Does skimming flow reduce population growth in horse mussels?

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Abstract

Skimming flow was induced in a field flow-through flume with model and live horse mussels as roughness elements. A growth experiment was conducted in the flume with locally available seawater and natural seston. Horse mussel population growth was compared in turbulent isolated element (control) and skimming flow (treatment) and with regulated natural seston levels, indicated by $C =$ bulk flow seston concentration, $C^1 =$ seston concentration in the benthic boundary layer, near the inhalant, which just meets the maintenance ration of the mussel population. We were able to control the bulk seston within the range: 1.2 to 5 times of C^1 during the growth experiment. No significant difference between control and skimming flow treatments was found in: tissue growth, RNA–DNA ratios, or condition factor. Extrapolating from the experimental results we predict that under minimum growth enhancing seston concentrations at a high horse mussel density (71 m^2), skimming flow does not reduce population growth.

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1. Introduction

This study was stimulated by the observation that horse mussels, *Modiolus modiolus* (Linnaeus, 1758), living on gravel/cobble and mottled gravel substrates in the upper Bay of Fundy, grew at a slower rate than those 30–40 km away on megarippled sandy substrates. Horse mussels form characteristic raised features on such substrates, termed bioherms (=mussel reefs), where they are partially buried in the sand (Wildish et al., 1998). One possible cause of slower growth by horse mussels living among cobbles is that the cobbles, and/or epi-benthic mussels themselves, change the boundary layer flow in such a way as to limit their food supply. Hydrodynamically, rough-turbulent, steady flows near the seabed are governed by the size, shape and density of roughness elements (reviewed in Nowell and Church, 1979; Green et al., 1998). Three types of flow pattern were confirmed by Nowell and Church (1979): isolated roughness, wake interference and skimming flow. In skimming flow the density of roughness elements, such as cobbles and mussels, causes flow penetration between roughness elements to be reduced. A sheared layer develops above the cobbles or mussels, thus reducing the exchange of sestonic particles across it.

Boundary layer conditions above a cobble substrate are hydrodynamically rough at velocities greater than a few cm s^{-1}. If the density and size of cobbles or epi-benthic mussels is sufficient to induce skimming flow, the seston supply in the interstices between the roughness elements will be more limited than in other types of turbulent flow. This is because of reduced mechanical transport of seston from the bulk flow across the sheared zone which develops just above the roughness elements, and the increased likelihood of seston depletion where high densities of filter feeders are present in the slowly circulating eddies between the roughness elements. Lassen et al. (2006) showed that exhalant jets from blue mussels influences the boundary layer flow in such a way as to increase downward mixing from the bulk layer above roughness elements. Skimming flow would be expected to reduce the mussel exhalant jet penetration of the bulk layer and hence reduce the biomixing effect.

The seston depletion index, SDI (Wildish and Kristmanson, 1997), predicts for turbulent flow conditions whether seston depletion is likely. The SDI (Table 1) compares the flux of seston due to mussel filtration, $PR\alpha$, divided by the flux driven by turbulent mass transfer, γU. Where the SDI values in Table 1 are >0.11, seston depletion can be expected. At SDI ~0.11 we can expect the seston concentration, C^1, at the bottom of the boundary layer and in eddies between the mussels to just meet the ration maintenance requirements of a given mussel population. C^1 is often expressed as $\mu g\ L^{-1}$ of chlorophyll a and equals 0.2 to $0.8C$ at SDI=0.11, where C is the seston concentration in the bulk of the flow above the sheared zone. An important consideration in setting up filter feeding growth experiments with natural seawater is the bulk seston concentration, C, in relation to C^1 during the growth period observed. Wildish and Kristmanson (1979) proposed three possible ranges of natural bulk seston concentrations which might be encountered by a given filter feeding population: $C \gg C^1$ and no mass transfer limitation was likely; $C^1 \sim 0.2$–$0.8C$, where turbulent mass transfer rates may be limiting, causing reduced population growth and/or density; and $C^1 > C$ where seston levels are insufficient to support a given population of filter feeders.

