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Feeding of Juvenile Purple Washington Clam, *Saxidomus purpuratus* (Sowerby): Effects of Algal Concentration and Temperature

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To find the optimal rearing conditions for *Saxidomus purpuratus* juvenile, filtering activity was estimated as functions of algal concentration and temperature by measuring the rates of clearance (CR) and ingestion (IR), when *S. purpuratus* was feeding. The clams were fed on unialgal diet of *Isochrysis galbana* at 6 algal concentrations (4.6×10^4~2.6×10^6 cells/ml) and at 6 temperatures (5, 10, 15, 20, 25, and 30℃). Algal concentration significantly affected the CR and the IR at all temperatures. At lower algal concentrations, CR increased, but decreased beyond a particular concentration. The maximum CR (CR_{max}) at 5, 10, 15, 20, 25, and 30℃ were 0.30, 1.73, 5.95, 15.17, 21.12, and 0.33 ℓ/g/h, respectively. Below the level of 5.6×10^5 cells/ml, IR increased as algal concentration increased, but was saturated at higher concentrations. To maintain high growth rate of *S. purpuratus*, *I. galbana* should be supplied with more than 5.6×10^5 cells/ml. The maximum IR (IR_{max}) at 5, 10, 15, 20, 25, and 30℃ were 2.2×10^8, 1.5×10^9, 3.4×10^9, 4.9×10^9, 5.3×10^9, and 1.0×10^8 cells/g/h, respectively. As for temperature, both CR_{max} and IR_{max} increased remarkably with raising temperature from 5 to 25℃, but rapidly decreased at 30℃. Between 15 and 25℃ CR_{max} and IR_{max} were higher and most stable. At this temperature range, the Q_{10}s for CR_{max} and IR_{max} were 3.5 and 1.6, respectively. Therefore the optimal thermal range for the juvenile is 15~25℃. The annual variation in IR_{max} predicted by natural seawater temperature shows that 'inactive period' (with lower IR_{max}) lasts for 5 months (from December to April). To ensure higher growth of juvenile during this inactive period at hatcheries, rearing temperature should be elevated to 15℃.

Key words: *Saxidomus purpuratus*, Juvenile, Algal concentration, Temperature, Clearance rate, Ingestion rate

Introduction

The purple Washington clam, *Saxidomus purpuratus* (Class Bivalvia, Family Veneridae) is a suspension-feeding bivalve and one of the most important food resources for human. Its natural distribution is restricted to the coasts of China, Japan, and Korea. It inhabits the soft bottoms with silty sand from intertidal to subtidal zones to a depth of ca. 20 m (Choe et al., 1999). Recently, commercial interest in this species has increased with strong demands and high prices. The commercial yields from the traditional exploitation by divers have been declining due to over-harvesting. Hence much attention has been paid to the culturing of the species. Although there are several studies on basic ecological aspects (Kim, 1971), reproductive biology (Kim, 1969; Chung et al., 1999; Kim et al., 2001a), and natural yields and growth (Kim et al., 2001b) of *S. purpuratus*, there has been no published report on its aquaculture.

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Thanks to the efforts made by the Taean Marine Hatchery, National Fisheries Research and Development Institute (NFRDI), Korea to rear the larvae and juveniles of *S. purpuratus*, mass production of seedling was possible in 2001. However, the seedling production could not be sustained even up to 2002, as optimal conditions for rearing juveniles were not known clearly. To find the optimum conditions of temperature and algal concentration for culturing the juveniles of S. *purpuratus*, the present investigation was undertaken.

Feed and temperature are important factors in determining the scope for growth of marine bivalves (Bayne et al., 1976; MacDonald and Thompson, 1986). They significantly influence the survival and growth of larvae, juveniles, and broodstocks (Mills, 2000). Filtering activity reflects the physiological status of bivalves and is affected significantly also by food and temperature (Bougrier et al., 1995; Heasman et al., 1996; Mills, 2000; Navarro et al., 2000). It is possible to identify optimal feed and thermal conditions for successful rearing of juveniles through measurements of filtering activity. To develop suitable aquaculture technique for rearing *S. purpuratus*, baseline data on the rates of clearance and ingestion were obtained exposing the juvenile to different algal concentrations and temperatures.

