J. Fish. Sci. Tech. 5(3), 183~190, 2002

JOURNAL OF
FISHERIES SCIENCE
AND TECHNOLOGY

Effect of Body Size on Feeding Physiology of an Intertidal Bivalve, *Glauconome chinensis* Gray (Glauconomidae)

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(Received March 2002, Accepted August 2002)

To determine the effect of body size on the clearance rate and ingestion rate of small intertidal bivalves, *Glauconome chinensis*, feeding experiments were conducted on individuals of 12 different size classes, from 4 to 16 mm in shell length. Relationships between morphological parameters were also determined. The clearance and ingestion rates of *G. chinensis* responded similarly to their body size, ranging from 1.3 to 28.2 mL/hr/ind. and from 24.0 to 458.5 μgC/hr/ind., respectively. Both rates increased significantly ($p<0.001$) as shell length increased from 4 to 9 mm, although neither rate changed significantly when shell length was in the range from 12 to 16 mm. The weight-specific clearance rate (CR_W) and ingestion rate (IR_W) decreased with increasing body size, with values from 1.0 to 3.1 L/hr/g and from 17.9 to 51.3 mgC/hr/g, respectively. The CR_W of *G. chinensis* was intermediate compared to those of larger bivalve species. The clearance rate (CR) relative to flesh dry weight (FDW) of *G. chinensis* were fitted well to the power function: $CR=0.43\times(FDW)^{0.71}$ ($r^2=0.89$). The exponent of fitting equation (0.71) of *G. chinensis* was higher than those of *Mytilus edulis* (Walne, 1972), *Crassostrea gigas* (Walne, 1972), and *Placopecten magellanicus* (MacDonald and Thompson, 1986).

Key words: *Glauconome chinensis*, Body size, Clearance rate, Ingestion rate

Introduction

It is well known that most physiological processes, such as feeding, growth, respiration, and reproduction, are influenced by the size of animals (Bayne et al., 1976). The dependence of clearance and ingestion rates of bivalves on body size is also well understood and has been studied comprehensively (Winter, 1973; Bayne et al., 1976; Werner and Hollibaugh, 1993; Yukihira et al., 1998). However, most studies on feeding of bivalves have dealt with large or commercially important species, such as 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). Studies on small but ecologically important species are relatively rare (Werner and Hollibaugh, 1993).

Glauconome chinensis Gray (Bivalvia: Glauconomidae) is a small bivalve that inhabits upper tidal flats containing silty sediments. Recently, we found that a tidal flat near Kunsan was dominated by *G. chinensis* at a density exceeding 8,000 ind./m^2 (Lee et al., unpubl. data). Species belonging to the genera *Glauconome* are suspension feeders and are important foods for fishes (Brewer and Willan, 1985; Brewer and Warburton, 1992). Therefore, despite their small size, the ecological importance of *G. chinensis* in the tidal flat community cannot be disregarded. To better understand its role as a primary consumer in the community food web, it is necessary to determine the clearance and ingestion rates as a function of body size.

Because there were no reports on the ecological or physiological characteristics of *G. chinensis*, this study examined the relationships between morphological parameters (shell length, total dry weight,

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shell dry weight, and flesh dry weight) and their effects on physiological parameters (clearance and ingestion rates). We selected the microflagellate *Isochrysis galbana* (Prymnesiophyceae) as prey for *G. chinensis* in feeding experiments. The relationships between parameters were established through regression analyses and several feeding parameters were obtained. This paper provides information about the feeding physiology of *G. chinensis* and will serve as a basis for understanding the role of small bivalves in tidal flat ecosystems.

Materials and Methods

Test organisms

G. chinensis were collected at Sura tidal flat, near Kunsan (35°55′59″N, 126°36′56″E), on the western coast of Korea. The clams were separated from sediments by sieving with a 2-mm mesh screen and transported to the laboratory within 1 hr of collection. The clams were divided into 12 size classes with 1 mm intervals from 4 to 16 mm (Table 1). They were rinsed with 5-μm filtered seawater and acclimated to the experimental temperature (20℃) for 24 hrs, and were maintained in a 20-L aquarium with filtered seawater in an undisturbed place under dim light (5 μE/m^2/sec). They were not fed during this period of acclimation.