Our aim was to determine experimentally whether the reductions in transfer rates of seston across the sheared layer created by skimming flow hydrodynamics were large enough to result in reduced mussel growth rates. The control flow conditions against which growth rates were compared was isolated roughness or wake interference turbulent flows, where the sheared layer was absent. The seston concentration provided in the horse mussel growth experiment was: $C^1=0.2$–$0.8C$, chosen because the latter was most likely to demonstrate reduced mussel growth rates caused by skimming flow hydrodynamics.

2. Materials and methods

2.1. Skimming flow recognition

Two methods to identify when skimming flow is present were available. If cobbles, or mussels, as roughness elements are distributed over the bottom in a regular pattern, then using the roughness density estimate of Nowell and Church (1979) skimming flow can be expected when:

$$NA_e/A_t > 1/12 \text{ to } 1/8 \tag{1}$$

where N is the density of roughness elements (number/m^2), A_e is the mean plan area of roughness elements and A_t is the total

area of bottom available for occupation by roughness elements. In this study we used model horse mussels to create skimming flow. For model mussels A_e was calculated as:

$$A_{e\ mussel} = \pi(\text{valve length} \times \text{valve height}/2). \tag{2}$$

A second method (Green et al., 1998) uses as a criterion the spatial concentration of roughness elements λ, where:

$$\lambda = kd/D^2 \tag{3}$$

where k is valve width, d is valve height and D is the centre-to-centre distance between roughness elements. When $\lambda \geq 0.2$, skimming flow is expected.

2.2. Growth experiment with horse mussels

Horse mussels were from a wild stock obtained from a mid-tidal level, rocky pool at Mathew Cove, Mascarene, Bay of Fundy ($45^0\ 10^1$ N $67^0\ 32^1$ W). The pool received ebb flow run-off when not tidally submerged. Densities of up to $136\ m^2$ were found with the mussels attached directly to the rock pool bottom. Some of the upper valves of the horse mussels were covered with an encrusting, calcareous alga (*Lithothamnion* sp). The horse mussels were acclimated in a 2 m diameter tank, supplied with near-ambient temperature, running, unfiltered seawater, for a few weeks before placing in flume experiments. An outdoor, flow-through flume (Wildish and Kristmanson, 1988) with centrally placed partition to divide the working section into two halves (Fig. 1) was used. The seawater was supplied to the flume by a 5 HP submersible pump and 4-inch plastic pipe that carried seawater, containing ambient levels of chlorophyll a, directly from 1.5 m depth in the estuary near the Biological Station floating wharf. Another 4-inch line carried "unfiltered" seawater, known to contain low levels of chlorophyll a, from the Biological Station supply to the flume mixing chamber. Both seawater supplies could be controlled by means of valves to adjust chlorophyll a. The chlorophyll a level was determined daily based on fluorometric measurements (see below for details). During the growth experiment we measured flow profiles at 3.05 and 4.05 m positions in both flow channels (Fig. 1). Free stream flows were measured at 3.05 m along the flume 5 times/week.

Horse mussels were divided into three groups ($n=19$–25) and prepared for the growth experiment by sacrificing one group to obtain initial measures of valve length, dry weight of soft tissue and combined dry weight of both valves. Linear regressions for these data ($R^2>0.84$) were used to predict the initial dry weight and valve weight of the two other groups of mussels used in the experiment. Mussels were randomly assigned to control and skimming flow treatments and measured for initial valve length. At the same time they were individually tagged by attaching a numbered tag on the valve with cyanoacrylate glue. Velcro circles were also stuck to the right valve as a means of attaching mussels at specified positions in the flume. Control mussels were placed in the flume so that there was 25 cm between rows and 15 cm between mussels in every other row (i.e. with one row having 1 mussel and the next row 2). Treatment mussels (5/row)

Table 1
Calculated SDI's for a horse mussel population

Density	Free stream U, cm s^{-1}				
No. m^{-2}	5	10	20	50	100
50	1.18	0.59	0.29	0.118	0.058
100	2.35	1.18	0.59	0.235	0.118
132	3.70	1.55	0.78	0.31	0.155

