Control of suspension feeding bivalve production by current speed

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ABSTRACT: Growth experiments confirm that production by a bed of blue mussels *(Mytilus edulis)* may be controlled by tidal current speed through its effect on seston supply. The mechanism of this effect involves a downstream seston depletion and is thus applicable only to populations of mussels. Individual physiological responses by mussels, such as increased filtration, ingestion and assimilation rates at higher current speeds, are not involved in the enhanced bivalve production observed.

INTRODUCTION

Bivalve production is considered to be the average rate of change of biomass, both positive and negative, of all individuals in a specified population for a given time interval and is thus equivalent to the average population growth. Factors which may affect the production of suspension feeding bivalve molluscs include: the quality and quantity of sestonic food (Stromgren & Craig, 1984), hydrodynamic factors at the sediment-water interface, the path length, density and mussel size within the bed (Wildish & Kristmanson, 1979), intrinsic physiological or behavioural factors, such as a seston concentration maximum beyond which feeding is inhibited (Schulte, 1975), and extrinsic, non-feeding factors such as predation (Seed, 1976) or tidal-current erosion (Wildish, 1983).

Convincing evidence that hydrodynamic factors are important in controlling growth and production of suspension feeding bivalves is lacking. The ability of current speed to control the growth of suspension feeding bivalve populations was in doubt because of apparently contradictory experimental results (Bayne et al., 1976; Vogel, 1981). Walne (1972) found that juveniles of all three species of bivalves, *Mytilus edulis, Ostrea edulis* and *Crassostrea gigas,* grew better in small experimental boxes at seawater flows of 3.3 than at 1.3 cm · sec^{-1}. Kirby-Smith (1972) investigated the growth of the bay scallop, *Argopecten irradians,* in an apparatus consisting of eight plastic pipes supplied with natural seawater, each at a different current speed, within the range 0.2–12.8 cm · sec^{-1}. Results showed that faster currents, contrary to the data of Walne (1972), inhibited shell growth and that maximum growth was observed at the slowest current speed.

In the trophic group mutual exclusion hypothesis, Wildish (1977) suggested that both deposit and suspension feeders are food limited and that an important limiting

factor is tidal current velocity. For suspension feeding animals, the mechanism of food limitation is considered to involve seston depletion. Wildish & Kristmanson (1979, 1984) have modelled the conditions under which seston depletion might occur and have experimentally verified a downstream seston depletion effect above a blue mussel bed (Wildish & Kristmanson, 1984). Experimental verification of seston depletion is a necessary, but not sufficient, step in establishing that suspension feeding animals may be food limited. It is the purpose of the growth experiments described here to establish whether production of small experimental populations of blue mussels may be growth limited by the seston depletion effect. A preliminary test is also made on the effect of current velocities and density on blue mussel production.

MATERIALS AND METHODS

Growth experiments with the blue mussel, *Mytilus edulis*, were made in an apparatus based on the design of Kirby-Smith (1972) with local mussels obtained from near low-water mark. A constant head box containing seawater pumped from near the Biological Station wharf, St. Andrews, N.B., supplied eight 1.5-m long plexiglass tubes of 7 cm internal diameter (Fig. 1). The flow rate through each tube was adjustable by
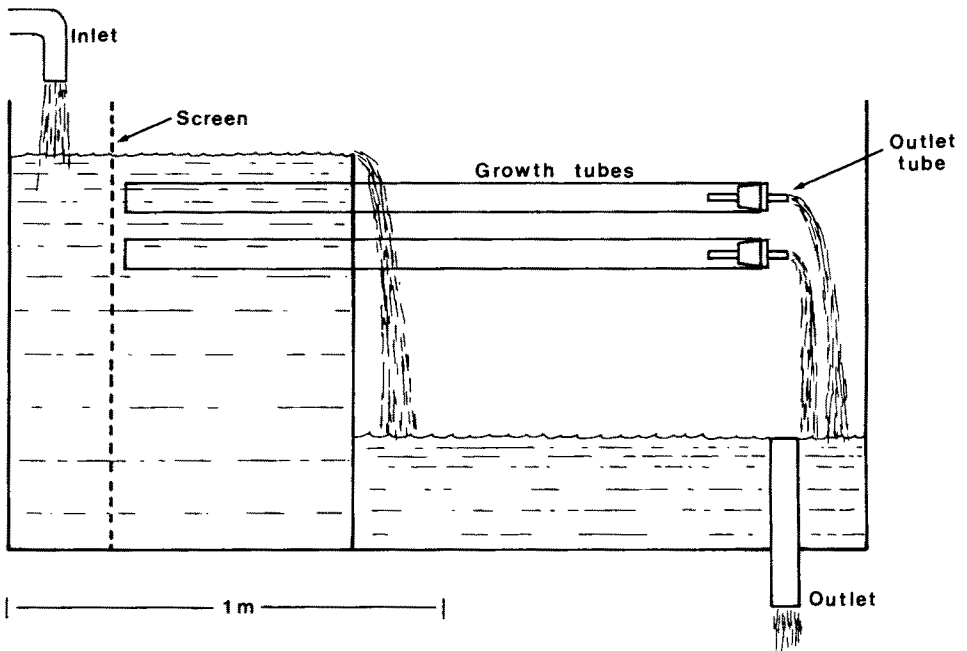