The strain of *I. galbana* was obtained from the Red Tide Research Center, Kunsan National University. The algae were cultivated at 20℃ in enriched f/2 seawater medium (Guillard and Ryther, 1962) without silicate, under continuous illumination of 100 μE/m^2/sec provided by cool-white fluorescent light. Cultures in the exponential growth phase were used for experiments.

Relationship between length and weight of *G. chinensis*

The relationship between shell length and flesh dry weight of *G. chinensis* was determined by an indirect method because the individual flesh dry weight of the smallest size class was less than the detection limit of the balance (0.001 g). Therefore, the flesh dry weight of individual *G. chinensis* was calculated by subtracting the regression equation between shell length and shell dry weight from that between shell length and total dry weight using the measured shell length of each individual. Two different sets of 10 individuals of each size class were used as the basis of each of the two regression equations.

To measure the shell length, the distance between anterior and posterior ends of the shell was measured to the nearest 0.01 mm using an electronic Vernier caliper (Mitutoyo Co.). To measure the total dry weight, the clams were rinsed with deionized water, dried in an oven at 90℃ for 48 hrs, and then weighed on an electronic balance to the nearest 0.001 g. To measure the shell dry weight, soft tissues were removed from the shells, which were then rinsed with deionized water, dried in an oven at 90℃ for 48 hrs and then weighed on an electronic balance to the nearest 0.001 g.

The relationships between shell length (SL) and total dry weight (TDW) and between shell length (SL) and shell dry weight (SDW) were determined by fitting curves to a power function as follows:

$$(\text{TDW or SDW}) = a(\text{SL})^b$$

Feeding experiments

Experiments were designed to compare the clearance and ingestion rates of *G. chinensis* as a function of body size when feeding on unialgal diet of *I. galbana*. Two (for size class 1) or three (for size classes 2~12) 270-mL polycarbonate bottles (Nalgene Co.) were used as feeding chambers. Bottles were filled with 250 mL of algal suspension (1.0×10^6 cells/mL) of *I. galbana*. Then, according to their size, 1 to 14 *G. chinensis* were transferred to each bottle (Table 1). Three control bottles containing *I. galbana* only (without *G. chinensis*) were also prepared. These controls were used to monitor changes in algal concentration due to growth, death, or attachment of algal cells to the bottle. The prepared bottles were incubated in an undisturbed place at 20℃ under 5 μE/m^2/sec of cool white fluorescent light for 3 hrs. To enumerate the concentrations of *I. galbana*, subsamples were taken at the beginning and the end of experiments.

For simplicity, algal cell concentrations were determined with a fluorometer (Turner Designs, Model 10-AU), based on the measurements of fluorescence (Brand et al., 1980). Ten-mL aliquots of the

Table 1. Shell length (mean ± SD), the number of individuals per incubation bottle, and the number of replicates for each size class in determination of clearance and ingestion rates of an intertidal bivalve, *G. chinensis*

Size class	Shell length (mm)	No. of ind.	No. of rep.
1	4.32 ± 0.05	14	2
2	5.46 ± 0.09	12	3
3	6.53 ± 0.06	10	3
4	7.46 ± 0.12	7	3
5	8.58 ± 0.09	5	3
6	9.51 ± 0.07	3	3
7	10.53 ± 0.33	2	3
8	11.38 ± 0.24	2	3
9	12.37 ± 0.24	1	3
10	13.24 ± 0.04	1	3
11	14.48 ± 0.28	1	3
12	15.25 ± 0.09	1	3

subsamples were transferred to test tubes with an autopipette and their fluorescence was measured. To determine the relationship between the fluorescence and the cell concentration of *I. galbana*, another set of 6 different concentrations were prepared. The fluorescence and cell concentrations of each suspension were determined five times and the relationship was expressed as a linear regression equation. This equation was used to convert the fluorescence data obtained from the feeding experiments into cell concentrations.

