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Growth Responses of the Filter-Feeding Clam *Gafrarium tumidum* to Water Flow: A Field Manipulation Experiment

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ABSTRACT: The effect of water flow on the growth of *Gafrarium tumidum* was studied in the field using open cages constructed with stainless steel net and perspex in which holes were drilled. Cages with different flows (25, 50 and 75% of the control) were made by varying the area of perspex being drilled. Reduction in flow rate was directly proportional to the undrilled area, and the mean flow rate of the different treatment groups varied from 3.12 cm/s for the 25% exposure to 12.48 cm/s for the control cages. At the end of the 3-month experiment, no significant differences in sediment characteristics were found among the treatments. Growth in shell length, shell weight and tissue dry weight was, however, positively correlated with flow rate. Percentage increases ranged from 3.0~8.3% for shell length, 9.9~23.1% for shell weight and 17.2~53.3% for tissue dry weight. Condition index of the clam was not significantly different among the treatments. Seston depletion effect could reduce growth in *G. tumidum* only when water flow was reduced to 25% of the control. *G. tumidum* also exhibited different responses in shell and tissue growth at low flow rates, in which shell growth continued to decrease as flow rate decreased whereas tissue growth was relatively independent of low flows at 25 and 50% of the control. It was suggested that when seston flux was reduced at slow flows, it would be a better strategy for *G. tumidum* to channel energy for gonad development instead of shell growth during the reproductive stage.

Key words: Clams, *Gafrarium*, Growth, Water flow

INTRODUCTION

The significance of water flow on growth in bivalves has been studied in laboratory flume and field experiments (for a review, see Wildish and Kristmanson 1997). With flow rate being carefully controlled in flume experiments, growth is commonly found to be unimodal with growth increasing with water flow until a threshold is reached. When flow increases further, growth becomes reduced (Kirby-Smith 1972, Wildish and Kristmanson 1985, 1988). Reduction in growth at low flows in siphonate bivalves can be caused by reduction in seston flux, especially at high population densities where seston is being depleted by individuals on the upstream which reduces growth of those in the downstream (Peterson and Black 1991). Disturbance of sediments is also lessened at low flow or under weak wind-wave effects (Emerson 1990, Fréchette and Grant 1991, Bock and Miller 1994), which reduces the resuspension of organic matter in the sediments including benthic algae, microfauna and detritus (Wildish 1977). High flows, however, can also be growth-inhibiting (Wildish et al. 1987, Wildish and Kristmanson 1988) and this is probably caused by substantial re-pumping of the exhalant water into the inhalant flow when ambient flow speed exceeds the pumping speed (Grizzle et al. 1992). Laboratory flume experiments are not without criticisms, as they are not easily able to mimic unsteady flows such as the tidal conditions or seston quantity and *quality the animals are experiencing in the natural environment* (Wildish and Kristmanson 1984, Eckman et al. 1989, Judge et al. 1992).

Compared with laboratory flume experiments, field studies on the relationship between flow and bivalve growth are scarce with most of the work being performed on the hard clam *Mercenaria mercenaria*, in which results obtained were not conclusive. Grizzle and Morin (1989) studied the growth of *M. mercenaria* at three sites with different current velocities and found that growth was lower at sites with low flow. Site-related differences in growth, however, could be attributed to other environmental variables which may also vary with sites, including seston quality, oxygen levels, inhibitory wind-wave effects, temperature and sediment characteristics (Judge et al. 1992, Wildish and Kristmanson 1997). The above shortcomings of field experiments could be remedied by manipulating current regimes in a single field location. Using channels with diverging, parallel, or converging walls, Judge et al. (1992) found that growth of *M. mercenaria* was not influenced by flow. The conclusion, however, was questioned by Wildish and Kristmanson (1997) as nothing is known of the temporal distribution of flow throughout the experiment.

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Here we describe the results of a study investigating the growth of a siphonate, filter-feeding clam *Gafrarium tumidum* under different flow rates in a field experiment. Flow rate was manipulated by using cages with variable degrees of exposure. *G. tumidum* is an infaunal bivalve commonly found in subtropical waters and is a dominant species on sheltered sandy shores in Hong Kong (Morton and Morton 1983). We are not aware of previous efforts to study how current flow affects growth in this subtropical bivalve.

MATERIALS AND METHODS

Experimental stainless steel cages (W: 28 cm; L: 36 cm; H: 15 cm) used in the experiment were made of aluminum bars (2.45 cm width) with stainless steel nets (dimensions: 6 mm × 6 mm) across the bars. To control the rate of water flow through the cages (which provided an exposure of 25%, 50%, 75%, 100% for water flow), four lateral sides of the cage above the sediment were covered by 2 mm thick transparent perspex plates (except for the control, i.e., 100% water flow). The number of holes (diameter: 6 mm) drilled was dependent on the flow rate to be achieved (Table 1) and the position of the holes was determined by a random number table. The top of the cage was kept open.

A field trial was conducted to test the design of the sediment cages in creating different flows, but otherwise maintaining similar concentration of seston and organic content in the seawater passing through the cages. The flow outside and inside the four types of experimental cages, which were placed in the sediment at 0.5 m below chart datum at a protected sandy shore lying deep in Tai Tam Harbour (Fig. 1), was measured using an electromagnetic current meter (Global Water, Model: FP101). For each cage, six 10 second readings were recorded haphazardly outside and inside the cage at 2 cm below the top during ebb tides and averaged to estimate the flow rate. Three replicates of 500 mL seawater samples outside and inside the cages were also collected immediately after flow measurements. The above measurements were conducted twice for each type of the experimental cages on separate occasions. In the laboratory, concentration of the total suspended particulate matter (TPM) of the seston was determined by filtering the seawater onto an ashed and pre-weighed 25 mm Whatman GF/C glass fibre filter rinsed with ~5 mL isotonic ammonium formate, dried in an oven (110℃ for 24 hours) and weighed. Particulate inorganic matter (PIM) was determined by ashing the seston with the filter paper in a muffle furnace at 450℃ for 6 hours. The particulate organic matter concentration (POM) was estimated by subtracting PIM from TPM, and organic content (f) was calculated from POM/TPM × 100% (Wong and Cheung 2003). The differences on flow rates, and mean TPM, POM, PIM and f between outside and inside the cages were compared using paired t-test (Zar 1996). The percentage f values were arcsine transformed prior to statistical comparison.