Materials and Methods

Test organisms

The measurements on the rates of clearance and ingestion were made at the Red Tide Research Center, Kunsan National University. *S. purpuratus* juveniles were obtained from a cohort reared at ambient seawater temperature in the Taean Marine Hatchery, NFRDI. One-year old juveniles (4.7~6.3 mm in shell length) were used for the feeding experiments. They were divided randomly into 6 groups. Each group consisted of ca. 200 individuals and was transferred into a 10 ℓ aquarium with 5 ㎛ filtered seawater (salinity: 30‰). Then, each aquarium was placed and maintained separately in 6 temperature-controlled incubators (initial temperature: 20℃) with 12 L : 12 D cycle of 5 μE/m^2/sec provided by cool-white fluorescent lights. Prior to feeding experiments, rearing temperature of each incubator was adjusted gradually (1℃/day) to the desired temperature (Table 1). On attaining it, the clams were acclimated for additional 2 days. During acclimation seawater was fully renewed everyday and the clams were fed 5×10^6 cells/ml of *I. galbana*. Mortality was checked everyday and dead individuals were removed immediately. On the day of feeding experiment, clams were rinsed twice with freshly filtered seawater and depurated at least for 6 hrs at the same temperature. Apparently healthy individuals were selected for the feeding experiments.

I. galbana was supplied from the Red Tide Research Center, Kunsan National University. It was grown at 20℃ with f/2 medium (Guillard and Ryther, 1962) without silicate, with continuous illumination of 100 μE/m^2/sec provided by cool-white fluorescent lights. Only cells in exponential growth phase were used for

Table 1. Selected sizes (shell length, SL; flesh dry weight, FDW) of *S. purpuratus* and the mean concentrations of *Isochrysis galbana* for determining the rates of clearance and ingestion at each experimental temperature

Temperature (℃)	Size of *S. purpuratus* (mean±SD)		Concentration of *I. galbana* (cells/ml)*
	SL (mm)	FDW (mg)	
5	5.61±0.32(n=54)	1.38±0.25(n=54)	2.0×10^5, 4.0×10^5, 5.6×10^5, 7.6×10^5, 1.2×10^6, 1.7×10^6
10	5.61±0.30(n=49)	1.38±0.23(n=49)	1.8×10^5, 2.3×10^5, 4.0×10^5, 5.8×10^5, 1.0×10^6, 1.4×10^6
15	5.65±0.30(n=40)	1.41±0.23(n=40)	1.2×10^5, 3.0×10^5, 4.2×10^5, 7.0×10^5, 1.3×10^6, 1.8×10^6
20	5.67±0.30(n=54)	1.43±0.22(n=54)	4.6×10^4, 1.6×10^5, 3.6×10^5, 7.2×10^5, 1.6×10^6, 2.5×10^6
25	5.72±0.14(n=42)	1.46±0.12(n=42)	1.2×10^5, 3.7×10^5, 9.0×10^5, 1.4×10^6, 1.9×10^6, 2.6×10^6
30	5.74±0.15(n=42)	1.47±0.13(n=42)	1.5×10^5, 3.1×10^5, 7.0×10^5, 1.1×10^6, 1.6×10^6, 1.8×10^6

*Mean algal concentration during incubation period (geometric mean of initial and final concentrations)

experiments. To acclimate to the experimental temperature, culture was transferred to the incubators 1 day before the feeding experiments.

Experimental design

Experiments were designed to measure the rates of clearance and ingestion of juvenile as a function of algal concentration, when feeding on unialgal diet of *I. galbana* at each experimental temperature (Table 1). Initial concentrations of *I. galbana* were established using an autopipette to deliver predetermined volumes of known concentrations to the chambers. Triplicate 100 ml polyethylene beakers were used as incubation chambers. Beakers were filled with 50 ml of algal suspension, and then 2 or 3 juveniles were transferred to each beaker. The beakers were placed in temperature-controlled incubators with 5μE/m^2/sec of cool-white fluorescent light for 1~4 hrs. To determine the actual concentrations of *I. galbana* at the beginning and the end of experiments, 10 ml aliquot of algal suspension was sub-sampled from each beaker and fixed with 5 % Lugol's solution, and more than 400 algal cells (in triplicate) in 1 ml Sedgwick-Rafter chambers were counted. After the experiments, the flesh dry weight (FDW) of each clam was measured. Soft tissue was removed from the shells, dried in an oven at 90℃ for 48 hrs, and weighed on an electronic microbalance (Sartørius Co.) to the nearest 0.01 mg.