Clearance rate and ingestion rate

The clearance rate (CR) was calculated as follows:

$$CR = V \times [\ln(C^*_t/C^*_0) - \ln(C_t/C_0)]/N \times t$$

where V = volume of algal suspension; C^*_0 and C^*_t = initial and final concentrations of *I. galbana* in control bottles, respectively; C_0 and C_t = initial and final concentrations of *I. galbana* in experimental bottles, respectively; N = number of *G. chinensis;* t = incubation time. The ingestion rate (IR) was calculated as follows:

$$IR = \langle C \rangle \times CR$$

where $\langle C \rangle$ = average concentration of *I. galbana* in experimental bottles during the incubation period (Frost, 1972). The ingestion rate was converted to the carbon equivalent by assuming that one *I. galbana* cell contains 0.022 ngC (Bougrier et al., 1997). The weight-specific clearance rate (CR_W) and ingestion rate (IR_W) were also calculated by standardizing the rates to the flesh dry weight; these rates were expressed in L/hr/g and mgC/hr/g, respectively. The relationships between shell length (SL) or flesh dry weight (FDW) and clearance rate (CR) or ingestion rate (IR) were determined by fitting curves to the following power function (Bayne et al., 1976):

$$(CR \text{ or } IR) = a(SL \text{ or } FDW)^b$$

Statistical analyses

The clearance and ingestion rates for different body sizes of *G. chinensis* were compared by one-way analysis of variance (ANOVA) using the SPSS program. Multiple comparisons were conducted using Tukey's HSD (Zar, 1984). Before statistical analyses, the clearance and ingestion rates were tested for normality and homogeneity of variance. If at least one of the above ANOVA requirements was not met, the data were $\log_{10}$ transformed, and then ANOVA was repeated. For all analyses, a significance level of $\alpha = 0.05$ was adopted.

Results

Relationship between length and weight of *G. chinensis*

The relationships between shell length and total dry weight and between shell length and shell dry weight of *G. chinensis* were fitted well to the power function (Fig. 1). The fitted equations for total dry weight (TDW, mg) versus shell length (SL, mm) and for shell dry weight (SDW, mg) versus shell length (SL, mm) were as follows:

$$TDW = 0.107 \times SL^{2.628},\ r^2 = 0.99$$
$$SDW = 0.111 \times SL^{2.545},\ r^2 = 0.98.$$

By subtracting the second equation from the first equation (TDW − SDW), the relationship between flesh dry weight (FDW, mg) and shell length (SL, mm) was obtained as follows:

$$FDW = 0.004 \times SL^{3.183}$$

Relationship between fluorescence and cell concentration of *I. galbana*

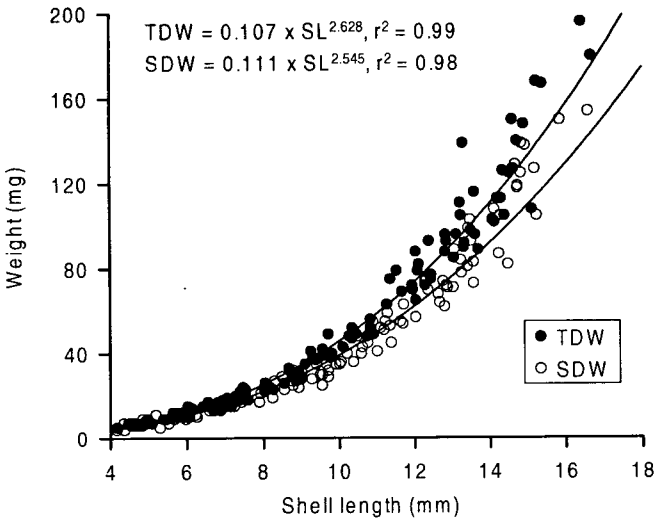

Fig. 1. Total dry weight (TDW; mg) and shell dry weight (SDW; mg) as a function of shell length (SL; mm) of *G. chinensis* (filled circle: TDW, open circle: SDW). The curves were fitted to power functions.

