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A Laboratory Study of the Effect of Phytoplankton Concentration, Water Flow and Their Interaction on the Growth of the Sandy Shore Suspension Feeding Clam *Gafrarium tumidum*

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ABSTRACT: The effects of water flow rate and phytoplankton concentration on the growth of the sandy shore clam *Gafrarium tumidum* was investigated in a laboratory flume study using a 3 × 3 factorial design. After 60 days, shell length, shell weight and tissue dry weight increased significantly with phytoplankton concentration. For the effect of flow rate, growth was faster when flow rate increased from low to medium level; further increases in flow rate, however, either did not sustain faster growth or resulted in a reduction in growth. The condition index (CI) of a standard-sized clam was significantly higher at low flow rate than at medium and high flow rates and was negatively correlated with phytoplankton concentration. The uncoupled growth of shell and tissue in response to flow rate and phytoplankton concentration may be adaptations to low food environments, so that energy can either be stored to sustain life or reserved for gametogenesis during the reproductive period.

Key words: Clams, Flume, *Gafrarium,* Growth, Phytoplankton concentration, Water flow

INTRODUCTION

Both laboratory flume and field experiments have been used to investigate the effects of water flow and food concentration on growth in bivalves (see review by Wildish and Kristmanson 1997). When compared to field experiments, a laboratory flume approach is advantageous in the sense that flow rate and food concentration can be controlled carefully, and different combinations of the two factors can be tested to reveal the relative contributions of these factors, along with their interactions on bivalve growth. Nevertheless, critics to this approach are concerned that the laboratory flume approach cannot easily mimic the natural fluctuations in flows, such as tidal conditions or seston quantity and quality, to which animals are exposed in their natural environment (Wildish and Kristmanson 1984, Eckman et al. 1989, Judge et al. 1992).

Growth is positively correlated with food concentration, but only up to a certain point; further increases in food concentration result in a reduction of growth in mussels (Winter 1978) and scallops (Cahalan et al. 1989). This is because at high food concentrations, growth is limited by the ability of the gills to remove particles from water (Winter 1978). The clearance rate of cockles *Cerastoderma edule*, however, was not significantly affected by water flow between 5 and 35 cm s^{-1} (Widdows and Navarro 2007).

A number of studies have shown that the effect of flow on growth in bivalves is unimodal with the fastest growth being obtained at medium flow (Grizzle et al. 1992, Wildish and Miyares 1990). Reduction in growth at low flows may be due to a reduction in seston flux and a depletion of seston by individuals on the upstream, especially within high population densities (Peterson and Black 1991). Growth inhibition at high flows, however, is probably caused by disruption of the bivalve pump by the pressure differential between inhalant and exhalant openings (Kirby-Smith 1972, Jørgensen et al. 1986, Eckman et al. 1989).

The present study investigated the effects of food concentration, water flow and their interactions on the growth of *Gafrarium tumidum*, a common sandy shore bivalve in Hong Kong. The levels of water flow and food concentration used were within the range experienced by this animal in the field to enable a determination of the relative significance of food concentration and flow on its growth. Results could also help predict inter-site differences in growth between habitats with different flow rates and food concentrations.

MATERIALS AND METHODS

A flume apparatus modified from Grizzle et al. (1992) was used in the experiment and constructed of fibreglass. The dimensions of the flume were 300 cm × 40 cm × 20 cm (L × W × H) and the flume was fed by a 2000 L capacity fibreglass header tank (Fig. 1). Water was maintained at a constant height (9 cm) in the header tank by a standpipe, and the constant, gravity-fed flow rate to the flume was controlled by ball valves. All pumping devices and valves were

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made of PVC. The working section, which included two sediment boxes lying side by side, were located in a trough of the flume 2.0 m from the water inflow point and 0.5 m from the outflow end. The size of each sediment box was 50 cm × 20 cm × 6 cm.

