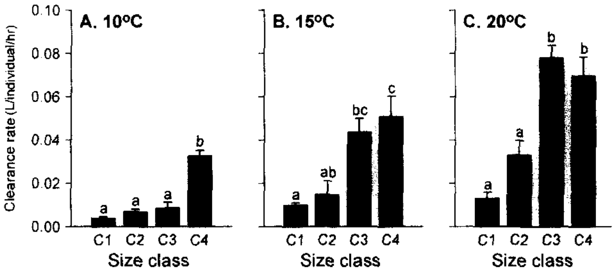

Fig. 5. Comparison of clearance rate (CR) among size classes of *Coecella chinensis* when feeding on *Isochrysis galbana* for each temperature. See Table 1 for C1, C2, C3, and C4. Bar indicates the standard error. Values with the same character are not statistically different ($p > 0.05$).

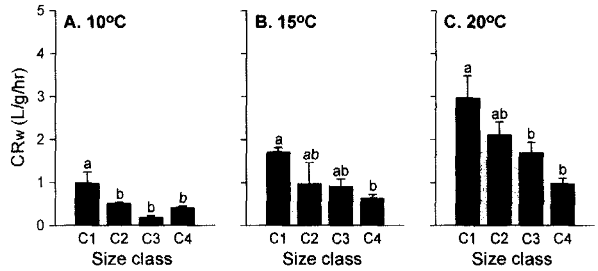

Fig. 6. Comparison of weight-specific clearance rate (CRw) among size classes of *Coecella chinensis* when feeding on *Isochrysis galbana* for each temperature. See Table 1 for C1, C2, C3, and C4. Bar indicates the standard error. Values with the same character are not statistically different ($p > 0.05$).

"standard" (0.616) and the "active" (0.797) metabolism. The temperature coefficient (Q_{10}) for a between 10 and 15℃ (3.61) was 1.6 times higher than that between 15 and 20℃ (2.20). Q_{10} between 10 and 20℃ was 2.82, which was higher than that of *Saxidomus purpuratus* (Lee *et al.*, 2002b). The higher Q_{10} in low temperature range was also found in other bivalves (Ali, 1970; Schulte, 1975; Shin and Lim, 2003). Shin and Lim (2003) stated that this trend is related to the nonlinear change in ciliary activity with increasing temperature.

The weight-specific CR (CR_w) decreased as body size increased. CR_w ranged from 0.14 to 1.60 L/g/hr at 10℃, 0.37 to 1.92 L/g/hr at 15℃, and 0.61 to 3.87 L/g/hr at 20℃. There were 5 to 12-fold differences between the maximum and minimum of CR_w. The relationship between FDW and CR_w also was fitted well to the power function (Fig. 4). The coefficient values (a) were identical to those from the relationship between FDW and CR (Table 2). The exponent values (b) were all negative and decreased as

Table. 5. Two-way ANOVA (model I) of the effects of size and temperature on the clearance rate (CR) of *Coecella chinensis* when feeding on *Isochrysis galbana* ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$).

Source of variation	SS	df	MS	F	p
Size	0.018	3	0.0060	30.08	$< 0.001^{***}$
Temperature	0.012	2	0.0058	29.45	$< 0.001^{***}$
Size × Temperature	0.003	6	0.0006	2.94	0.016^{*}
Error	0.010	48	0.0002		

temperature increased.

The reduction in CR_w with increasing body size is a general phenomenon in bivalves (Bayne *et al.*, 1976). The CR_w obtained in this study (0.1-3.9 L/g/hr) is comparable to those for *Mytilus edulis* (Winter, 1973; Cranford and Hill, 1999), *Crassostrea virginica* (Strychar and MacDonald, 1999), *Placopecten magellanicus* (Cranford and Hill, 1999), *Brachidontes pharaonis* (Sarà *et al.*, 2000), or *Glauconome chinensis* (Lee *et al.*, 2002a), but lower than others for *Mytilus edulis* (Clausen and Riisgård, 1996; Björk and Gilek, 1997), *Potamocorbula amurensis* (Werner and Hollibaugh, 1993), *Argopecten ventricosus-circularis* (Sicard *et al.*, 1999), spat of *Pinctada maxima* (Mills, 2000), or juvenile of *Saxidomus purpuratus* (Lee *et al.*, 2002b) (Table 4).