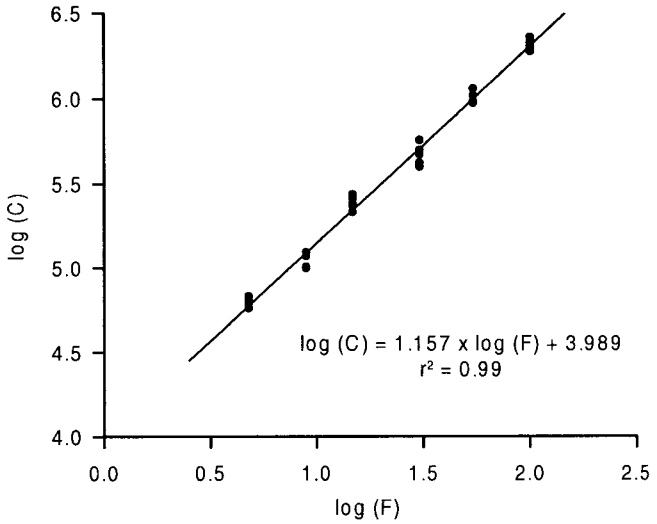

Fig. 2. Relationship between logarithm of cell concentration (C; cells/mL) and logarithm of fluorescence (F; relative unit) of *I. galbana*.

The fluorescence and cell concentration of *I. galbana* showed a strong linear relationship when the fluorescence ranged from 4 to 100 (Fig. 2). All of the fluorescence data measured in feeding experiments were within this linear range.

Clearance rate and ingestion rate

The clearance rate (mean ± SD) of *G. chinensis* fed on a diet of *I. galbana* ranged from 1.3 ± 0.3 to 28.2 ± 11.9 mL/hr/ind. (Fig. 3). One-way ANOVA showed that body size affected clearance rate significantly ($F=32.8$, $p<0.001$). As shell length increased from 4 to 9 mm (flesh dry weight from 0.47 to 4.04 mg), clearance rate increased rapidly and significantly ($p<0.001$). As shell length (and flesh dry weight) increased further, the clearance rate increased gradually but not significantly ($p=0.087$). The exponents of the fitting equations for shell length and flesh dry weight were 2.254 and 0.712, respectively.

The weight-specific clearance rate (CR_w) decreased with increasing flesh dry weight (Fig. 4), with CR_w values (mean ± SD) from 1.0 ± 0.2 to 3.1 ± 0.6

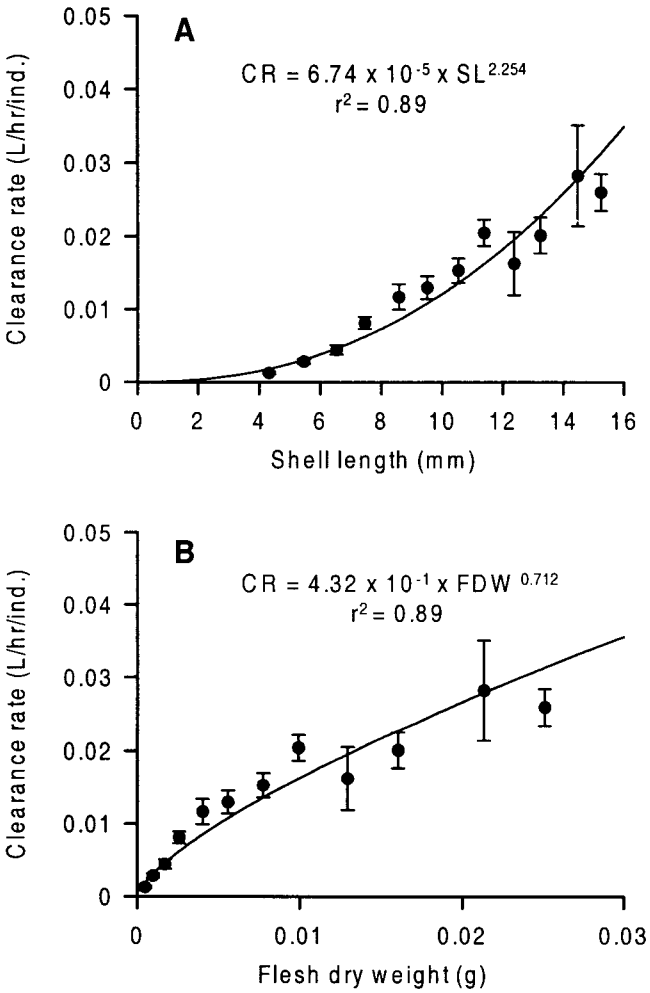

Fig. 3. The clearance rates (CR; L/hr/ind.) of *G. chinensis* as functions of (A) shell length (SL; mm) and (B) flesh dry weight (FDW; g) when feeding on *I. galbana*. Symbols represent treatment mean ± 1 SE. The curves were fitted to power functions.