Based on the water flow data at the site where the clams were collected (Cheung and Shin unpublished data), and on information on seston concentrations (in terms of concentration of total suspended particulate matter) in coastal waters in Hong Kong (Wong and Cheung 2001), three flow velocities, low, medium and high (circa 5, 15, and 25 cm s^{-1}, respectively) and three phytoplankton concentrations, low, medium and high (4.0×10^4, 7.5×10^4, and 15×10^4 cells mL^{-1}, respectively) were selected for the flume experiment. In each flume, the sediment collected from the natural habitat of the test species was defaunated by drying the sediment in an oven at 60℃ for 48 h prior to placement in the sediment box.

The experiment lasted for 60 days (Grizzle et al. 1992) in a re-circulating filtered seawater system. As temperature affects bivalve growth rates (Emerson et al. 1994, Grant 1996), seawater was maintained at 20±1℃ in an air-conditioned laboratory with a 12h-12h light-dark cycle. Flow speed in each flume was measured daily using an electromagnetic current meter. Salinity, temperature and dissolved oxygen in each of the three header tanks were measured by refractometer, thermometer and dissolved oxygen meter, respectively. Unicellular algal culture of *Dunaliella tertiolecta* was offered as food during the experiment; the average cell size was circa 10 μm. After cell densities were counted microscopically in the culture media, a volume was calculated to give a known concentration in the experimental flume. Water samples were collected every day using an isokinetic technique (Hinds 1982) as described by Grizzle et al. (1992). A 1 cm (internal diameter) tygon tube was placed on the bottom of the flume in front of the sediment box, with its opening directed upstream. The opposite end of the tube was extended through one of the openings in the outflow end of the flume and positioned at a height just below the water surface, but at a point beyond the water spilling from the flume. One plastic bottle (300 mL) was filled for measurement of seston density from the end of the tube according to Wong and Cheung (1999). In such an arrangement, water flowing through the tube was at approximately the same speed as the water moving along the bottom of the flume.

The velocity distribution in a uniform channel flow is known to be approximately logarithmic and is given by the following equation:

$$v = 2.5\ V_f \ln (y/y_o) \quad \text{(French 1994)}$$

where v is the flow rate (cm s^{-1}) at y (cm) from the bottom, V_f is the shear velocity (cm s^{-1}), and y_o (cm s^{-1}) is the constant of integration with the order of magnitude as the viscous sublayer thickness. The above equation was used to determine the actual flow rate at 2 mm above the sediment surface where the siphon of the clam was positioned. To obtain V_f and y_o for the above equation, water flow rate was measured at the centre of the sediment box and at 2 cm, 4 cm and 7 cm above sediment surface by a flow meter at the low, medium and high flow rates (see Fig. 1). The V_f and y_o were obtained by a trial and error approach to minimize the mean square error. The fitted profiles at different flow rates is shown in Fig. 2 and y_o was calculated as 1.0×10^{-6} cm s^{-1}, and V_f at low, medium and high flows were 0.12, 0.35 and 0.59 cm s^{-1},

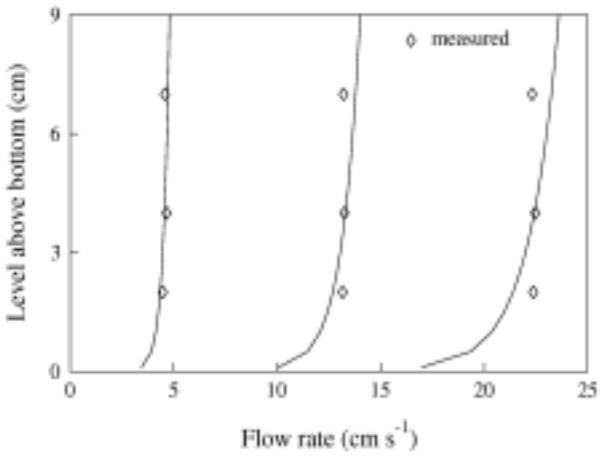

Fig. 2. Fitted curves relating height above sediment surface (cm) and the water flow rate (cm s^{-1}) in the flume experiment.