3. Effects of temperature and body size on CR and CR_w

Two-way ANOVA showed that there were significant differences in CR of *Coecella chinensis* among different size classes (F = 30.08, $p < 0.001$) and temperatures (F = 29.45, $p < 0.001$) (Table 5). Body size was the most important factor contributing to total variation of CR. The interaction between body size and temperature was also significant (F = 2.94, p = 0.016) indicating that the change in CR with the body size was dependent on the temperature. One-way ANOVA also showed that there were significant differences in CR among size classes at all temperatures and among temperatures for all size classes (Table 6). Multiple comparisons showed that CR (L/individual/hr, mean ± S.E.) was significantly different between size class C3 and C4 at 10℃ (0.009 ± 0.003 vs. 0.033 ± 0.002, $p < 0.001$), between C1 and C4 at 15℃ (0.010 ± 0.001 vs. 0.051 ± 0.009, p = 0.007), and between C2 and C3 at 20℃ (0.033 ± 0.007 vs. 0.078 ± 0.006, p = 0.003) (Fig. 5). There were no significant differences among size class ranges C1-C3 (p = 0.384) at 10℃, C1-C2 (p = 0.970), C2-C3 (p = 0.084) and C3-C4 (p = 0.910) at 15℃, and C1-C2 (p =

Table. 6. One-way ANOVA of the effects of size and temperature on the clearance rate (CR) of *Coecella chinensis* when feeding on *Isochrysis galbana* ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$). See Table 1 for C1, C2, C3, and C4.

Variable	SS	df	MS	F	p
Size					
Temperature = 10℃	0.0032	3	0.0011	59.6	$< 0.001^{***}$
Temperature = 15℃	0.0065	3	0.0022	7.3	0.003^{**}
Temperature = 20℃	0.0116	3	0.0039	13.7	$< 0.001^{***}$
Temperature					
Size class = C1	0.0002	2	0.0001	10.9	0.005^{**}
Size class = C2	0.0023	2	0.0012	6.7	0.008^{**}
Size class = C3	0.0083	2	0.0042	37.1	$< 0.001^{***}$
Size class = C4	0.0044	2	0.0022	6.3	0.009^{**}

Table. 7. Two-way ANOVA (model I) of the effects of size and temperature on the weight-specific clearance rate (CR_w) of *Coecella chinensis* when feeding on *Isochrysis galbana* ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$).

Source of variation	SS	df	MS	F	p
Size	9.66	3	3.22	15.15	$< 0.001^{***}$
Temperature	17.40	2	8.70	40.94	$< 0.001^{***}$
Size × Temperature	3.07	6	0.51	2.41	$< 0.001^{***}$
Error	10.20	48	0.21		

Table. 8. One-way ANOVA of the effects of size and temperature on the weight-specific clearance rate (CR$_{w}$) of *Coecella chinensis* when feeding on *Isochrysis galbana* ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$). See Table 1 for C1, C2, C3, and C4.

Variable	SS	df	MS	F	p
Size					
Temperature = 10℃	1.29	3	0.43	9.7	$< 0.001^{***}$
Temperature = 15℃	2.97	3	0.99	4.9	0.013^{*}
Temperature = 20℃	8.82	3	2.94	7.5	0.002^{**}
Temperature					
Size class = C1	6.74	2	3.37	11.6	0.004^{**}
Size class = C2	8.78	2	4.39	10.5	0.001^{**}
Size class = C3	3.91	2	1.96	14.6	0.002^{**}
Size class = C4	1.04	2	0.52	15.8	$< 0.001^{***}$

0.325) and C3-C4 (p = 0.879) at 20℃.

There were also significant differences in CR$_{w}$ of *Coecella chinensis* among different size classes (F = 15.15, p < 0.001) and temperatures (F = 40.94, p < 0.001) (Table 7). Temperature is the most important factor contributing to total variation of CR$_{w}$. The interaction between body size and temperature was also significant (F = 2.41, p < 0.001) indicating that the change in CR$_{w}$ with body size was dependent on the temperature. One-way ANOVA also showed that there were significant differences in CR$_{w}$ among size classes at all temperatures and among temperatures for all size classes (Table 8). Multiple comparisons showed that CRw (L/g/hr, mean ± S.E.) was significantly different between size class C1 and C2 at 10℃ (1.00 ± 0.24 vs. 0.52 ±0.02, p = 0.013), between C1 and C4 at 15℃ (1.71 ± 0.09 vs. 0.64 ± 0.07, p = 0.008), and between C1 and C4 at 20℃ (2.97 ± 0.50 vs. 0.99 ± 0.11, p = 0.002) (Fig. 6). There were no significant differences among size class ranges C2-C4 (p = 0.148) at 10℃, C1-C3 (p = 0.063) and C2-C4 (p = 0.667) at 15℃, and C1-C2 (p = 0.204) and C2-C4 (p = 0.069) at 20℃.

It is noticeable that the CR$_{w}$ (which is already standardized by body size) was still affected by body size. This implies that the differences in CR among different size class should be considered in energetic point of view. Smaller individuals need more energy per unit biomass for growth, and the energy requirement for growth decreases as body size increases. Therefore, although the absolute rate (CR) increased, the standardized rate (CR$_{w}$) decreased as body size increased.

This study provided the basic information on the changes in CR of *Coecella chinensis* with temperature and body size through short-term experiments. The optimal range of temperature could not obtained because the temperature range was relatively narrow. Considering that *C. chinensis* inhabits upper zone of tidal flat where the temperature fluctuation is great, further studies should include the physiological responses at extreme (both high and low) temperatures.

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