Based on $PR\alpha/\gamma U$, given that $R=12.7$ L h^{-1} (calculated from mean dry tissue weight at the end of experiment 3 and a regression fitting for horse mussels in Mohlenberg and Riisgard, 1979), $\alpha=1$ and $\gamma=0.003$.
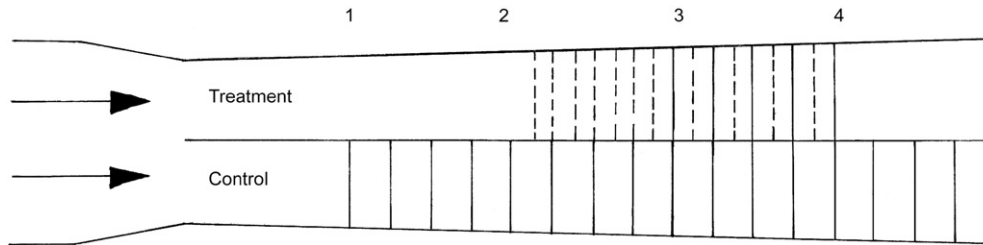
Fig. 1. Diagrammatic plan view of part of the 5 m long, flow-through field flume. Numbers indicate the distance from the origin of the working section of the flume. Live mussel rows indicated by solid lines, model mussel rows by dashed lines. Individual live mussels are not shown. Flow direction indicated by arrows.

were also placed at 25 cm intervals beginning at 3 m along the flume. Seven rows of model mussels (5/row) preceded live mussels at a spacing of 12.5 cm between rows. Model were interspersed between live mussel rows to give the same spacing (Fig. 1).This ensured that path length and mussel density differences occupied by live animals: control=4.25 m and 22 m^2; skimming flow=1.0 m and 71 m^2, met the theoretical threshold criteria for skimming and control flows. The experiment was started on 21/06/2005 and terminated 36 days later. Final measures included individual RNA/DNA ratios, valve length, total dry weight of both valve and tissue dry weight.

2.3. Determining C^1

In a preliminary experiment with blue mussels using the same experimental protocol as described herein we offered a natural seston concentration (mean=0.35 μg L^{-1}) which serendipitously proved to be close to the maintenance ration for the blue mussel population tested (not shown). This was consistent with the population growth results obtained: that is no change in condition factor, near zero growth in valve length and tissue weight and no change in RNA/DNA ratios. We assumed that the seston concentration equivalent to the maintenance ration would be similar in both blue and horse mussels. However, because of the larger size of horse mussels their C^1 will actually be greater than for blue mussels, perhaps by as much as 2 times. Nevertheless the seston concentration during growth experiments in the flume was controlled within the range 0.2–0.8C^1 based on $C=C^1$=0.35 μg L^{-1} for blue mussels; to ensure seston depletion. Then the permissible range of chlorophyll a becomes:

High $C = 0.35 \mu gL^{-1}(1/0.2) = 1.75 \mu gL^{-1}$ and
Low $C = 0.35 \mu gL^{-1}(1/0.8) = 0.44 \mu gL^{-1}$.

2.4. Measured variables for the mussel growth experiments

2.4.1. Temperature
This was measured at 30-minute intervals with a Stow Away Tidbit (Anset Computer Corp., Bourne, MA, U.S.A.) secured on the bottom near the working section entrance.

2.4.2. Velocity
Flow profiling in the flow-through flume was made at positions indicated by the distance into the flume (3.05 and 4.05 m), both in the treatment and control channels. A straight shafted 403 StreamFlo probe from Nixon Instrumentation,

Cheltenham, Gloucestershire, U.K., was used for making mid-channel profiling measurements. Free stream flow measurements were made with the same probe at mid-depth, 6–9 cm above bottom with 10 replicated readings, each of which was integrated over 10 s. Flow profiling with an 11 mm diameter rotor was in 1 cm increments with 10 replicated readings of 10 s each.