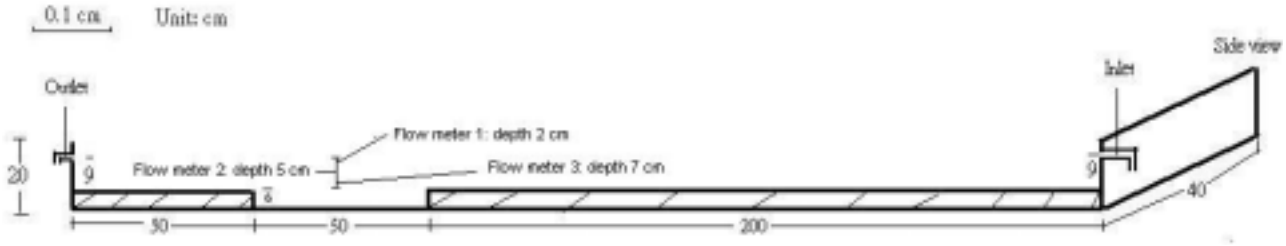

Fig. 1. The setup of the flume apparatus. Note that the depth of the flow meter position is denoted from the water surface.

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respectively. Substituting V_f and y_o into the above equation, the actual flow rates at 2 mm above sediment surface were 3.66, 10.68 and 18.00 cm s^{-1} at low, medium and high flow rates, respectively.

Three flumes were used for each flow rate and phytoplankton concentration as replicates. In each experimental flume, 12 juvenile individuals of *G. tumidum*, with mean shell length of 26.84 ± 1.27 mm (SD), were placed in two sediment boxes and allowed to bury themselves in the sediment. The number of individuals chosen was equivalent to the density that was found at the collection site. At the start of the experiment, the shell length of each bivalve was measured and numbered with permanent ink. Initial shell weight and tissue dry weight used to calculate growth rate were estimated from regressions relating to tissue dry weight/shell weight to shell length (Cheung and Shin 2007). The equations are:

$$\text{Shell weight (g)} = 0.49 \times \text{Shell length (mm)} - 8.20 \quad (R^2 = 0.98,\ F = 1699.38,\ p<0.001)$$

$$\text{Tissue dry weight (g)} = 0.03 \times \text{Shell length (mm)} - 0.71 \quad (R^2 = 0.92,\ F = 311.33,\ p<0.001)$$

The condition index (CI) of each individual was calculated as the ratio between tissue dry weight (g) and the total dry weight (g) (tissue dry weight + shell weight). The regression relating initial shell length (SL) (mm) and CI was calculated using 29 individuals with shell length ranging from 22.50 to 42.45 mm. Tissue dry weight, shell dry weight and shell length of each individual were measured. The relationship is shown as follows:

$$CI = -0.155 + (0.0101 \times SL) - (0.000127 \times SL^2) \quad (R^2 = 0.77,\ F = 44.62,\ p<0.001)$$

At the end of the experiment, the bivalves were removed from the flumes, put into plastic bags and frozen. Shell length, shell weight and tissue dry weight were determined for each bivalve. Shell weight and tissue dry weight were measured after drying in an oven at 60℃ for 24 h. CI covariates with shell length. To remove the confounding effect of shell length on CI, the values of CI obtained from different treatments at the end of the experiment were converted to values for a standard-sized individual with a shell length of 32.48 mm. This was the mean final shell length of *G. tumidum* obtained from all the treatments.

Since all clams were tagged at the start of the experiment, percentage increases in shell length, shell weight and tissue dry weight could be calculated for each individual. Data obtained from two sediment boxes in the same flume were pooled. Three flumes from each treatment became replicates. Different treatments were then compared by using a balanced, design-nested, one-way ANOVA with individual flumes being assigned as a random factor nested within three flow rates and three phytoplankton concentrations. Normality of the data was checked by using the Kolmogorov-Smirnov test and homogeneity of variances was checked by Bartlett's test of the statistical software Sigmastat 3.0. Significant treatment effects were further examined by Tukey multiple comparison procedure.