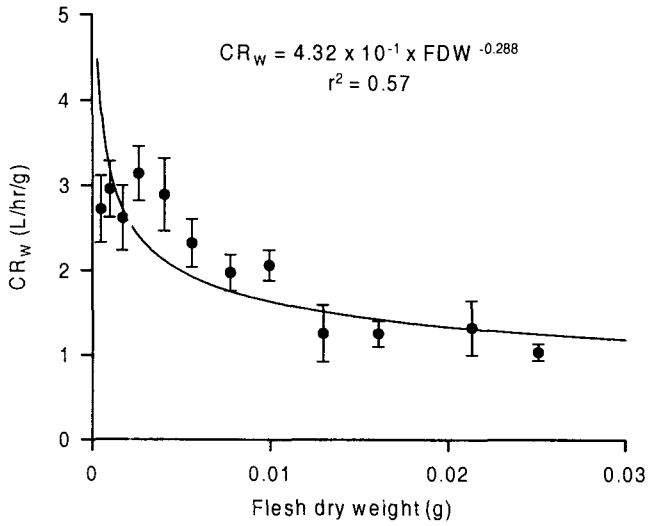

Fig. 4. The weight-specific clearance rate (CR_W; L/hr/g) of *G. chinensis* as a function of flesh dry weight (FDW; g) when feeding on *I. galbana*. Symbols represent treatment mean ± 1 SE. The curve was fitted to a power function.

L/hr/g. Body size also affected CR_W significantly ($F=6.6$, $p<0.001$). Smaller size classes with shell lengths from 4 to 9 mm (flesh dry weights from 0.47 to 4.04 mg) had higher CR_W than larger size classes with shell lengths from 10 to 16 mm (flesh dry weights from 5.59 to 25.11 mg). Multiple comparisons showed that CR_W values did not differ significantly when shell length was in the range from 4 to 12 mm (flesh dry weight from 0.47 to 9.92 mg) ($p=0.262$) or from 9 to 16 mm (flesh dry weight from 5.59 to 25.11 mg) ($p=0.158$).

Ingestion rate exhibited quite similar patterns to clearance rate. The ingestion rates (mean ± SD) of *G. chinensis* ranged from 24.0 ± 3.9 to 458.5 ± 137.7 μgC/hr/ind. (Fig. 5). One-way ANOVA showed that body size affected ingestion rate significantly ($F=45.9$, $p<0.001$). As shell length increased from 4 to 10 mm (flesh dry weight from 0.47 to 5.59 mg), ingestion rate increased rapidly and significantly ($p<0.001$). As shell length (or flesh dry weight) increased further, ingestion rate increased gradually but not significantly ($p=0.155$). The exponents of the fitting equations for shell length and flesh dry weight were 2.273 and 0.718, respectively.

The weight-specific ingestion rate (IR_W) decreased with increasing flesh dry weight (Fig. 6), with IR_W