The growth response experiment was conducted using natural sediment and the filter-feeding clam *G. tumidum* collected from a sheltered sandy shore at Ting Kok, Tolo Harbour, Hong Kong. In the laboratory, the sediment was defaunated by drying in an oven at 60℃ for 48 hours prior to placement in the cages, to a depth of 9 cm. To prevent sediment leaking out from the cage, a fine mesh (1 mm) was placed inside the cage up to the height of the sediment before placing the defaunated sediment. Particle size was determined by the wet sieving method and expressed as median

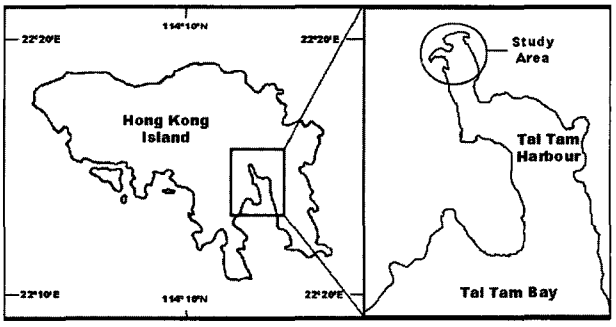

Fig. 1. Map showing the location of the experimental site.

Table 1. Relationship between percentage of exposure to water flow and number of holes (diameter: 6 mm) drilled for each cage (− = cage not covered by perspex)

Percentage of exposure	No. of holes on each side of the cage		Total number of holes on four sides of the cage	Total area of exposure (cm^2)
	Length	Width		
Control, 100%	−	−	−	237.5
75%	180	135	630	178.1
50%	120	90	420	118.8
25%	60	45	210	59.4

diameter (Md, ø unit), quartile deviation (QD, ø unit) and quartile skewness (Sk_q, ø unit) (Buchanan 1984). Total organic carbon (TOC) was determined using the modifications of the Schollenberger chromic acid oxidation technique (Buchanan 1984). Total Kjeldahl nitrogen (TKN) was analyzed as NH_4-N after a modified Kjeldahl combustion method (Allen 1989). Total phosphorus (TP) was analyzed as PO_4-P by calorimetric method after acid extraction (Allen 1989).

Six juveniles of *G. tumidum*, with shell length circa 24 mm, were placed in each experimental cage and allowed to bury in the sediment (Fig. 2). Three cages were used for each flow rate as replicates. The number of individuals chosen was equivalent to the density that found in Ting Kok, the collection site of the clam (Shin and Cheung 2005). Before the experiment started, each individual was numbered with a plastic tag. Shell length was measured by vernier calipers to the nearest 0.01 mm. To determine the relationships between shell length, shell weight and tissue dry weight, the tissue of 30 clams with shell length from 22 to 43 mm (each measured to 0.01 mm) was dried separately in an oven at 85℃ for two days and their shell weight and tissue dry weight determined by an electronic balance to the nearest 0.1 mg. Regression analysis showed the following linear relationships: shell weight (mg) = 490.2 × shell length (mm) − 8197.8 ($n = 30$, $r^2 = 0.98$, $p<0.001$) and tissue dry weight (mg) = 31.4 × shell length (mm) − 708.0 ($n = 30$, $r^2 = 0.92$, $p < 0.001$). These relationships were used to determine the initial shell weight and tissue dry weight of the clams from their shell length used in the experimental cages. Individuals in different replicates and treatments were not significantly different at the beginning of the experiment in terms of shell length (treatment: $F = 0.34$, $p = 0.98$; replicate: $F = 0.71$, $p = 0.68$), shell weight (treatment: $F = 0.34$, $p = 0.98$; replicate: $F = 0.71$, $p = 0.68$) and tissue dry weight (treatment: $F = 0.34$, $p = 0.80$; replicate: $F = 0.71$, $p = 0.68$) as tested by nested ANOVA. All sediment cages and the clams were transplanted to Tai Tam Harbour as in the field trial, 24 km away from the clam collection site. The cages were placed haphazardly into the sediment at 0.5 m below chart datum at the experimental site.

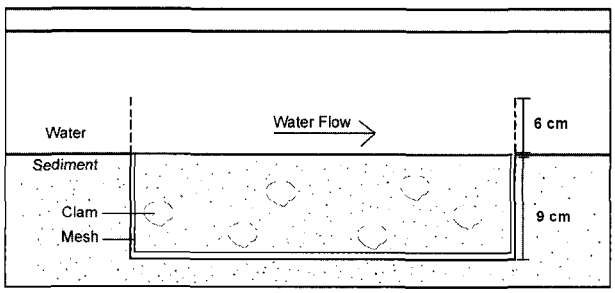

Fig. 2. The design of the sediment cages used in this experiment.

The field transplant experiment lasted for 3 months in the summer (28th July~25th October 2004), so as to register the growth of *G. tumidum* in the sediment cages. During the transplant period, temperature, salinity and dissolved oxygen in the near-bottom (2 to 16 cm) water at the field site were measured about once a week. Any fouling organisms on the cages were removed to ensure no clogging of the perforations in the cages. Water samples collected were divided into two aliquots; one for determination of chlorophyll *a*, and another for determination of seston concentration and quality. Magnesium carbonate (1 mL, 1%) was added to each replicate and filtered through Whatman GF/C glass fiber filter paper. The remains retained on the filter paper were extracted with 90% acetone under refrigeration for 20 hours and centrifuged. The extinction of the resultant solution was measured with a spectrophotometer at wavelengths of 665, 645 and 630 nm, and the chlorophyll *a* concentration was calculated with the Richards formula (Strickland and Parsons 1972). Concentrations of TPM, POM and PIM of the seston were determined as in the field trial. Water flow velocities within the experimental cages were also measured *in-situ* as in the field trial. For each cage, six 10 second readings were recorded haphazardly 2 cm below the top of the cage (4 cm above sediment) during ebb tides and averaged to estimate the flow rate through the cage. Current speeds at the field site were also measured, at four heights, including 2, 4, 8 and 16 cm above the bottom (Grizzle and Morin 1989) during ebb tides. At each height, six 10 second readings were measured and averaged to estimate the speed at that height. To determine the relationship between water flow rate and tides, water flow rate at the study site was measured at different times in a tidal cycle on 26th (Day 1) and 28th (Day 2) July 2005. Each hour six readings of water flow rate were taken as replicates next to the cages at the study site and 4 cm above the sediment by a current meter.

At the end of 3 months, all sediment cages were retrieved from the field site and brought back to the laboratory. The clams were sieved, collected, checked for markings, and measured for the final shell length. Other animals present in the sediment were also collected and identified. The final shell weight and tissue dry weight were determined according to the relationships as established at the beginning of the experiment. Sediment particle size, TOC, TKN and TP were also analyzed following the methods described above.