Calculation of the rates of clearance (CR) and ingestion (IR)

The clearance rate (CR) was calculated using the equation of Coughlan (1969) as:

$$CR = V \cdot \ln(C_0/C_t)/(FDW \cdot t) \quad (1)$$

where V is the volume of algal suspension, C_0, the initial concentration of *I. galbana*, C_t, the final concentration of *I. galbana*, *FDW*, the flesh dry weight of *S. purpuratus*, and t is the incubation time. To determine the functional response of *S. purpuratus* to algal concentration, clearance rate data were fitted to an exponential equation (Riisgård, 1988):

$$CR = a/C^* \cdot e^{(-b/C^*)} \quad (2)$$

where C^* is the mean algal concentration during incubation period (geometric mean of C_0 and C_t), a and b are the parameters estimated by curve-fitting. Parameter a explains the magnitude of the clearance rate and parameter b denotes the algal concentration at which the clearance rate is maximal. Maximum clearance rate (CR_{max}) was calculated by substituting algal concentration with estimated b value to the above equation.

Ingestion rate (IR) was calculated as:

$$IR = CR \cdot C^* \quad (3)$$

To determine the functional response of *S. purpuratus* to algal concentration, the ingestion rate data were fitted to a Michaelis-Menten equation (Båmstedt et al., 2000):

$$IR = IR_{max} \cdot C^*/(K_{IR} + C^*) \quad (4)$$

where IR_{max} is the maximum ingestion rate, K_{IR}, the half-saturation constant (i.e. the algal concentration, where IR = $IR_{max}/2$).

Statistical analyses

Data obtained for the rates of clearance and ingestion at different algal concentrations for each tested temperature were compared by one-way ANOVA on SPSS program. Multiple comparisons were conducted using Tukey's HSD (Zar, 1984). Before the statistical analyses, data on the rates of clearance and ingestion were tested for normality (Shapiro-Wilk's test) and homogeneity of variance (Bartlett's test). If at least one of the above ANOVA requirements was not met, the data were transformed into $\log_{10}$, and then ANOVA was repeated. For all analyses, a significance level of $\alpha = 0.05$ was used.

Results

Clearance rate (CR)

Clearance rate (CR, mean ± SD) of juveniles of *S.*

purpuratus fed on unialgal diet of *I. galbana* at seawater temperature of 5℃ ranged from 0.10 ± 0.02 to 0.32 ± 0.10 ℓ/g/h (Fig. 1A). Algal concentration affected significantly the CR (ANOVA, $P<0.001$). With increasing algal concentration from 2.0×10^5 to 4.0×10^5 cells/ml, the CR increased slightly but subsequently decreased progressively, as the algal concentration increased further, and reached the minimum, when algal concentration was the highest. Multiple comparisons showed that there were no significant differences in CRs, when algal concentration ranged from 2.0×10^5 to 7.6×10^5 cells/ml, 5.6×10^5 to 1.2×10^6 cells/ml, and 1.2×10^6 to 1.7×10^6 cells/ml. When CR data were fitted to the equation (2), the maximum CR (CR_{max}) was estimated as 0.30 ℓ/g/h.

In general, the trends obtained for the relationship between CR and algal concentration at other temperatures remained more or less similar to that at 5℃, but the level of CR shifted higher and higher with increasing temperature up to 25℃. For instance, the increases in CR were from 0.48±0.11 to 2.32±0.64 ℓ/g/h (ANOVA, $P<0.001$) at 10℃ (Fig. 1B), 1.39±0.33 to 5.67±2.50 ℓ/g/h (ANOVA, $P=0.005$) at 15℃ (Fig. 1C), 1.70±0.31 to 13.73±1.14 ℓ/g/h (ANOVA, $P<0.001$) at 20℃ (Fig. 1D) and 1.86±0.37 to 19.27±2.68 ℓ/g/h (ANOVA, $P<0.001$) at 25℃ (Fig. 1E).