2.4.3. Seston
Fluorometric determination of the chlorophyll a concentration of seawater was made by the method of Strickland and Parsons (1968) in a 10-AU Turner Designs fluorometer. Seawater samples of 0.2–0.5 L were drawn from upstream of the live mussels in 5 replicates. In addition a "quick" method was devised to measure chlorophyll a in living microalgae on a daily basis. Chlorophyll a was measured fluorometrically once or twice daily, directly from 5 replicate seawater samples (10 ml drawn upstream of live mussels) without filtration or acetone extraction. The relationship between extracted chlorophyll a (y) as μg L^{-1}and live microalgal chlorophyll a collected by the "quick" method in the same units (x) was:

$$y = 0.2214x + 0.172 \quad N = 20, \ R^2 = 0.99. \tag{4}$$

2.4.4. Mussels
Mussel growth rate was determined as the percentage valve length increment (mm) or dry weight increment (g)/day:

$$(L_1 - L_2)*100/(L_0N) \tag{5}$$

and

$$(W_1 - W_0)*100/(W_0N) \tag{6}$$

where N=time in days, L_0=initial valve length in mms, L_1=final length in mms, and W_0=initial tissue dry weight in g, W_1=final

Table 2
Environmental characteristics of seawater during horse mussel growth experiment

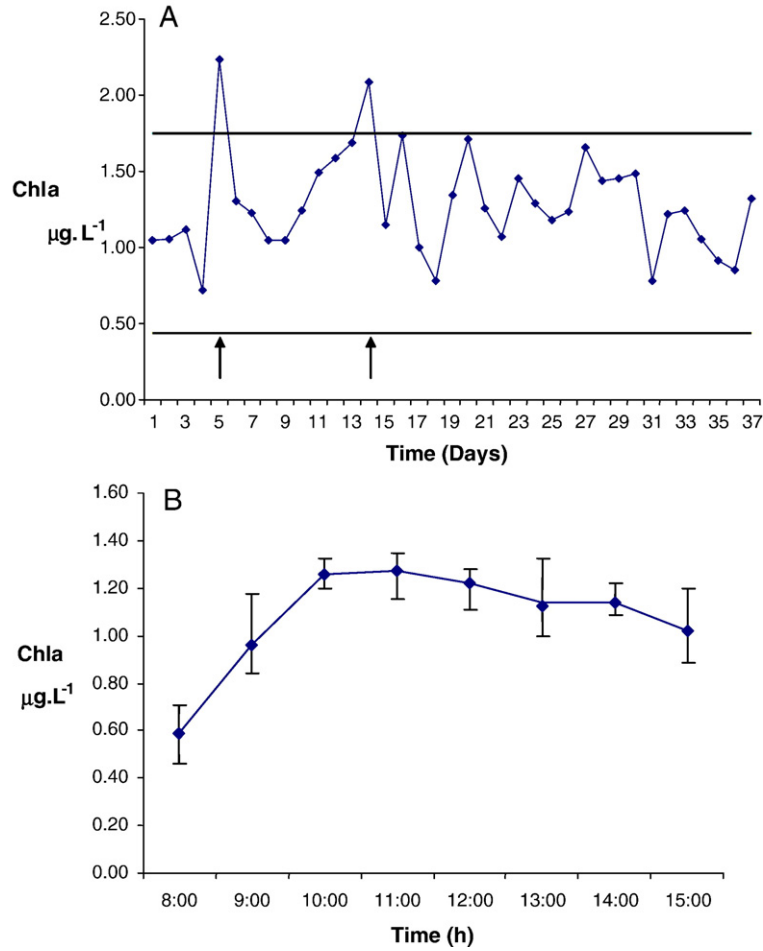| Variable	Minimum	Maximum	Mean	SD	N
Temperature °C	8.40	12.60	10.38	0.834	1722
Chlorophyll a (μg L^{-1})					
Acetone extraction	0.37	1.56	0.90	0.352	25
Live microalgae	0.72	2.24	1.28	0.339	185
Free stream ($\bar{U}$ cm s^{-1})					
Control	6.71	13.09	8.63	0.97	160
Skimming flow	4.25	13.15	7.97	1.01	160

Fig. 2. Chlorophyll *a* concentrations in seawater measured by "quick" method, expressed as acetone extract determination. A. Daily chlorophyll *a* during experiment Arrows indicate flow adjustments. B. Tidal periodicity of chlorophyll *a* at the Biological Station wharf on 22/07/2005. L.W. was at 0700 and H.W. at 1305 D.S.T.

dry weight in g. We also calculated the static physiological condition factor, CF, recommended by Lucas and Beninger (1985)

$$CF = (W/V)*100 \tag{7}$$

where W = the dry tissue weight (g) and V = the total dry weight of both valves (g).