RESULTS

During the experimental period, salinity was maintained between 29.5 and 30.0‰, temperature 19.7 and 20.4℃, and dissolved oxygen 6.9 and 7.3 mg l^{-1}. Measurements of low, medium and high flow rates in the flumes ranged from 4.9 to 5.2, 14.9 to 15.2, and 24.9 to 25.3 cm s^{-1}, respectively. Seston densities in the low, medium and high phytoplankton concentrations ranged from 3.9 to 4.0 × 10^4, 7.4 to 7.6 × 10^4, and 14.7 to 15.0 × 10^4 cells mL^{-1}, respectively. Shell length increased with flow rate ($F = 1626.9$, $p<0.001$), phytoplankton level ($F = 5260.6$, $p<0.001$) and the interaction between flow rate and phytoplankton level ($F = 110.9$, $p<0.001$). The growth in shell length ranged from 0.11% day^{-1} at low flow and low phytoplankton level to 0.54% day^{-1} at medium flow and high phytoplankton level (Fig. 3a). At each flow rate, the percentage increase in shell length increased significantly with phytoplankton level (Table 1). A significant increase in shell length was obtained when flow rate increased from low to medium level. Further increase in flow rate either did not enhance a faster growth (at low and medium phytoplankton level) or resulted in a reduction in growth rate (at high phytoplankton level) (Table 2).

Shell weight increased with flow rate ($F = 149.3$, $p<0.001$), phytoplankton level ($F = 506.5$, $p<0.001$) and the interaction between flow rate and phytoplankton level ($F = 6.72$, $p<0.001$). The growth in shell weight ranged from 0.23% day^{-1} at low flow and low phytoplankton level to 1.35% day^{-1} at medium flow and high phytoplankton level (Fig. 3b). At each flow rate, shell weight increased significantly with phytoplankton level (Table 1). Similar to shell length, a significant increase in shell weight was obtained when flow rate increased from low to medium level. Further increases in flow rate either did not enhance a faster growth (at low and medium phytoplankton level) or resulted in a reduction in growth rate at high phytoplankton level (Table 2).

Tissue dry weight increased with flow rates ($F = 60.7$, $p<0.001$) and phytoplankton level ($F = 197.7$, $p<0.001$), but not the interaction between flow rates and phytoplankton level ($F = 2.0$, $p = 0.141$). The increase in tissue dry weight ranged from 0.19% day^{-1} at low flow and low phytoplankton level to 1.29% day^{-1} at medium flow and high phytoplankton level (Fig. 3c). At each flow rate,

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tissue dry weight increased significantly with phytoplankton level (Table 1). A significant increase in tissue dry weight was obtained when the flow rate increased from low to medium level. Further increase in flow rate, however, did not enhance a faster growth (Table 2).

The seston flux (phytoplankton concentration × flow rate) significantly affected the growth in shell length ($F = 1312.7$, $p < 0.001$), shell weight ($F = 547.3$, $p<0.001$) and tissue dry weight ($F = 314.6$, $p<0.001$) with all growth parameters increasing significantly with flux (Fig. 4 a~c) except at a flux of 55×10^4 cells cm^{-2} s^{-1}, of which the growth was much more enhanced and comparable to the value at 135×10^4 cells cm^{-2} s^{-1}. At the highest flux (270×10^4 cells cm^{-2} s^{-1}), growth in shell length and shell weight was lowered.