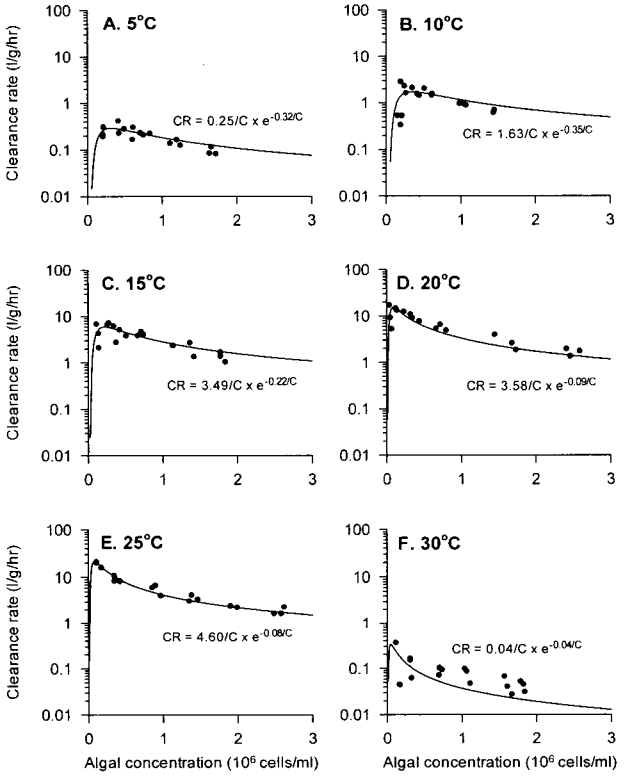

Fig. 1. Clearance rate (CR) of juvenile purple Washington clam *S. purpuratus* as a function of algal concentration (*Isochrysis galbana*) at different temperatures (A: 5℃, B: 10℃, C: 15℃, D: 20℃, E: 25℃, F: 30℃). CR data were fitted to an exponential function [eq. (2)]. Equations for fitted curves are shown in each figure.

On reaching the respective maxima, the CR began to decrease progressively with further increase in algal concentration and reached the minimum at the respective highest concentrations. Hereto the level of minimum CR was progressively shifted towards higher value with increasing temperature. However, the CR was low at 30℃ and ranged between 0.04±0.01 and 0.15±0.02 ℓ/g/h (Fig. 1F) but there was no significant difference at different algal concentrations (ANOVA, $P=0.275$).

Multiple comparisons of the data among different algal concentrations for each temperature showed that there were no significant differences in the CR, when algal concentrations ranged from 2.3×10^5 to 5.8×10^5 cells/ml, 4.0×10^5 to 1.0×10^6 cells/ml, and 1.0×10^6 to 1.4×10^6 cells/ml at 10℃, 1.2×10^5 to 1.3×10^6 cells/ml and 1.3×10^6 to 1.8×10^6 cells/ml at 15℃, 4.6×10^4 to 3.6×10^5 cells/ml, 3.6×10^5 to 7.2×10^5 cells/ml, 7.2×10^5 to 1.6×10^6 cells/ml, and 1.6×10^6 to 2.5×10^6 cells/ml at 20℃, and 9.0×10^5 to 1.4×10^6 cells/ml, 1.4×10^6 to 1.9×10^6 cells/ml, and 1.9×10^6 to 2.6×10^6 cells/ml at 25℃, respectively. At 30℃, the CR decreased progressively with increasing algal concentrations and reached the minimum at the highest algal concentration.

When the CR data were fitted to the equation (2), the estimated CR_{max} increased from 0.30 ℓ/g/h at 5℃ to 1.73, 5.95, 15.17 and 21.12 ℓ/g/h at 10, 15, 20 and 25℃, respectively. However, it rapidly fell to 0.33 ℓ/g/h at 30℃.