2.4.5. RNA–DNA ratios

Each tissue was analyzed for RNA–DNA ratios in small samples as described in Robinson and Ware (1988). A small portion of mantle tissue was removed during preparation for dry weight determination. The mantle tissue was stored in small, numbered vials at −80 °C. The nucleic acids in the mantle tissues of the mussels were measured using the LePecq and Paoletti (1966) fluorometric technique, modified by Karsten and Wollenberger (1972, 1977). This technique is based on the enhanced fluorescence of nucleic acids after introduction of the dye ethidium bromide (2,7 diamino-10-ethyl-9-phenyl-phenanthidinium bromide) and is sensitive to small amounts of nucleic acids at concentrations down to 0.05 µg ml^{-1} for RNA and 0.1 µg ml^{-1} for DNA. A frozen sample of mantle tissue (approximately 12 mm^3) was homogenised in 4 ml of ice-cold phosphate buffered saline (PBS) with a Polytron tissue grinder

at 24,000 rpm for two 10 s treatments. Three replicate aliquots (0.5 ml) were taken for both DNA and total nucleic acid determinations. For the DNA determinations, RNAse was added to the three aliquots for DNA along with heparin. No RNAse was added to the total nucleic acid aliquots and was replaced with PBS. Samples were incubated for 30 min at 37 °C. Fluorescence
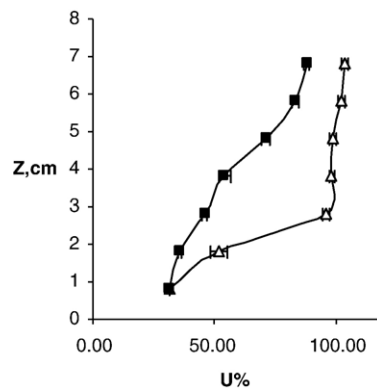

Fig. 3. Mid-channel flow profiles at a point 3.05 m along the working section of the flow-through flume in control and skimming flow channels of experiment 2. *U* is expressed as a percentage of the mean flow. Open triangles — control channel, filled squares skimming flow channel.

Table 3

Specific daily growth (fitted by Eqs. (5) — valve length and (6) — dry tissue weight),RNA–DNA ratios and condition factors (fitted by Eq. (7)) for horse mussels during the 36 days of the experiment

Growth measure	Control	Skimming flow	Mann–Whitney test		
	Median	Median	W	N	P-value
% Valve increment	0.003	0.008	262.0	50	0.332
% Dry tissue increment	0.69	0.96	245.0	50	0.194
RNA–DNA ratios					
After	2.39	2.18	388.5	50	0.143
Condition factor					
Before	11.71	11.29	406.5	50	0.070
After	13.79	14.77	234.0	50	0.130

"Before" estimates are based on samples and length/weight regression of a preliminary batch ($N=19$) of mussels, sacrificed at the beginning of the experiment. Non-parametric test between all control and skimming flow treatment mussels.

was read on a Turner fluorometer (Model 112) and compared with known standard curves for RNA and DNA.

2.4.6. Statistical analysis

Free stream mean flows in each side of the flume were compared by t-test at a confidence interval of 95%. Because some growth data was not normally distributed, e.g. some standard deviations > mean and standard skewness and kurtosis values were > 2, we employed a non-parametric test. The null hypothesis that the differences between median control and skimming flow growth measures and RNA–DNA ratios was zero was determined with the Mann–Whitney (=Wilcoxon) W test. The probability level used throughout was $P>0.05$.