For the growth response experiment, treatment and replicate effects on growth in shell length, and shell and tissue dry weight were analyzed using a balanced design nested ANOVA with individual cages assigned as a random factor nested within the three treatments. Normality of the data was checked by using the Kolmogorov-Smirnov test and homogeneity of variances by Bartlett's

test using the statistical software Sigmastat 3.0. Significant treatment effects were further examined by the Tukey multiple comparison procedure. Percentage data were arcsine transformed to achieve normality prior to analysis (Zar 1996).

RESULTS

Results of the field trial showed that the flow data measured outside and inside the experimental cages were significantly different ($t = 4.03$, $p<0.05$). However, the mean TPM, POM, PIM and f of the seston in the seawater collected outside and inside the experimental cages were not statistically different ($p>0.05$) (Table 2).

For the growth response experiment, all hydrographic parameters at the experimental site changed significantly with time ($p<0.001$) as tested by Kruskal-Wallis one-way ANOVA (Fig. 3 a~e). Water temperatures ranged from 28.15 to 34.28℃ and pH from 8.06 to 8.50. Heavy rainfall decreased the salinity in August to half of its values in early September. Precipitation was reduced in autumn bringing salinity to highest values at the end of the experiment. As the site was relatively free from human disturbance, dissolved oxygen levels were high and centered at 7.2 mg/L. Particulate inorganic matter formed the bulk of the total particulate matter (> 70%) with organic content (f) varying from 10.4% on 7th Oct 2004 to 30.0% on 28th Sep 2004. There was a marked temporal variation in chlorophyll *a* concentrations with two troughs identified, one in early September and another in late October. Flow rate during ebb tides changed significantly with time ($F = 35.78$, $p<0.001$) and water depth ($F = 571.84$, $p<0.001$) but not their interaction ($F = 0.90$, $p = 0.62$) as tested by two-way ANOVA (Fig. 3e). Flow rate increased with distance from the sediment surface except for those at 8 cm and 16 cm, which were statistically insignificant ($t = 1.16$, $p = 0.25$).

Flow rate during ebb tides varied significantly with treatment cages ($F = 2720.8$, $p<0.001$) and time ($F = 100.48$, $p<0.001$) (Fig. 4) as tested by nested ANOVA. Reduction in flow rate was directly proportional to the reduction in the surface area of the cage above the sediment (Fig. 5) with a correlation coefficient of 0.999 ($n = 44$, $p<0.001$) as tested by the Pearson product moment correlation. The flow rate in control cages was similar to that outside the cages ($p>0.05$) with significantly higher flow rate outside the cages only in 2 out of the 11 samplings on 12th Aug 2004 ($F = 6.80$, $p<0.05$) and 7th Oct 2004 ($F = 5.43$, $p<0.01$).

Table 2. Comparisons of water flow, total particulate matter (TPM), particulate organic matter (POM), particulate inorganic matter (PIM) and organic content (f) outside and inside experimental cages

Variable	Mean value (1 SD)	Paired t-test		
Flow (m/s)	0.75 (0.52)	$t = 4.03$,	$df = 7$,	$p<0.05$
TPM (mg/L)	−0.15 (1.36)	$t = -0.31$,	$df = 7$,	$p = 0.76$
POM (mg/L)	−0.25 (0.85)	$t = -0.83$,	$df = 7$,	$p = 0.44$
PIM (mg/L)	0.10 (0.85)	$t = 0.38$,	$df = 7$,	$p = 0.75$
f (%)	−0.03 (0.10)	$t = -0.72$,	$df = 7$,	$p = 0.50$

At the end of the growth response experiment, characteristics of the sediments in cages including TOC, TKN and TP were not significantly different from the initial values obtained from the sediments sampled randomly on the collection site at Ting Kok at the beginning of the experiment, but final values in cages were significantly different from the initial values in terms of Md and QD (Table 3). Differences in TOC, TKN and TP among cages at the end of the experiment were not significant as analyzed by one-way ANOVA (TOC: $F = 0.73$, $df = 3,8$, $p = 0.56$; TKN: $F = 2.02$, $df = 3,8$, $p = 0.19$; TP: $F = 2.04$, $df = 3,8$, $p = 0.19$). Particle size distribution of the sediments among cages at the end of the experiment in terms of Md, QD and Sk_q was also not significantly different (Md: $F = 2.34$, $df = 3,8$, $p = 0.15$; QD: $F = 0.64$, $df = 3,8$, $p = 0.61$; Sk_q: $F = 0.55$, $df = 3,8$, $p = 0.67$).

After 3 months, growth of shell length, shell weight and tissue dry weight in *G. tumidum* varied significantly with flow rate, with highest growth rate being obtained for the control, followed by 75% flow rate. Increase in shell weight and tissue dry weight was similar between 50% and 25% flow rate but the increase in shell length at 50% flow rate was significantly higher than at 25% (Table 4). Percentage increase in shell length varied from 3.0% for the lowest flow rate to 8.3% for the control. Percentage increase in shell weight varied from 9.9 to 23.1% and that in tissue dry weight from 17.2 to 53.3% when the flow rate increased from 50 to 100% (control). Except for juveniles of few polychaete species (Nereidae and Syllidae) which were found in the sediment of some of the experimental cages, no large filter-feeding bivalves were found settled over the study period.

Water flow rate was positively correlated with tidal height on both dates (26th July: $r = 0.92$, $p<0.001$; 28th July: $r = 0.98$, $p<0.001$) with the rate gradually being increased during flood tide and decreased during ebb tide. The mean water flow rate in a tidal cycle on Day 1 and Day 2 was 12.38 and 9.83 cm/s, respectively (Fig. 6). Using pooled data from the two days, water flow rate could be predicted from tidal height using the following linear equation:

$$\text{Water flow rate (cm/s)} = 2.504 + 6.317 \times \text{Tidal height (m)} \quad (n = 27,\ r^2 = 0.79,\ p<0.001)$$

Mean tidal height in the study period (28th Jul ~ 25th Oct 2004)

was estimated at 1.58 m according to the record obtained from the Hong Kong Observatory (http://www.hko.gov.hk/tide/eWAGtide.htm) at Waglan Island 10.7 km from our study site. Using the above equation, mean water flow rate at the study site was estimated at 12.48 cm/s and considered as the mean flow rate of the control group with 100% exposure. Mean water flow rates of different treatment groups were calculated according to their percentage exposure (i.e., 75%, 50%, 25%). Relationships between daily incre-