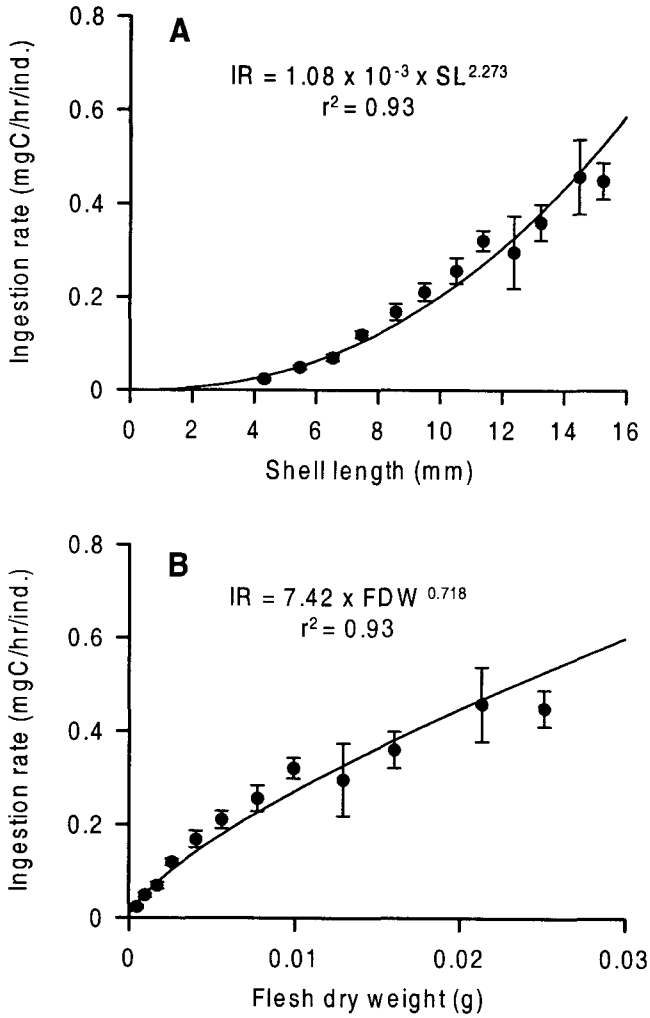

Fig. 5. The ingestion rates (IR; mgC/hr/ind.) of *G. chinensis* as functions of (A) shell length (SL; mm) and (B) flesh dry weight (FDW; g) when feeding on *I. galbana*. Symbols represent treatment mean ± 1 SE. the curves were fitted to power functions.

values (mean ± SD) from 17.9 ± 2.7 to 51.3 ± 8.3 mgC/hr/g. Body size also affected IR_W significantly ($F=9.5$, $p<0.001$). Smaller size classes with shell lengths from 4 to 10 mm (flesh dry weights from 0.47 to 5.59 mg) showed higher IR_W than larger size classes with shell lengths from 11 to 16 mm (flesh dry weights from 7.74 to 25.11 mg). Multiple comparison showed that IR_W did not differ significantly when shell length was in the range from 4 to 12 mm (flesh dry weight from 0.47 to 9.92 mg) ($p=0.067$) or from 10 to 16 mm (flesh dry weight from 7.74 to 25.11 mg ($p=0.229$).

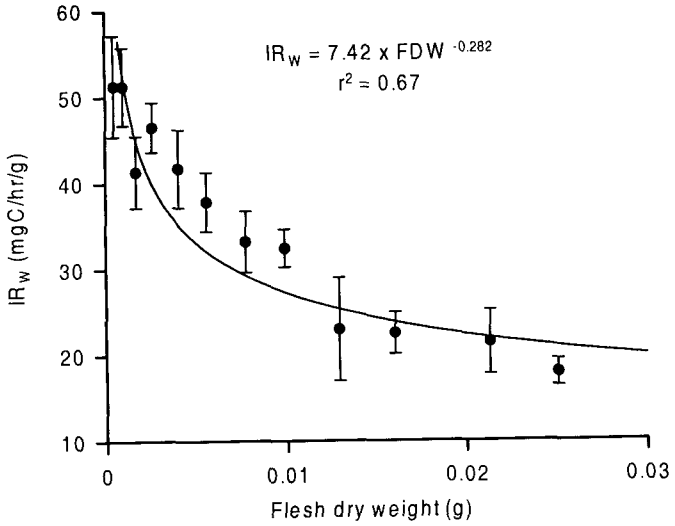

Fig. 6. The weight-specific ingestion rate (IR_W; mgC/hr/g) of *G. chinensis* as a function of flesh dry weight (FDW; g) when feeding on *I. galbana*. Symbols represent treatment mean ± 1 SE. The curve was fitted to a power function.

Discussion

We found that the CR_W of *G. chinensis* decreased as their body size increased (Fig. 4). Reduction in CR_W with increasing body size is a general phenomenon (Bayne et al., 1976). The CR_W obtained in this study (1.0~3.1 L/hr/g) is comparable to those for *Mytilus edulis* (Winter, 1973), *Crassostrea virginica* (Strychar and MacDonald, 1999), and *Brachidontes pharaonis* (Sarà et al., 2000) (Table 2). Specifically, our CR_W is higher than some values for *M. edulis* and *Placopecten magellanicus* (Cranford and Hill, 1999), but lower than others for *M. edulis* (Clausen and Riisgård, 1996; Björk and Gilek, 1997), *Potamocorbula amurensis* (Werner and Hollibaugh, 1993), *Argopecten ventricosus-circularis* (Sicard et al., 1999), and spat of *Pinctada maxima* (Mills, 2000).