3. Results

Chlorophyll a data (Table 2) collected during this experiment does not reflect the natural concentrations in surface waters near the Biological Station. This was because the seston concentration was adjusted by opening or closing seawater valves as explained in the methods section. The aim of maintaining the chlorophyll a concentration within 0.44–1.75 µg L^{-1}, was achieved during a period of relative chlorophyll a stability with adjustments needed on two occasions only (Fig. 2A). Tidal effects on chlorophyll a (Fig. 2B) were found to be <0.6 µg/L, so we did not adjust the daily measurements to a standard tidal time. The measured mean value of chlorophyll a (Table 2), 0.90 µg L^{-1} for the standard acetone extraction method, lies within these two calculated values. If horse mussel C^1 is two times greater than for blue mussels, 0.70 µg L^{-1}, then our measured flume chlorophyll a, C, is still within the 0.2–$0.8C^1$ range for horse mussels.

Free stream flows in each channel were significantly different (Table 2) with the skimming flow mean being slightly lower than that of the control ($t=5.95$, $df=318$). Flow profiling (Fig. 3) confirmed that skimming flow was created in the treatment, but not control side, of the flume.

The back-calculated condition factor at the beginning of the experiment was not significantly different between control and skimming flow mussels, suggesting no bias in their selection. By the end of the growth period the condition factor had significant-

ly increased for both control ($W=519$, P-value$=0.000$) and treatment ($W=574$, P-value$=0.000$) mussels. For both treatments valve growth (Table 3) was small and the condition factor increases explained by the more substantial tissue growth. These results are consistent with the seston offered during the experiment being higher than the maintenance ration as our calculations predicted.

High variance was found in the tissue growth data of Table 3 (standard deviations > means, skewness and kurtosis values >2.0) and non-parametric testing found no significant differences between the two treatments for any pair of medians shown in Table 3. There were no significant differences between control and skimming flow mussels for RNA–DNA (Table 3). Consequently we accept the null hypothesis of no difference in growth between the two treatments.

Seston depletion effects were expected at the flows, mussel densities and seston concentrations used in our experiment (Table 1) so the data shown in Table 4 was analyzed further by comparing the up- and downstream mussel beds. Results suggest that there was no significant difference for any of the growth

Table 4

Final valve length, soft tissue growth, RNA–DNA ratios and final condition factor of individual mussels

Position in flume	Controls				Skimming flow			
	Valve length mms	RNA–DNA ratios	Growth % day	CF	Valve Length mms	RNA–DNA ratios	Growth % day	CF
1	66	4.81	1.34	13.87	77	1.99	1.95	15.53
2	64	2.44	1.5	14.43	73	2.36	1.23	12.85
3	(75	3.90	0.2	8.93)	61	1.88	2.24	16.15
4	62	2.33	2.36	16.63	59	2.87	1.33	16.91
5	69	1.77	0.31	13.73	70	2.99	1.09	11.43
6	71	2.39	0.93	20.06	63	2.18	1.53	14.62
7	67	3.46	0.41	14.08	67	3.74	0.96	15.12
8	55	2.52	1.75	14.87	77	2.11	0.46	14.45
9	78	1.08	0.69	15.62	(53	1.20	0.22	6.58)
10	69	2.05	−0.05	12.39	57	1.86	2.35	14.54
11	68	2.17	0.91	15.36	61	1.85	0.9	15.45
12	66	1.63	0.15	14.65	68	2.34	0.52	16.77
13	68	2.23	0.71	10.75	55	1.04	2.64	15.85
14	70	2.18	0.8	13.47	53	1.91	4.27	14.44
15	62	2.61	1.84	15.54	73	1.61	0.18	16.74
Median		2.33	0.8	14.43		1.99	1.23	15.12
Mean		2.5	0.92	14.68		2.13	1.46	15.06
SD		0.93	0.7	2.13		0.69	1.09	1.54
16	67	1.69	1.7	13.79	63	1.14	0.75	13.67
17	70	2.39	0.18	13.32	64	2.40	1.49	19.44
18	(59	2.88	−0.01	13.61)	66	2.81	0.39	14.77
19	75	2.07	−0.18	9.13	65	2.36	0.64	13.03
20	65	3.60	1.74	17.26	61	2.89	0.53	15.89
21	73	3.56	0.53	11.89	67	1.68	0.03	12.67
22	63	3.59	1.43	12.77	67	2.33	−0.1	15.89
23	77	2.89	−0.19	11.57	77	2.29	1.16	18.05
24	67	2.09	−0.03	14.99	62	2.45	0.13	12.47
25	74	1.23	0.49	12.75	55	1.90	3.58	11.79
Median		2.64	0.34	12.77		2.35	0.59	14.22
Mean		2.6	0.57	13.05		2.23	0.86	14.77
SD		0.84	0.77	2.27		0.52	1.08	2.54