Fig. 1. Side elevation diagram of the Kirby-Smith growth tube apparatus

changing the outlet pipe diameter and was measured by collecting a timed sample of known volume. Plastic mesh inserts, divided into ten equal compartments, were slid into each of the tubes. In the current speed experiment, four mussels (size range 0.5–11.8 g wet weight) were selected so that each could be identified by size and were placed in

each compartment so that the total weight in each was the same. In the density experiment, a mussel size range of 1.5–3.59 g wet weight was selected to minimise individual differences. Mean sizes for each treatment were 2.53 g with two nominal current speeds and four densities tested. Individual mussels in this experiment were marked with a numbered half-circular tag of 1.5-cm diameter, glued to one of the valves. Wet weight to the nearest 1 mg was obtained for each mussel initially (W_0) and on termination of the experiment (W_1). Growth was expressed as the mean percentage change in weight per day per mussel:

$$\frac{W_1 - W_0}{W_0 \times N} \times 100$$

where N was the duration of the experiment in days. The plan area occupied by the 40 mussels in each tube of the current speed experiment was $1.5 \times 0.07 = 0.11 \text{ m}^2$, equivalent to a density of a 364 mussels/m². In the density experiment, density was calculated in the same way. Because equal weights of mussels were allocated to each compartment, it was possible to compare treatments directly without adjusting for initial weight which affects the growth achieved by an individual mussel. Daily seawater temperatures were recorded and current speed estimates made by dividing the observed flow rate $(\text{cm}^3 \cdot \text{sec}^{-1})$ by the area of the tube cross section (cm^2).

Analysis of seston depletion in a Kirby-Smith growth tube is dependent on the ratio, F, of the seawater which is filtered by mussels to the total flow. F for each experimental compartment can be estimated from:

$$F = \frac{nXY}{138.5 \text{ U}}$$

where n is the compartment number starting with inlet = 1 ... outlet = 10, Y is the mean mussel pumping rate treated here as a constant of $2 \text{ l} \cdot \text{hr}^{-1} \cdot \text{mussel}^{-1}$, X is the number of mussels in each compartment, U is the current speed in $\text{cm} \cdot \text{sec}^{-1}$, and the value 138.5 converts U to the flow units of the numerator.

RESULTS

At current speeds less than $1.95 \text{ cm} \cdot \text{sec}^{-1}$, greater growth was observed in the inlet half of the tubes (Table 1). One-tailed t-tests showed that at the five slowest current speeds inlet growth was significantly greater at $p = 0.10$ for all treatments and for the two intermediate current speeds $(0.45 \text{ and } 0.75 \text{ cm} \cdot \text{sec}^{-1})$ the significance level reached $p = 0.05$. At $1.95 \text{ cm} \cdot \text{sec}^{-1}$ and two higher current speeds, growth was statistically equal at both inlet and outlet ends of the tubes. This is because, at slower current speeds, mussels near the inlet capture a major proportion of seston and cause depletion further down the tube. Seston depletion was also found in the low flow treatments of the Kirby-Smith (1972) bay scallop experiments and has been experimentally examined in a simulated benthic boundary layer (Wildish & Kristmanson, 1984).