The CI of a standard-sized individual ranged between 0.022 ± 0.004 (SD) (medium flow, high phytoplankton level) and 0.035 ± 0.001 (SD) (low flow, low phytoplankton level), and varied significantly with flow rate ($F = 74.59$, $p<0.001$), phytoplankton level ($F = 226.45$, $p<0.001$) and the interaction between flow rate and phytoplankton level ($F = 9.71$, $p<0.001$). The CI at low flow was significantly higher than that at medium and high flow ($p<0.001$); the difference between medium and high flow, however,

Table 1. Multiple comparisons between phytoplankton concentrations on the percentage increase in shell length, shell weight and tissue dry weight at different flow rates

Growth parameter	Flow rate	*F*	*p*	Multiple comparisons between phytoplankton concentrations*
Increase in shell length (%)	Low	2,641.8	< 0.001	Low < Medium < High
	Medium	1,166.3	< 0.001	Low < Medium < High
	High	1,076.3	< 0.001	Low < Medium < High
Increase in shell weight (%)	Low	1,220.6	< 0.001	Low < Medium < High
	Medium	401.9	< 0.001	Low < Medium < High
	High	439.0	< 0.001	Low < Medium < High
Increase in tissue dry weight (%)	Low	574.2	< 0.001	Low < Medium < High
	Medium	298.4	< 0.001	Low < Medium < High
	High	200.0	< 0.001	Low < Medium < High

*Values were arranged in ascending order. Bonferroni adjustment was made with significant level at $p<0.017$ (or 0.05/3).

Table 2. Multiple comparisons between flow rates on the percentage increase in shell length, shell weight and tissue dry weight at different phytoplankton concentrations

Growth parameter	Phytoplankton concentration	*F*	*p*	Multiple comparisons between flow rates*
Increase in shell length (%)	Low	468.3	< 0.001	Low < Medium = High
	Medium	1,231.7	< 0.001	Low < High = Medium
	High	172.4	< 0.001	Low < High < Medium
Increase in shell weight (%)	Low	141.7	< 0.001	Low < High = Medium
	Medium	416.8	< 0.001	Low < Medium = High
	High	66.2	< 0.001	Low < High < Medium
Increase in tissue dry weight (%)	Low	73.2	< 0.001	Low < High = Medium
	Medium	243.6	< 0.001	Low < Medium = High
	High	37.6	< 0.001	Low < High = Medium

*Values were arranged in ascending order. Bonferroni adjustment was made with significant level at $p<0.017$ (or 0.05/3).

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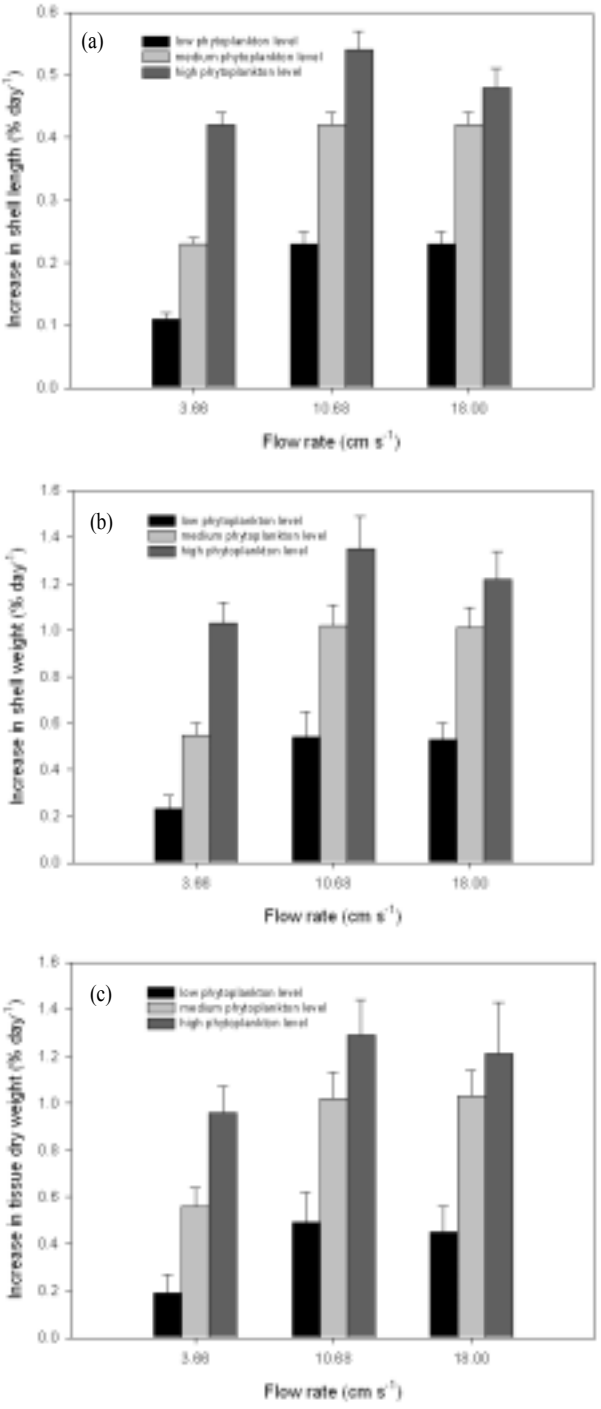