Horse mussels are arranged in upstream/downstream order as placed at the beginning of the experiment. Numbers 1–15 are upstream (=first 3 rows of treatment side), 16–25 downstream (=last 2 rows of treatment side). Mussels shown in parenthesis were heavily encrusted with calcareous microalgae.

measures shown in Table 4. Thus for tissue growth the median growth % day (Table 4) for up-/downstream mussels was not significantly different within controls ($W=49.0$, P-value$=0.157$), or within skimming flow treatments ($W=44.0$, P-value$=0.09$). The absence of significant up-/downstream effects is surprising since the median tissue growth of downstream mussels was 57.5% less for controls and 52% less for skimming flow mussels. These results may be explained by:

- the low number ($N=25$) of live mussels used; given that the theory assumes an infinite path length and hence many mussels in the bed,
- a much higher variance in tissue growth rates (Table 4) of downstream mussels where one SD was greater than the mean for both treatments (not so for upstream mussels).

RNA–DNA ratios of individual mussels did not correlate with tissue growth rate and the upstream/downstream differences of this variable were also not significantly different (Table 4). The lack of correlation is because the two measures are operating over different time scales and growth in tissue mass integrates over the whole experimental period, whilst RNA–DNA ratios apply to short-term effects near the end of the growth period.

4. Discussion

Our results suggest that skimming flow does not result in reduced population growth rates. An upstream/downstream analysis of growth rates shows that in both treatments the downstream mussels experienced a 52–58% decrease, although the difference was not significant because of the low sample number used. If more mussels were included in the experiment, necessitating a longer path length flume, the upstream/down-stream differences may become significant. A characteristic feature of seston depletion effects in horse mussel population experiments is that it results in great variability of growth rates and increasing growth variability with greater seston depletion (Table 4). The recognition of high growth rate variability might be employed in future studies to infer seston depletion effects among mussel populations. Our results are consistent with seston depletion effects controlling population growth of horse mussels and suggest that additional effects due to skimming flow are absent or likely to be small.

Further work is needed to verify our conclusion that skimming flow is unimportant in explaining the differences between popu-lation growth rates of mussels from different benthic habitats. One useful approach would be to increase the number of mussels, and hence flume path length used, and to provide a means of increasing the flow speeds used. Both of these presented unresolved technical challenges with the flume design used in this experiment. Sampling within the benthic boundary layer was also difficult in this flume and future studies will require an *in situ* seston sampling system through the flume bottom or sidewall.

To put our results in an ecological context skimming flow is one of many other environmental variables that could influence population growth rates of mussels (see Bertness and Grosholz, 1985; Seed and Suchanek, 1992). Our laboratory experiment

used natural seston at realistic field concentrations and at one live horse mussel density of 71 m^2, which is close to the maximum density recorded in the sand with bioherms province (78 m^2), and with the model mussels of the treatment side (156 m^2) reaches the higher densities of gravel/cobble provinces in the upper Bay of Fundy (Wildish et al. 1998). The experiment was carried out at relatively low current velocities (~ 8 cm s^{-1}), whereas depth-averaged tidal flows in this part of the Bay of Fundy reach maxima of 105 cm s^{-1} (Greenberg et al., 2005), although no field studies of benthic boundary layer flows in horse mussel habitats have been undertaken. Clearly, there is a need to repeat skimming flow experiments at higher velocities.

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