If the seawater passing down a Kirby-Smith tube could be suitably separated, it would all be filtered by the mussels when it reached the first compartment where $F \geq 1.0$. If mussel-filtering efficiency were 100 %, then beyond this compartment there would be no seston available for downstream mussels. In reality, the concentration of seston

Table 1. Wet weight growth of blue mussels of 0.5–11.8 g initial wet weight in a Kirby-Smith growth tube apparatus for eight current speeds at constant density of 364 mussels · m^{-2}. Experiment initiated on 15. 10. 82 terminated 31 days later. S.E. = standard error

Current speed cm · sec^{-1}		Overall percentage losing weight	Growth as mean percentage wet weight g · day^{-1} · mussel^{-1}			
			Compartments			
			Overall 1–10		Inlet 1–5	Outlet 6–10
$\overline{X}$	S.E.		$\overline{X}$	S.E.		
0.10	0.005	59	0	0.03	0.05	− 0.05
0.13	0.003	60	− 0.06	0.06	0.02	− 0.15
0.40	0.010	29	0.22	0.06	0.33	0.15
0.45	0.012	40	0.13	0.17	0.44	− 0.13
0.75	0.025	22	0.12	0.07	0.26	− 0.01
1.95	0.018	15	0.27	0.04	0.30	0.31
3.50	0.079	13	0.28	0.04	0.30	0.30
3.89	0.077	18	0.29	0.08	0.34	0.27

available for mussel feeding is not a simple function of downstream distance, as is implied by the fractional flow analysis, because of the mixing of the unfiltered and mussel-filtered seawater and less than perfect mussel-filtering efficiency. For laminar flows, mixing in the radial direction of the tube is weak and a significant proportion of the seston supply bypasses the mussels. By contrast, in turbulent flows, mixing in the radial direction is more effective and consequently the seston supply remains greater in its passage along the tube than in laminar flows. Individual compartment growth rates and compartments where F > 1.0 are shown in Table 2. The transition from laminar to turbulent flow in an empty tube would occur at about 3 cm·sec^{-1}.

With mussels and plastic mesh inserts in the tube, the transition will be less sharp

Table 2. Mean percentage change in weight per day per mussel for each compartment at different current speeds. Compartment 1 is at the inlet end. Data in italics: F > 1.0; elsewhere F < 1.0. Note that outlet-limited growth is present up to U = 0.75 cm · sec^{-1}

Compartment No.	Current speed (cm · sec^{-1})							
	0.10	0.13	0.40	0.45	0.75	1.95	3.50	3.89
1	0.24	0.00	0.46	0.28	0.26	0.27	0.17	0.36
2	*0.17*	0.00	0.25	0.35	0.43	0.19	0.11	0.22
3	*− 0.01*	*0.34*	0.65	− 0.10	0.17	0.24	0.34	0.53
4	*− 0.14*	*− 0.43*	0.22	2.04	0.03	0.26	0.42	0.38
5	*− 0.02*	*0.21*	− 0.04	0.22	0.32	0.29	0.34	0.10
6	*− 0.03*	*− 0.37*	0.12	− 0.56	0.03	0.23	0.22	0.70
7	*0.04*	*− 0.13*	*− 0.15*	− 0.13	0.06	0.62	0.35	0.14
8	*− 0.05*	*− 0.03*	*0.05*	*− 0.03*	− 0.77	0.19	0.32	0.09
9	*− 0.08*	*− 0.11*	*0.57*	*0.04*	0.18	0.14	0.36	0.33
10	*− 0.10*	*− 0.07*	*− 0.02*	*− 0.09*	0.26	0.27	0.17	0.02

but the flow rates tested will encompass both laminar and turbulent conditions. This interpretation is supported by the presence of a transitional area in our data (Table 2) where $F < 1.0$, in tubes up to $U = 0.75 \text{ cm} \cdot \text{sec}^{-1}$, and where seston depletion is confirmed by the presence of greater inlet than outlet growth (Table 1). At $U \geqslant 1.95$ $\text{cm} \cdot \text{sec}^{-1}$, no evidence of differences in inlet versus outlet growth is present (Table 1) and in all cases $F \leqslant 0.30$, consistent with seston depletion effects being absent. In these conditions and with an increase in current speed up to $3.89 \text{ cm} \cdot \text{sec}^{-1}$, there is no increase in overall growth and each of the three higher current speed treatments in Table 1 results in statistically equal growth ($p = .001$).