Ingestion rate (IR)

Ingestion rate (IR, mean±SD) of the juveniles of *S. purpuratus* fed on unialgal diet of *I. galbana* at seawater temperature of 5℃ ranged from 5.0×10^7±1.3×10^7 to

$1.7\times10^8\pm0.2\times10^8$ cells/g/h (Fig. 2A). The IR was significantly affected by the algal concentration (ANOVA, P=0.003). It increased with increasing algal concentration from 2.0×10^5 to 4.0×10^5 cells/ml. As algal concentration increased further, the IR was saturated and fluctuated between 1.3×10^8 and 1.7×10^8 cells/g/h. Multiple comparisons showed that there were no significant differences in the IRs, when algal concentration ranged from 2.0×10^5 to 4.0×10^5 cells/ml, and 4.0×10^5 to 1.7×10^6 cells/ml. When the IR data were fitted to the equation (4), the maximum IR (IR_{max}) and the half-saturation constant (K_{IR}) were estimated as 2.2×10^8 cells/g/h and 3.5×10^5 cells/ml, respectively.

In general, the trends obtained for the relationship between IR and algal concentration at other temperatures remained more or less similar to that at 5℃, but the level of IR shifted higher and higher with increasing temperature of up to 25℃. For instance, the increases in IR were from 8.6×10^7 to 9.8×10^8 cells/ml at 10℃ (ANOVA, P<0.001, Fig. 2B), 5.4×10^8 to 3.0×10^9 cells/ml at 15℃ (ANOVA, P=0.001, Fig. 2C), 4.3×10^8 to 4.5×10^9 cells/ml at 20℃ (ANOVA, P<0.001, Fig. 2D) and 2.3×10^9 to 5.2×10^9 cells/ml at 25℃ (ANOVA, P=0.003, Fig. 2E).

On reaching the respective maxima, the IR was saturated with further increase in algal concentration but the respective maximum reached higher and higher with increasing temperature up to 25℃. However, the IR was low at 30℃ and ranged between 1.9×10^7 to 8.3×10^7 cells/ml and reached the maximum at the algal concentration of about 1.8×10^6 cells/ml (ANOVA, P=0.020, Fig. 2F)

Multiple comparisons of the data obtained for each temperature showed that there were no significant differences in IR, when algal concentrations ranged from 2.3×10^5 to 4.0×10^5 cells/ml and 5.8×10^5 to 1.4×10^6 cells/ml at 10℃, 1.2×10^5 to 3.0×10^5 cells/ml, 3.0×10^5 to 4.2×10^5 cells/ml, and 4.2×10^5 to 1.8×10^6 cells/ml at 15℃, 4.6×10^4 to 1.6×10^5 cells/ml, 1.6×10^5 to 3.6×10^5 cells/ml, and 3.6×10^5 to 2.5×10^6 cells/ml at 20℃, 1.2×10^5 to 3.7×10^5 cells/ml and 3.7×10^5 to 2.6×10^6 cells/ml at 25℃, and 1.5×10^5 to 7.0×10^5 cells/ml and 3.1×10^5 to 1.8×10^6 cells/ml at 30℃, respectively.

When the IR data were fitted to the equation (4), the IR_{max} increased from 2.2×10^8 cells/g/hr at 5℃ to 1.5×10^9, 3.3×10^9, 4.9×10^9 and 5.3×10^9 cells/g/hr at 10, 15, 20 and 25℃, respectively. At 30℃, the IR_{max} decreased down to 1.0×10^8 cells/g/hr. The corresponding values for K_{IR} were 3.5×10^5, 5.1×10^5, 2.9×10^5, 2.0×10^5, 1.5×10^5 and 4.7×10^5 cells/ml at 5, 10, 15, 20, 25 and 30℃, respectively.