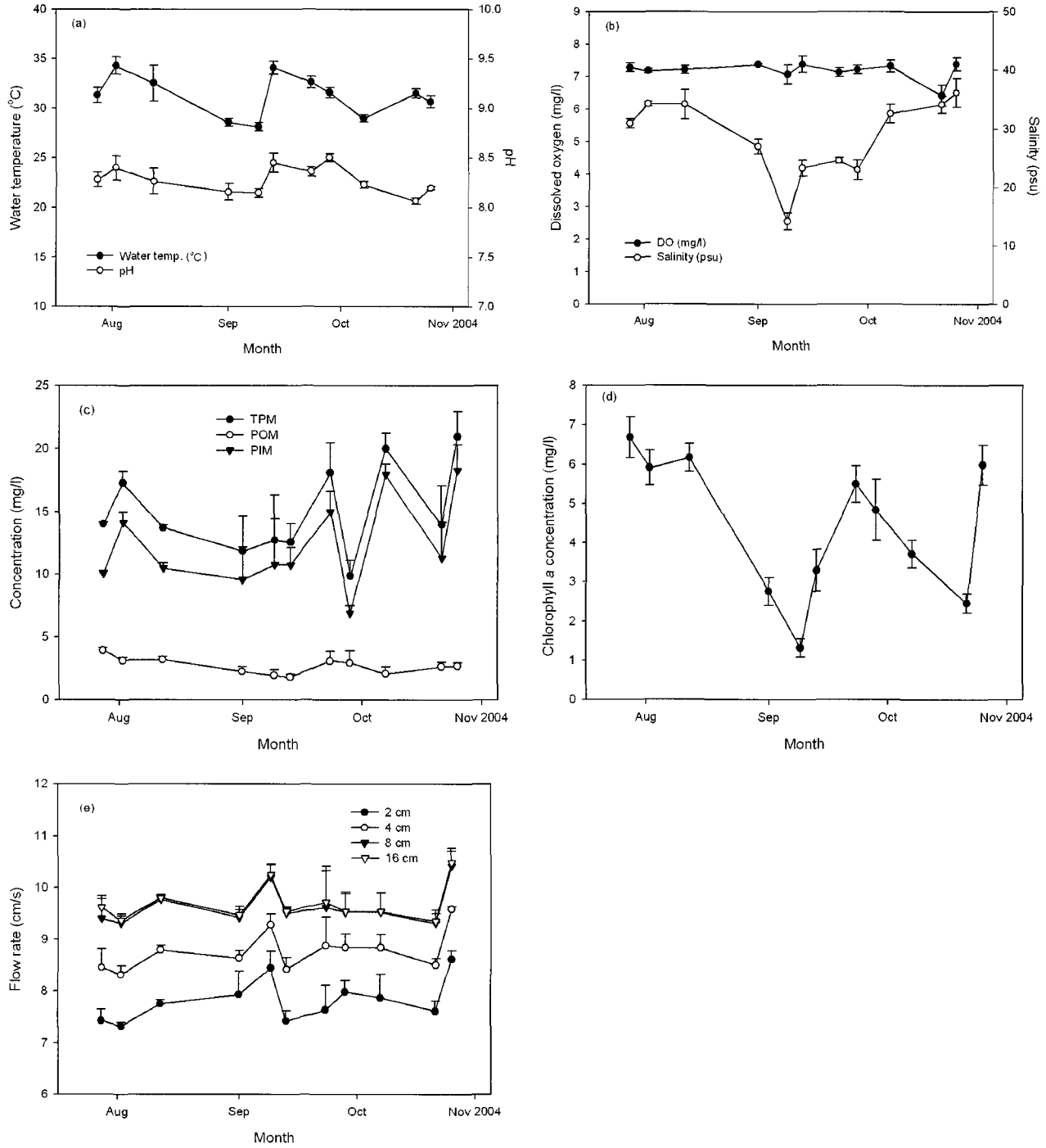

Fig. 3. Hydrographic parameters (1 SD) of the study site during the experimental period. (a) water temperature and pH, (b) dissolved oxygen level and salinity, (c) total particulate matter (TPM), particulate organic matter (POM) and particulate inorganic matter (PIM), (d) chlorophyll a concentration, and (e) water flow rate.

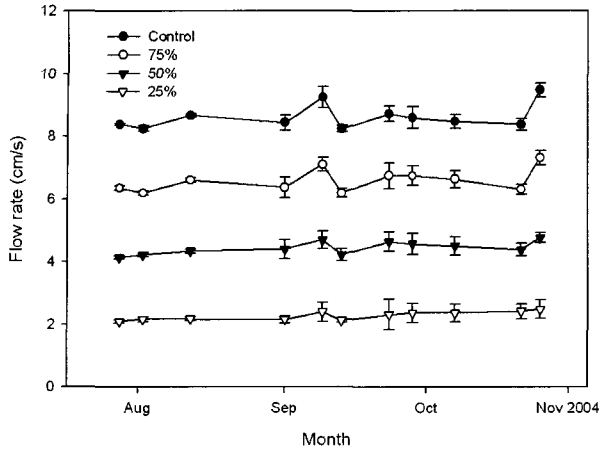

Fig. 4. Temporal variations of water flow rate in cages (± SD) with different percentages of exposure.

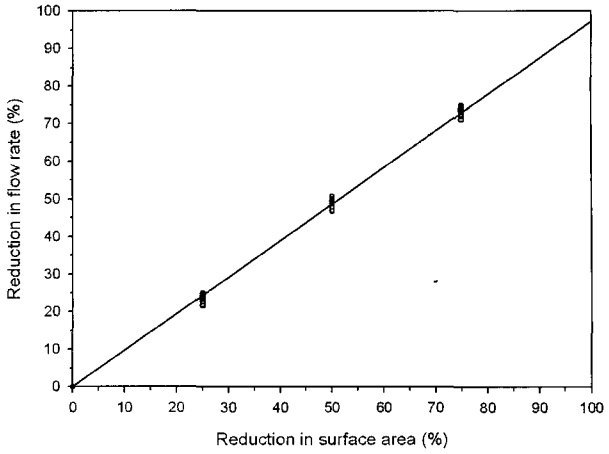

Fig. 5. Relationship between reduction in water flow rate and reduction in the area exposure of the cages.