We found a statistically significant relationship between the clearance rate (CR) and flesh dry weight (FDW) based on the equation $CR=a(FDW)^b$. Parameter a determines the absolute value of the clearance rate; it depends on various conditions such as body size or prey concentration (Winter, 1973). The a value of *G. chinensis* is much lower than those for other bivalves (Table 3). It may be due to the small size of *G. chinensis*. Parameter b is the slope of the regression line resulting from the data being plotted on a double logarithmic scale; it indicates the relative increase in the clearance rate with body size. The b value for *G. chinensis* obtained in this study is in good accordance with that obtained by Winter (1973); it is higher than b values for *M. edulis, C. gigas, Ostrea edulis, Venerupis decussata* and *Venus mercenaria* (Walne, 1972), *Pinctada margaritifera* and *Pinctada maxima* (Yukihira et al., 1998) and *Placopecten magellanicus* (MacDonald and Thompson, 1986). According to Thompson and Bayne (1972), however, our value represents "routine" metabolism, which is intermediate bet-ween the "standard" (0.616) and the "active" (0.797) metabolism.

From the results of statistical analyses, we can divide the size classes in the shell length of *G. chinensis* into 3 groups: 4 to 9 mm, 9 to 12 mm and 12 to 16 mm. In the 4 to 9 mm range, all the measured rates changed greatly and significantly with body size. In the 9 to 12 mm range, clearance and ingestion rates not standardized to flesh dry weight

Table 2. 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 (mg)	CR_W (L/hr/g)	Reference
Mytilus edulis	8.5~56.5	3~1,186	1.1~11.3	Winter (1973)
Mytilus edulis	25~30	40~100	18	Clausen and Riisgård (1996)
Mytilus edulis	14.8	9,600	2.7~26.6	Björk and Gilek (1997)
Mytilus edulis	77~82	1,800~3,000	0.12~2.11	Cranford and Hill (1999)
Potamocorbula amurensis	10~20	9~72	5.0~17.8	Werner and Hollibaugh (1993)
Crassostrea virginica	–	–	2.5~3.0	Strychar and MacDonald (1999)
Argopecten ventricosus-circularis	11.8	14	8.7~17.8	Sicard et al. (1999)
Placopecten magellanicus	91~97	6,100~9,300	0.06~1.05	Cranford and Hill (1999)
Brachidontes pharaonis	30	–	0.8~3.0	Sarà et al. (2000)
Pinctada maxima (spat)	4.3	11	17~54	Mills (2000)
Glauconome chinensis	4~16	0.5~25	1.0~3.1	This study

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

Species	*a*	*b*	Reference
Mytilus edulis	3.85	0.25	Walne (1972)
Mytilus edulis	2.41	0.74	Winter (1973)
Crassostrea gigas	10.39	0.27	Walne (1972)
Ostrea edulis	8.80	0.23	Walne (1972)
Venerupis decussata	4.56	0.28	Walne (1972)
Venus mercenaria	4.53	0.18	Walne (1972)
Pecten irradians	4.74	0.82	Chipman and Hopkins (1954)
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	This study

showed statistical significance, but the standardized rates did not. In the 12 to 16 mm range, none of the rates differed significantly. These results indicate that the increase in metabolic rates with body size is fastest when the shell length is from 4 to 9 mm, intermediate when the shell length is from 9 to 12 mm and slowest or nearly zero when the shell length is over 12 mm. Therefore, physiological experiments using *G. chinensis* larger than 12 mm in shell length will give the most stable results.

This study did not consider the effects of endogenous factors acting on *G. chinensis* in the long term, such as circadial-, tidal- and lunar rhythms. Because numerous studies have revealed that the behavioral and physiological processes of marine organisms have endogenous rhythms (Ameyaw-Akumfi and Naylor, 1987; Palmer, 1995; Kim et al., 1999), it is necessary to study the endogenous control of feeding physiology of suspension feeders through long term experiments.

Acknowledgements

We thank Yeong Tae Kim and Ki Hyun Kim for technical supports. This paper was funded by grants from the Korea Research Foundation ('99 Brain Korea 21) and KOSEF ('99 RRC).

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