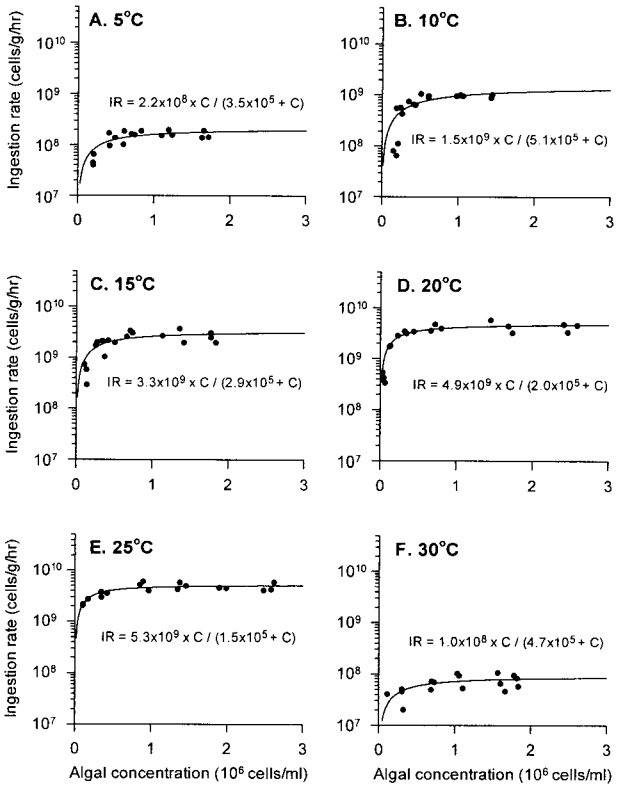

Fig. 2. Ingestion rate (IR) of juvenile purple Washington clam *S. purpuratus* as a function of algal concentration (*Isochrysis galbana*) at different temperatures (A: 5℃, B: 10℃, C: 15℃, D: 20℃, E: 25℃, F: 30℃). IR data were fitted to a Michaelis-Menten equation [eq. (4)]. Equations for fitted curves are shown in each figure.

Discussion

This study has established that the algal concentration and temperature strongly influenced the rates of clearance (CR) and ingestion (IR) of *S. purpuratus* juvenile. CR changed significantly from 0.04 to 19.3 ℓ/g/h (ca. 480-fold change) with increasing algal

concentration and temperature. In general, the CR was maximal at all temperature, when algal concentration was relatively low and then decreased as the concentration increased. This trend of CR is common to many suspension feeders (Bayne et al., 1976; Mills, 2000). Reduction in CR at high algal concentration may be due to increase in food availability. As algal cells become more abundant, clams require to filter less volume of water to obtain the same amount of food. The CR values (0.04~19.3 ℓ/g/hr) obtained for *S. purpuratus* are comparable to 0.8~3.0 ℓ/g/h of *Brachidontes pharaonis* (Sarà et al., 2000), 8.7~17.8 ℓ/g/h of *Argopecten ventricosus-circularis* (Sicard et al., 1999), 18 ℓ/g/h of *Mytilus edulis* (Clausen and Riisgård, 1996), and 5.0~17.8 ℓ/g/h of *Potamocorbula amurensis* (Werner and Hollibaugh, 1993), but are lower than 17.3~54 ℓ/g/h of *Pinctada maxima* (Mills, 2000).

The IR also changed significantly from 1.9×10^7 to 5.2×10^9 cells/g/h (ca. 270-fold change) according to algal concentration and temperature. It showed asymptotic relationships with algal concentration at all the tested temperatures, i.e. IR increased at lower algal concentration, then was saturated as algal concentration increased further. When the algal concentrations were above 5.6×10^5 cells/ml, IR showed no statistical differences, regardless of temperature. In other words, the ability to obtain the algal cells by *S. purpuratus* juveniles will not increase above this algal concentration. Therefore, to maintain its high growth rate algae should be supplied at the concentration of at least 5.6×10^5 *I. galbana* cells/ml.

Temperature effects on the CR_{max} and IR_{max} of *S. purpuratus* were remarkable (Fig. 3). At 5℃ the CR_{max} was as low as 0.3 ℓ/g/h. It increased with temperature and was the highest (21.1 ℓ/g/h) at 25℃, and then rapidly decreased at 30℃. Thermal conditions at 30℃ seem critical stress to *S. purpuratus*. The Q_{10}s for CR_{max} were 20.1 for the thermal range of 5~15℃, 8.8 for 10~20℃, 3.5 for 15~25℃, and 0.02 for 20~30℃. The trend for IR_{max} was also similar to CR_{max}. It increased from 5 to 25℃, and then rapidly decreased at 30℃. The Q_{10}s for IR_{max} were 15.3, 3.4, 1.6 and 0.02