Table 3. Comparisons of initial and final values of sediment characteristics, including total organic carbon (TOC), total Kjeldahl nitrogen (TKN), total phosphorus (TP), median diameter (Md), quartile deviation (QD), and quartile skewness (Sk_q) by Student *t*-test for cages with different percentages of flow rate as compared with the control (dw = dry weight)

Variable	Treatment	Mean value (1 SD)	Student *t*-test		
TOC (mg/g dw)	Initial	0.193 (0.020)			
	Final: Control	0.200 (0.005)	$t = -0.63$,	$df = 4$,	$p = 0.57$
	75%	0.204 (0.011)	$t = -0.86$,	$df = 4$,	$p = 0.44$
	50%	0.212 (0.024)	$t = -1.09$,	$df = 4$,	$p = 0.34$
	25%	0.215 (0.010)	$t = -1.75$,	$df = 4$,	$p = 0.15$
TKN (mg/g dw)	Initial	0.063 (0.008)			
	Final: Control	0.065 (0.005)	$t = -0.20$,	$df = 4$,	$p = 0.86$
	75%	0.071 (0.005)	$t = -1.28$,	$df = 4$,	$p = 0.27$
	50%	0.069 (0.003)	$t = -1.01$,	$df = 4$,	p = 0.37
	25%	0.063 (0.004)	$t = 0.09$,	$df = 4$,	$p = 0.93$
TP (mg/g dw)	Initial	0.021 (0.002)			
	Final: Control	0.018 (0.001)	$t = 2.03$,	$df = 4$,	$p = 0.11$
	75%	0.021 (0.001)	$t = 0.15$,	$df = 4$,	$p = 0.89$
	50%	0.021 (0.002)	$t = 0.22$,	$df = 4$,	$p = 0.84$
	25%	0.019 (0.002)	$t = 1.16$,	$df = 4$,	$p = 0.31$
Md (ø unit)	Initial	−0.097 (0.042)	$t = 18.31$,	$df = 4$,	$p<0.001$
	Final: Control	−0.651 (0.031)	$t = 8.07$,	$df = 4$,	$p<0.001$
	75%	−0.534 (0.084)	$t = 19.75$,	$df = 4$,	$p<0.001$
	50%	−0.586 (0.006)	$t = 5.07$,	$df = 4$,	$p<0.01$
	25%	−0.491 (0.128)	$t = 3.86$,	$df = 4$,	$p<0.05$
QD (ø unit)	Initial	1.169 (0.047)			
	Final: Control	1.011 (0.053)	$t = 4.67$,	$df = 4$,	$p<0.01$
	75%	1.036 (0.016)	$t = 2.71$,	$df = 4$,	$p = 0.05$
	50%	1.064 (0.048)	$t = 2.70$,	$df = 4$,	$p = 0.05$
	25%	1.047 (0.063)			
Sk_q (ø unit)	Initial	0.148 (0.004)			
	Final: Control	0.139 (0.008)	$t = 1.83$,	$df = 4$,	$p = 0.14$
	75%	0.141 (0.006)	$t = 1.72$,	$df = 4$,	$p = 0.16$
	50%	0.147 (0.006)	$t = 0.31$,	$df = 4$,	$p = 0.77$
	25%	0.141 (0.011)	$t = 1.02$,	$df = 4$,	$p = 0.37$

Table 4. Comparisons of percentage increase (1 SD) in shell length, shell weight and tissue dry weight of *Gafarium tumidum* in cages with different percentages of flow rate as compared with the control

		Control	75%	50%	25%	
Increase in shell length (%)	replicate 1	8.56 (1.67)	6.29 (1.20)	4.38 (1.50)	2.88 (1.02)	
	replicate 2	8.29 (1.18)	6.84 (0.88)	4.02 (1.21)	3.02 (1.25)	Treatment effect (df = 3, F = 60.33, p<0.001)
	replicate 3	8.03 (1.59)	6.84 (0.53)	3.95 (1.33)	2.99 (1.43)	Replicate effect (df = 8, F = 0.17, p = 0.994) NS
Mean		8.30 (1.42)	6.66 (0.90)	4.12 (1.29)	2.96 (1.17)	Multiple comparisons: Control > 75% > 50% > 25%
Increase in shell weight (%)	replicate 1	26.19 (4.99)	18.23 (5.97)	13.58 (5.37)	12.22 (2.95)	
	replicate 2	22.36 (5.66)	18.19 (4.57)	10.05 (3.59)	9.00 (5.40)	Treatment effect (df = 3, F = 29.96, p<0.001)
	replicate 3	20.63 (3.99)	16.45 (1.98)	12.71 (4.02)	8.52 (4.07)	Replicate effect (df = 8, F = 1.24, p = 0.295) NS
Mean		23.06 (5.21)	17.62 (4.30)	12.12 (4.41)	9.91 (4.34)	Multiple comparisons: Control > 75% > 50% = 25%
Increase in tissue dry weight (%)	replicate 1	50.32 (12.17)	36.74 (13.40)	12.16 (3.17)	16.82 (6.67)	
	replicate 2	53.78 (16.52)	36.28 (12.36)	21.24 (7.96)	20.85 (6.26)	Treatment effect (df = 3, F = 38.15, p<0.001)
	replicate 3	55.91 (12.41)	31.64 (20.16)	18.18 (8.18)	18.58 (11.66)	Replicate effect (df = 8, F = 0.57, p = 0.796) NS
Mean		53.33 (13.22)	34.88 (14.93)	17.20 (7.51)	18.75 (8.21)	Multiple comparisons: Control > 75% > 50% = 25%

NS - Statistically insignificant at 95% probability level.

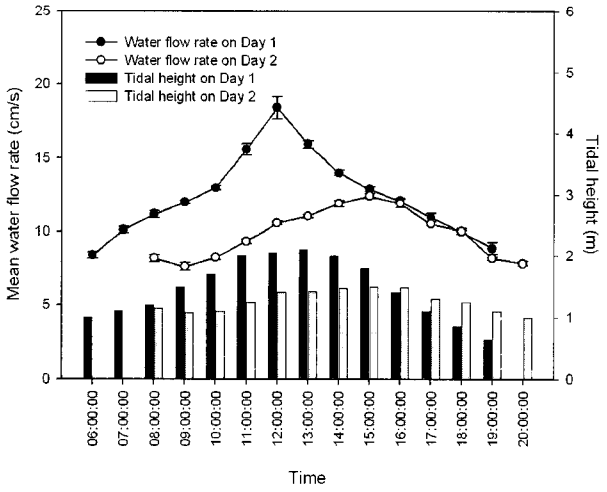

Fig. 6. Temporal variations of water flow rate (± SD) and tidal height in a complete tidal cycle on two days.