Fig. 3. Increase in (a) shell length, (b) shell weight and (c) tissue dry weight (% day^{-1}) of *Gafrarium tumidum* under different combinations of flow rate and phytoplankton concentration.

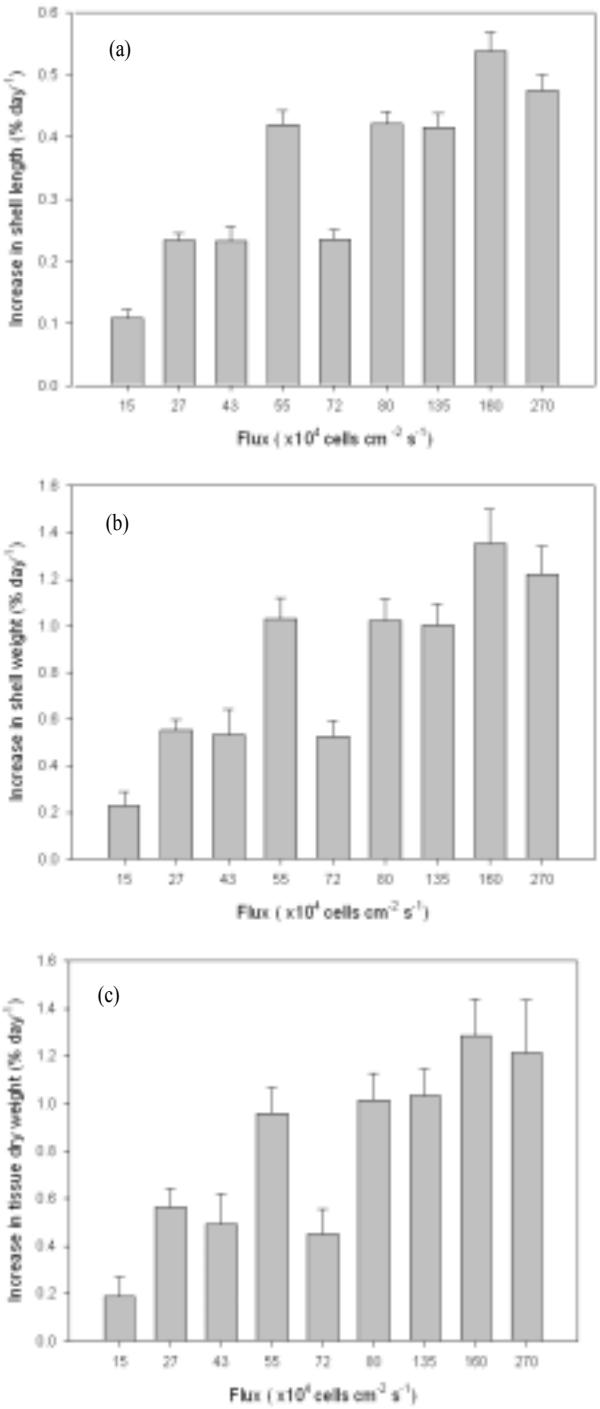

Fig. 4. Relationships between seston flux (× 10^4 cells cm^{-2} s^{-1}) and growth (% day^{-1}) in (a) shell length, (b) shell weight and (c) tissue dry weight in *Gafrarium tumidum*.

was insignificant (p = 0.116) (Fig. 5). The CI at low phytoplankton levels was higher than that at medium and high phytoplankton levels (p<0.001), and the CI at the medium level was also higher than that at the high level (p<0.001).