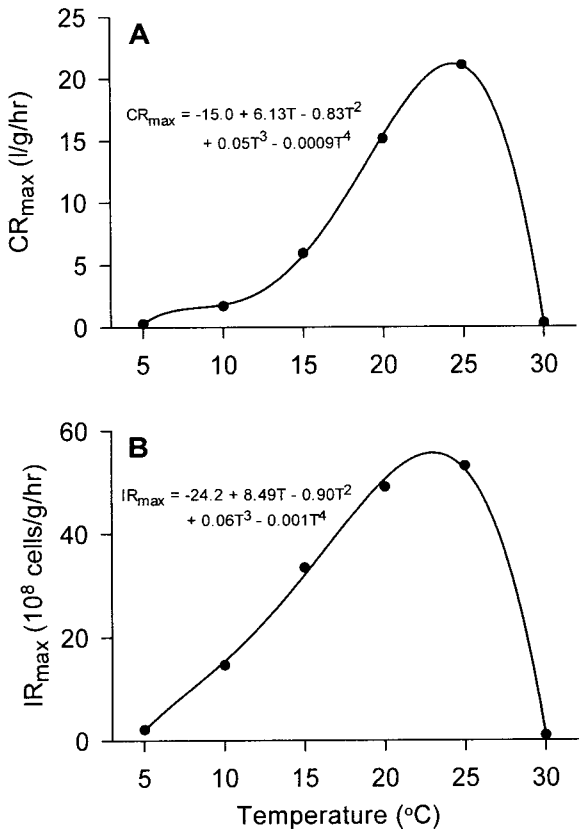

Fig. 3. Maximum clearance rate (CR_{max}, A) and maximum ingestion rate (IR_{max}, B) of juvenile purple Washington clam *S. purpuratus* as a function of temperature (T). CR_{max} and IR_{max} data were fitted to 4th order polynomial equations. Equations for fitted curves are shown in each figure.

for the thermal ranges of 5~15℃, 10~20℃, 15~25℃ and 20~30℃, respectively. Within the thermal range of 15~25℃, both CR_{max} and IR_{max} were higher and varied little (3.5-fold change for CR_{max} and 1.6-fold for IR_{max}). Therefore, the optimal thermal range for *S. purpuratus* juvenile is 15~25℃. At temperature lower than 15℃, reduction in the growth is expected. At higher than 25℃, the clams suffer thermal stress.

From the relationship between the IR_{max} and temperature (Fig. 3B), it is possible to predict the annual variation in IR_{max} from the annual variation in seawater temperature (Fig. 4). The curve of the IR_{max} was fitted by a 4th order polynomial equation. The curve shows lower IR_{max} during January~April and December (indicated as 'inactive period'). Higher IR_{max}, and hence faster growth can be expected from

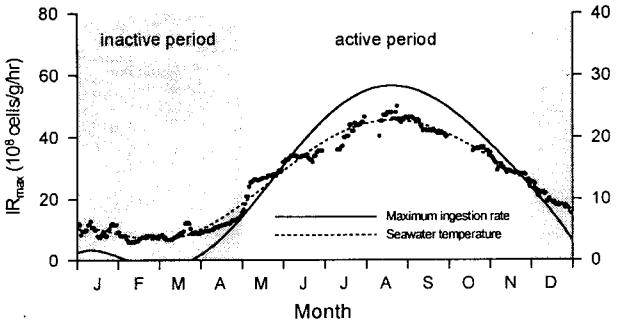

Fig. 4. Annual variations in the maximum ingestion rate (solid line; predicted by the equation in Fig. 3B) of juvenile purple Washington clam *S. purpuratus* and temperature measured at the Taean Marine Hatchery, NFRDI during 2001 (filled circle). Dotted line: fitted curve for seawater temperature.

May to November ('active period'). Surprisingly, the 'inactive period' lasts for 5 months. In general, most of aquaculturists assume that reduced growth is limited to winter only. However, our data clearly show that the inactive period extends from December to April, because the water temperature is less than 15℃ during this period. Therefore, rearing temperature at hatcheries should be elevated during this inactive period to ensure higher growth of *S. purpuratus* juvenile.

With short-term experiments, this study has shown the acute response of *S. purpuratus* to algal concentration and temperature. However, long term studies on survival and growth efficiency should be undertaken for better understanding the optimal rearing conditions required for *S. purpuratus* juvenile.

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