ments in shell length, shell weight and tissue dry weight and water flow rate (Fig. 7 a~c) were best described by the following quadratic equations:

$$SL = 0.004 + 0.0013\ FR + 2.7\times10^{-5}\ FR^2$$
(F = 137.49, df = 2,9, p<0.001)

$$SW = 3.9873 + 0.2554\ FR + 0.0303\ FR^2$$
(F = 44.39, df = 2,9, p<0.001)

$$DW = 0.3356 - 0.0456\ FR + 0.0058\ FR^2$$
(F = 31.77, df = 2,9, p<0.001)

where SL = daily increment in shell length (mm/d)
SW = daily increment in shell weight (mg/d)
DW = daily increment in tissue dry weight (mg/d)
FR = mean flow rate (cm/s)

Condition index of *G. tumidum* at the end of the experiment was calculated as the ratio between tissue dry weight (DW) and shell weight (SW), i.e., DW/SW. The mean ratio was 0.030, 0.029, 0.027 and 0.028 for the control, 75%, 50% and 25% flow rate, respectively and was not significantly different among treatments (F = 0.47, p = 0.70) and replicates (F = 0.91, p = 0.51).

DISCUSSION

The field trial study demonstrated the applicability of the design of the experimental cages in producing significant different flows but maintaining similar concentrations (as expressed in TPM) and quality (as expressed in POM and *f*) of seston outside and inside the cages. Our results suggested that the food availability, in terms of concentration and quality, in the water within all the experimental cages was statistically similar. However, owing to the difference in flows, the flux (flow rate × concentration) of seston through the different types of cages would differ significantly and

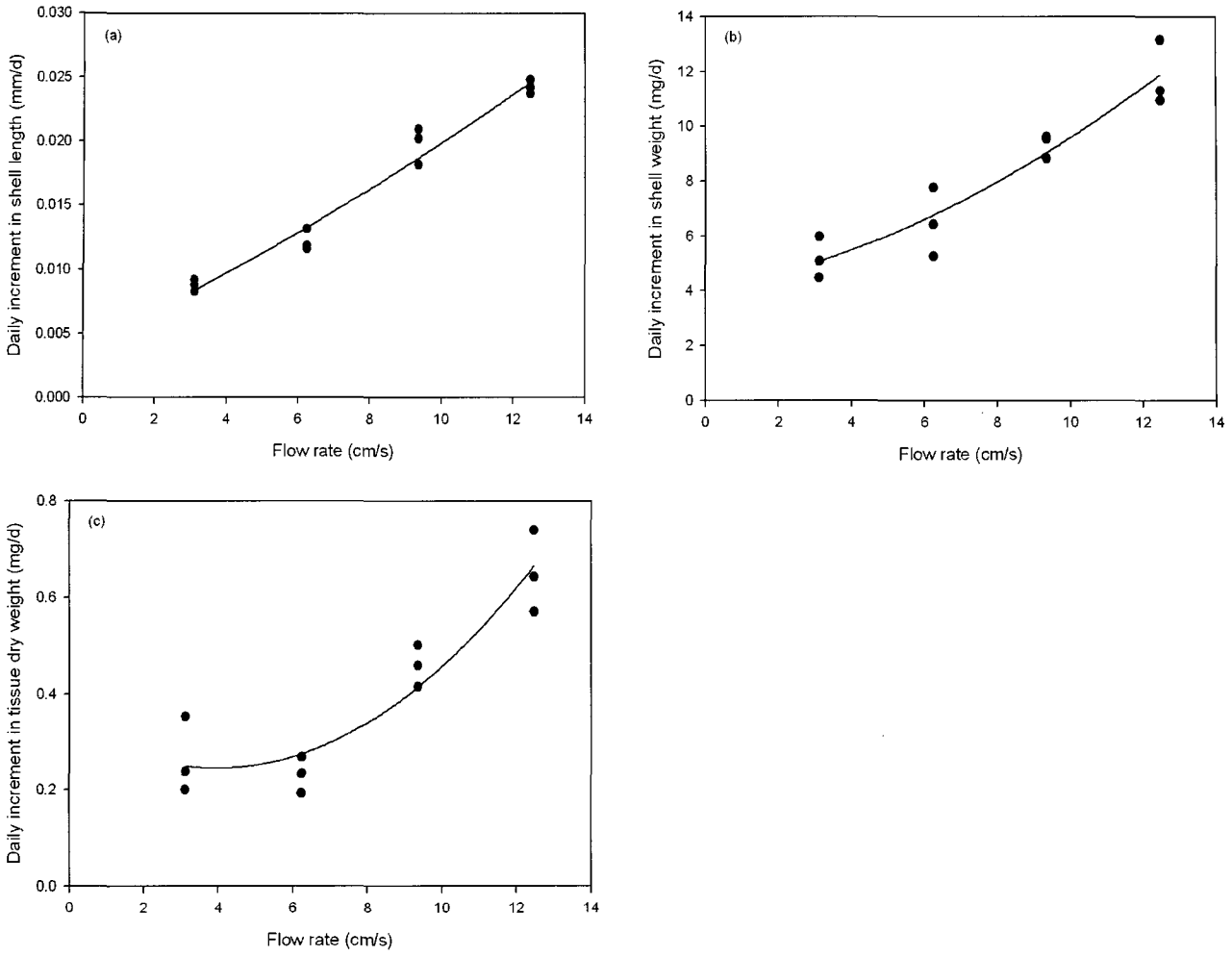

Fig. 7. Relationship between daily increment in (a) shell length, (b) shell weight, and (c) tissue dry weight of *G. tumidum* and water flow rate. Equations describing the relationships are shown in the text.

be a limiting factor affecting the growth of the filter-feeding clam *G. tumidum*.

Growth in *G. tumidum* increased with the estimated average flow rate in the present study from 3.12 to 12.48 cm/s. Studies of a number of infaunal bivalves have demonstrated a positive relationship between growth and flow rate until a threshold beyond which growth is reduced. In a laboratory flume experiment, Emerson (1990) found growth of soft tissue of the soft-shell clam *Mya arenaria* directly proportional to flow rate from 0.1 to 6 cm/s. Grizzle et al. (1992) compared growth of the siphonate *Mercenaria mercenaria* and non-siphonate *Crassostrea virginica* in a multiple-channel flume. In a limited range of free-stream velocities (< 8 cm/s), growth of both bivalves was unimodal with maximum growth of *M. mercenaria* obtained at 2 to 4 cm/s and that of *C. virginica* at 1 cm/s. Enhanced growth at a higher flow rate was also obtained in field experiments. Grizzle and Morin (1989) studied growth of *M. mercenaria* in three sediments at three sites in a lagoon in New Jersey, United States and found that growth was not affected by sediment type but was enhanced at sites with faster water flow. Wildish and Kristmanson (1997), however, commented that differences in growth obtained by Grizzle and Morin (1989) may not be related to flow rate but a result of inter-site differences in environmental variables such as seston quality, dissolved oxygen levels, or inhibitory wind-wave effects.