DISCUSSION

The present study has demonstrated a positive correlation between phytoplankton concentration and growth in *G. tumidum* at

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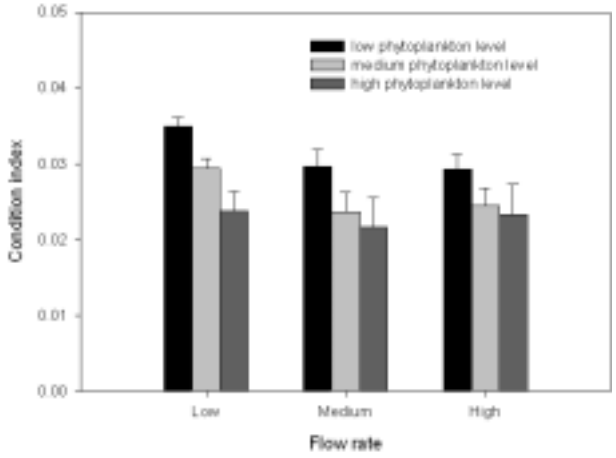

Fig. 5. Condition index of *Gafrarium tumidum* under different combinations of flow rate and phytoplankton concentration.

all flow rates. The phytoplankton concentration effect on growth, however, was not linear, with a greater relative increase in growth when food concentration increased from low to medium levels as compared with that from the medium to high levels. For example, at a flow rate of 3.66 cm s^{-1}, the increase in shell length, shell weight and tissue dry weight was 195%, 139% and 195%, respectively when phytoplankton concentration increased from low to medium levels (an increase of 88%); there was a corresponding increase in shell length, shell weight and tissue dry weight. When phytoplankton concentration increased from medium to high levels (an increase of 100%), the increase in measurements was only 71%, 87% and 71%, respectively (Fig. 3 a～c). Such differences in relative growth at different phytoplankton concentrations were even more pronounced at higher flow rates. This indicates that growth was gradually approaching maximum as phytoplankton concentration increased and was evident, as shown by the relatively similar growth between flow rates of 10.68 and 18 cm s^{-1} at the highest phytoplankton concentration. Positive correlations were established between food concentration and growth in mussels *Mytilus edulis* (Winter 1978) and scallops *Argopecten irradians* (Cahalan et al. 1989) up to certain food concentrations. However, further increases in food concentration showed a reduction in growth. The slowing of a growth increase at high food concentrations is probably caused by the ingestion being limited by the capacity of gills to remove particles from the water (Winter 1978; Cahalan et al. 1989). Unlike other studies in which the food range utilized was larger than those that might normally be encountered in the field (Cahalan et al. 1989), the food range used in this research was within the ambient levels experienced by *G. tumidum*. This may help explain why no inhibition of growth was observed even at the highest phytoplankton concentration.