The relationship between growth and hence productivity and flow rate may be interpreted as a population response to seston depletion as flow reduced. Wildish and Kristmanson (1979, 1984) have modeled the conditions under which seston depletion might occur. Laboratory studies (Wildish and Kristmanson 1985) and field investigations (Wildish and Kristmanson 1984) have demonstrated downstream seston depletion effects which together with reduction in feeding time during low tide could result in a 59% lower growth

for mid-intertidal than subtidal suspension feeding bivalves (Peterson and Black 1991). Growth of *M. mercenaria* in field channels was inversely proportional to distance from inflows (Hadley and Manzi 1984). To determine if seston depletion effect is significant, Wildish and Kristmanson (1997) developed a seston depletion index (SDI) which is calculated as:

$$SDI = \frac{PR\alpha}{\gamma U}$$

where P = density of suspension feeders, number/m^2
R = average filtration rate of each individual in the population, m^3/hr
α = average filtration efficiency (0% to 100%) of each individual in the population
γ = a dimensionless hydrodynamic term approximately equal to 0.003 and dependent on roughness
U = velocity at the top of the benthic boundary layer, m/hr

Significant seston depletion is expected to be observed if the index value is > 0.11. Although no filtration rate (clearance rate) was obtained for *G. tumidum*, filtration rate of a similar-sized venerid clam *Tapes philippinarum* sympatric with *G. tumidum* at our study site was found to be 0.92 L/hr (or 9.2×10^{-4} m^3/hr) at TPM of 10.5 mg/L (unpubl. data). As the average flow rate at 4 cm above sediment was estimated at 12.48 cm/s which was found to be 10% lower than that at 8 cm above sediment over the experimental period (i.e., the top of the benthic boundary layer), U was estimated at 13.73 cm/s (or 494.21 m/hr) for the control to the lowest flow rate of 3.43 cm/s (123.55 m/hr) for the 25% exposure cage during the study period. Assuming 100% filtration efficiency for *G. tumidum* (Newell and Shumway 1993), SDI was estimated at 0.04, 0.05, 0.07 and 0.15 for the flow rates at 13.73, 10.30, 6.87 and 3.43 cm/s, or 100%, 75%, 50% and 25% exposure, respectively. This indicates that seston depletion effect may have an impact on the growth of *G. tumidum* only when flow rate was reduced to 25% of the control.

Reduced growth under low flow may also be an individual's response to seston flux. For siphonates such as *M. mercenaria* and *G. tumidum* in our study, when ambient flow is substantially less than the pumping speed at the inhalant siphon, seston would be quickly depleted. Under such conditions, an increase in water flow will subsidize the animal's energy return from pumping (Grizzle and Morin 1989; Emerson 1990; Grizzle et al. 1992). Besides, disturbance of sediments at higher flow rates (Emerson 1990) or by wind-wave energy (Fréchette and Grant 1991; Bock and Miller 1994) may also enhance growth due to resuspension of organic matter including benthic algae, microfauna and detritus (Wildish 1977). However, in their experimental studies using sediment traps, Grémare et al. (1998) showed a negative correlation between available proteins in the suspended sediments and gross sedimentation rates, suggesting that resuspension might decrease the quality of the suspended material used as food by the filter feeders. At our study site, the bay is well protected from strong winds and waves (Fig. 1). Hence, wind-wave effects on water flow within the cages would be minimal.

Inhibition of growth under higher flow rates was reported for the giant scallop *Placopecten magellanicus* at > 10 cm/s (Wildish et al. 1987, Wildish and Kristmanson 1988) and for the blue mussel *Mytilus edulis* at > 25 cm/s (Wildish and Miyares 1990). The mechanism involves the disruption of the bivalve pump by pressure differential between inhalant and exhalant openings (Jørgensen et al. 1986). At increasing flow speeds, the ambient flow at the inhalant aperture creates a pressure greater than that of the bivalve pump at the exhalant aperture, resulting in reduction in the pump capacity and filtration or feeding rate. Such pressure differential and hence pumping rate, however, could be augmented with different orientation of the mussel siphons relative to the pressure gradient in unidirectional flow condition (Carter et al. 2001). In the present field investigation, growth of the clam *G. tumidum* increased with flow. New settlements of infauna within the cages over the 3-month study period comprised mainly small, swimming nereid and syllid polychaetes, which would not significantly affect interspecific competition with the clams for food or alter near-bed currents. The results thus suggest that either the flow rate of the control cages (average at 12.48 cm/s) recorded at our field site may not reach the level that affects the bivalve pump activity or the clams in the experimental cages oriented themselves in such a way that the inhalant flow could be maximized. Some bivalves are also known to adjust feeding such that growth obtained at inhibitory (high) flow and optimum flow is comparable (Wildish and Kristmanson 1988). Whether *G. tumidum* is able to adjust its feeding rate according to flow is unknown and deserves further investigations.

Responses in shell and tissue growth to flow were different in *G. tumidum* at low flow rates, with shell growth continuing to decrease as flow rate decreased, whereas tissue growth was relatively independent of flow. Grizzle and Morin (1989) demonstrated highest shell growth but lowest tissue growth in *M. mercenaria* at the site with medium flow, and lower shell growth but higher tissue growth at sites with fast or slow flow. Uncoupled growth of shell and soft tissue may be a result of a tradeoff in energy allocation between shell and tissue growth when food is limiting. Extrinsic factors such as food availability and temperature, and intrinsic factors including

reproductive state and age may affect energy allocation between shell, soma and gonad (Seed 1980, Bayne and Newell 1983, Hilbish 1986). A number of bivalves in Hong Kong such as *Gafrarium pectinatum*, *Corbicula fluminea* and *Brachidontes variabilis* undergo bimodal reproductive cycles with gametogenesis bringing the gonads to maturation in spring (Mar ~ June) and autumn (Sep ~ Nov), at a time when sea temperatures are rising and falling respectively about their mid-summer peak. The mid summer cessation in reproductive activity is probably caused by a marked decline in salinity which divides an annual reproductive cycle into two (Morton 1990). The time when the tissue weight of *G. tumidum* was determined (October) coincided with active gametogenesis. Our results may suggest that when seston flux is reduced at slow flows, it would be a better strategy for *G. tumidum* to channel energy for gonad development instead of shell growth during the reproductive stage.

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LITERATURE CITED

Allen SE. 1989. Chemical Analysis of Ecological Materials. 2nd ed. Blackwell Scientific Publications, Oxford.

Bayne BL, Newell RC. 1983. Physiological energetics of marine molluscs. In: The Mollusca, Vol 4 (Saleuddin ASM, Wilbur KM, eds). Academic Press, London, pp 409-515.

Bock MJ, Miller DC. 1994. Seston availability and daily growth in *Mercenaria mercenaria* on an intertidal sandflat. Mar Ecol Prog Ser 114: 117-127.

Buchanan JB. 1984. Sediment analysis. In: Methods for the Study of Marine Benthos, 2nd ed (Holme NA, McIntyre AD, eds). Blackwell Scientific Publications, Oxford, pp 41-65.

Carter RN, Wildish DJ, MacDonald BA. 2001. The effects of velocity and seston concentration on the exhalant siphon area, valve gape and filtration rate of the mussel *Mytilus edulis*. J Exp Mar Biol Ecol 261: 91-111.

Eckman JE, Peterson CH, Cahalan JA. 1989. Effects of flow speed, turbulence, and orientation on growth of juvenile bay scallops *Argopecten irradians concentricus* (Say). J Exp Mar Biol Ecol 132: 123-140.

Emerson CW. 1990. Influence of sediment disturbance and water flow on the growth of the soft-shell clam, *Mya arenaria* L. Can J Fish Aquat Sci 47: 1655-1663.

Fréchette M, Grant J. 1991. An *in situ* estimation of the effect of wind driven resuspension on the growth of the mussel *Mytilus edulis* L. J Exp Mar Biol Ecol 148: 201-213.

Grémare A, Amouroux J-M, Charles F, Medernach L, Jordana E, Nozais C, Vetion G, Colomines J-C. 1998. Temporal changes in the biochemical composition of particulate organic matter sedimentation in the Bay of Banyuls-sur-Mer. Oceanol Acta 21: 783-792.

Grizzle RE, Langan R, Howell WH. 1992. Growth responses of suspension-feeding bivalve molluscs to changes in water flow: differences between siphonate and non-siphonate taxa. J Exp Mar Biol Ecol 162: 213-228.

Grizzle RE, Morin PJ. 1989. Effect of tidal currents, seston, and bottom sediments on growth of *Mercenaria mercenaria*: results of a field experiment. Mar Biol 102: 85-93.

Hadley NH, Manzi JJ. 1984. Growth of seed clams, *Mercenaria mercenaria*, at various densities in a commercial scale nursery system. Aquaculture 36: 369-378.

Hilbish TJ. 1986. Growth trajectories of shell and soft tissue in bivalves: seasonal variation in *Mytilus edulis* L. J Exp Mar Biol Ecol 96: 103-113.

Jørgensen CB, Famme P, Kristensen HS, Larsen HS, Mohlenberg PS, Riisgård HU. 1986. The bivalve pump. Mar Ecol Prog Ser 34: 69-77.

Judge ML, Coen LD, Heck KL. 1992. The effect of long-term alteration of *in situ* water currents on the growth of *Mercenaria mercenaria* in the northern Gulf of Mexico. Limnol Oceanogr 37: 1550-1559.

Kirby-Smith WW. 1972. Growth of the bay scallop: The influence of experimental currents. J Exp Mar Biol Ecol 8: 7-18.

Morton B. 1990. The life cycle and sexual strategy of *Gafrarium pectinatum* (Bivalvia: Veneridae) in a Hong Kong mangrove. Malacol Rev 23: 53-62.

Morton B, Morton J. 1983. The Seashore Ecology of Hong Kong. Hong Kong University Press, Hong Kong.

Newell CR, Shumway SE. 1993. Grazing of natural particulates by bivalve molluscs: a spatial and temporal perspectives. In: Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes (Dame RF, ed). Springer-Verlag, Berlin, pp 85-148.

Peterson CH, Black R. 1991. Preliminary evidence for progressive food depletion in incoming tide over a broad tidal sand flat. Est Coast Shelf Sci 32: 405-413.

Seed R. 1980. Shell growth and form in the Bivalvia. In: Skeletal Growth of Aquatic Organisms (Rhoads RC, Lutz RA, eds). Plenum Press, New York, pp 23-67.

Shin PKS, Cheung SG. 2005. A study of soft shore habitats in Hong Kong for conservation and education purposes. Final Report, Environment and Conservation Project 23/99. City University of Hong Kong, Hong Kong.

Strickland JDH, Parsons TR. 1972. A Practical Handbook of Seawater Analysis. Fisheries Research Board of Canada, Ottawa.

Wildish DJ. 1977. Factors controlling marine and estuarine sublittoral macrofauna. Helgol wissenschaftliche Meeresunters 30: 445-454.

Wildish DJ, Kristmanson DD. 1979. Tidal energy and sublittoral macrobenthic animals in estuaries. J Fish Res Board Can 36: 1197-

1206.

Wildish DJ, Kristmanson DD. 1984. Importance to mussels of the benthic boundary layer. Can J Fish Aquat Sci 41: 1618-1625.

Wildish DJ, Kristmanson DD. 1985. Control of suspension feeding bivalve production by current speed. Helgo Meeresunters 39: 237-243.

Wildish DJ, Kristmanson DD. 1988. Growth response of giant scallops to periodicity of flow. Mar Ecol Prog Ser 42: 163-169.

Wildish DJ, Miyares MP. 1990. Filtration rate of blue mussels as a function of flow velocity: preliminary experiments. J Exp Mar Biol Ecol 142: 213-219.

Wildish DJ, Kristmanson DD. 1997. Benthic Suspension Feeders and Flow. Cambridge University Press, Cambridge.

Wildish DJ, Kristmanson DD, Hoar RL, DeCoste AM, McCormich SD, White AW. 1987. Giant scallop feeding and growth response to flow. J Exp Mar Biol Ecol 113: 207-220.

Wong WH, Cheung SG. 2003. Site-related differences in the feeding physiology of the green mussel *Perna viridis* (L.): a reciprocal transplantation experiment. Mar Ecol Prog Ser 258: 147-159.

Zar JH. 1996. Biostatistical Analysis, 3rd ed. Prentice Hall, New Jersey.

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