In contrast to phytoplankton concentration, the effect of flow rate on growth was either positive, until reaching a plateau at the medium flow, or unimodal with a reduction in growth at the highest flow. Our field study of the effect of flow on growth of *G. tumidum* (Cheung and Shin 2007) demonstrated a positive correlation between growth and an average flow rate of 3.12 to 12.48 cm s^{-1}, which agreed with the results of the present laboratory study due to the fact that the highest flow in the field study was similar to the medium flow in the laboratory observations (12.48 cm s^{-1} versus 10.68 cm s^{-1}). Unimodal growth was observed both in clams *Mercenaria mercenaria* and oysters *Crassostrea virginica* with the maximum growth being obtained at 2 to 4 cm s^{-1} for the former and 1 cm s^{-1} for the latter (Grizzle et al. 1992). Inhibition of growth for blue mussels *Mytilus edulis* occurred at > 25 cm s^{-1} (Wildish and Miyares 1990). This is a similar flow rate to where growth inhibition occurred in *G. tumidum* in the present study. The mechanism of growth inhibition at high flow rates involves the disruption of the bivalve's pump by a pressure differential between the inhalant and exhalant openings such that particle capture is inhibited (Kirby-Smith 1972, Jørgensen et al. 1986, Eckman et al. 1989) either by a decrease in pumping rates, shunting of water around the gill, constriction of the mantle margins or any combination of these responses (Wildish et al. 1987).

Flux was a good predictor of growth in *G. tumidum* except at the highest flux rates (270×10^4 cells cm^{-2} s^{-1}), at which growth was inhibited. The growth at 55×10^4 cells cm^{-2} s^{-1} was much more enhanced than was predicted from the relationship between flux and growth. The study shows that the growth at 55×10^4 cells cm^{-2} s^{-1} was greater than that at 43 and 72×10^4 cells cm^{-2} s^{-1}. This indicates that food concentration was more important in determining growth than flow rate as phytoplankton concentration at 55×10^4 cells cm^{-2} s^{-1} was higher than that at 43 and 72×10^4 cells cm^{-2} s^{-1}, although the flow rate for the former was the smallest (3.66 cm s^{-1} versus 10.68 cm s^{-1} at 43×10^4cells cm^{-2} s^{-1} and 18 cm s^{-1} at 72×10^4 cells cm^{-2} s^{-1}). The inhibition of growth at 270×10^4 cells cm^{-2} s^{-1} was also caused by the high flow rate which was 18 cm s^{-1} as compared with the medium flow (10.68 cm s^{-1}) at 160×10^4 cells cm^{-2} s^{-1}. Cahalan et al. (1989) showed that flux could only weakly predict growth rates of scallops *Argopecten irradians* with the effects of algal concentration being more pronounced than the effects of flow on growth. They, therefore, suggested to decouple the components of flux, flow rate and food concentration, in order to predict growth rates. Despite these current findings, and those of Cahalan et al. (1989), where the experimental sediment surface area was small, the effect of flow on growth could be more significant in the field. Under low flow conditions, seston could be depleted by individuals on the upstream. Our field study (Cheung

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and Shin 2007) showed that seston depletion effect could have significant effect on growth when flow rate was < 3.43 cm s^{-1}. Growth could also be enhanced at high flows due to more mixing and higher total volumes of water (and food) moving over the bivalves (Wildish and Kristmanson 1985, Eckman 1987). Under high flow regime, in addition to phytoplankton, the presence of microphytobenthos on the sediment surface may be an important alternative food source to the bivalves (Pinckney and Zingmark 1991). Such benthic microalgae can be resuspended at high flows and consumed by the bivalves during filter feeding.

CI indicates relative growth of shell and tissue, with a higher value being obtained when tissue growth was faster than shell growth and vice versa. Both flow rate and phytoplankton concentration had negative effects on CI, with the lowest flow and phytoplankton levels resulting in the highest values of condition. Similar results were obtained in a field study which reduced seston flux at slow flows, thereby channelling more energy to tissue growth in *G. tumidum* (Cheung and Shin 2007). The highest shell growth but lowest tissue growth in *M. mercenaria* occurred at the site with medium flow, and lower shell growth but higher tissue growth at sites with fast or slow flow (Grizzle and Morin 1989). Such an uncoupled growth of shell and tissue may be a result of a tradeoff in energy allocation between shell and tissue growth when food is limited. As more energy is channelled to tissue growth under low food environments, energy can be stored to sustain life or reserved for gametogenesis during the reproductive period.

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