Density influenced the percentage of mussels losing weight as well as the overall mean growth achieved (Table 3) at the slow current speed. As with current speed

Table 3. Growth of blue mussels of 1.5–3.5 g initial wet weight in a Kirby-Smith growth tube apparatus at two current speeds and four densities. Duration of the experiment was 34 days (initiated on 11. 7. 1983)

Current speed $\text{cm} \cdot \text{sec}^{-1}$		Density No./m²	Overall percentage losing weight	Growth as mean percentage wet weight $g \cdot \text{day}^{-1} \cdot \text{mussel}^{-1}$			
						Compartments	
				Overall 1–10		Inlet 1–5	Outlet 6–10
$\overline{X}$	S.E.			$\overline{X}$	S.E.		
0.10	0.005	91	0	0.23	0.05	0.33	0.13
0.10	0.004	273	8	0.22	0.05	0.39	0.08
0.09	0.004	455	14	0.13	0.04	0.25	0.02
0.08	0.003	909	20	0.10	0.02	0.18	0.02
1.47	0.031	91	0	0.57	0.10	0.51	0.64
1.53	0.025	273	0	0.59	0.07	0.56	0.61
1.42	0.034	455	0	0.59	0.06	0.70	0.47
1.32	0.038	909	2	0.59	0.04	0.67	0.51

experiment, this effect is due to seston depletion because one-tailed t-tests show that growth at the inlet end is significantly greater ($p = 0.05$) than at the outlet end in all four low current-speed treatments. The growth data also indicate that seston was of higher quality and/or concentration during the density experiment than in the current-speed experiment. The mean temperature during the former was 12.9 °C which is nearly 2 °C higher than in the current-speed experiment and this may have influenced seston supply and bivalve growth response.

The fractional volume of seawater filtered by the mussels at the high current speed is $F < 1.0$ for most compartments but for compartment 10 at the highest density $F > 1.0$. This suggestion of seston depletion is confirmed by significantly greater ($p = 0.05$) inlet than outlet growth at the two highest densities of Table 3. However, this effect is small because overall growth for each of the high current speed densities is statistically indistinguishable (Table 3). By contrast, most of the compartments at the low current speed have $F > 1.0$ (Table 4). Because F is affected by density even the first compartment

Table 4. Mean percentage change in weight per day per mussel for each compartment at a current speed of ~0.09 cm · sec⁻¹ and various densities. Data in italics: $F > 1.0$

Compartment No.	No. of mussels per compartment			
	1	3	5	10
1	0.51	0.67	*0.40*	*0.40*
2	0.24	*0.53*	*0.23*	*0.24*
3	0.16	*0.09*	*0.05*	*− 0.04*
4	0.53	*0.22*	*0.11*	*0.02*
5	0.23	*0.18*	*0.35*	*0.23*
6	0.28	*0.05*	*0.02*	*0.03*
7	*0.06*	*0.17*	*0.04*	*− 0.03*
8	*0.17*	*0.09*	*0.00*	*0.04*
9	*0.13*	*0.05*	*0.02*	*0.01*
10	*0.03*	*0.02*	*0.01*	*0.02*

with 10 mussels experiences refiltering (Table 4) and it is thus not surprising that growth was significantly greater at the inlet when compared to the outlet end (Table 3).

DISCUSSION

Our results with blue mussels in a Kirby-Smith growth tube apparatus appear to contradict results for bay scallops obtained by Kirby-Smith (1972). Some growth data (Wildish et al., unpublished) obtained with sea scallops in a flume confirm Kirby-Smith's result at least in some conditions of current speed and seston concentrations. Reanalysis of these and Kirby Smith's (1972) data suggests that growth may not be an inverse, but a ramp, function of current speed with an upper current speed beyond which growth is limited due to an individual physiological or behavioural closing response by the scallop.

The growth results obtained here confirm that production of a blue mussel bed may be limited by the available seston supply. Our results also show the effect of current speed on seston supply and mussel growth, although the results obtained are strongly apparatus-specific, depending also on mussel sizes and mussel bed length used. We suggest that blue mussel, like scallop, production is a ramp function of current speed. Thus at lower current speeds growth is limited by the seston depletion effect, whilst at intermediate currents (defined by the hydrodynamic conditions in relation to seston supply and mussel bed size) speed has no effect on mussel production. We suggest that blue mussels may also respond to much higher current speeds by a physiological closing, although, because the maximum current speed tested in our experiments was only ~ 4 cm·sec⁻¹, we have no evidence on this point.

We have also established that density influences the rate of seston supply and can result in downstream depletion and reduced growth under some flow conditions.

Our results are consistent with available physiological and ecological data. Thus Hildreth (1976) showed that an individual mussel would not adjust its pumping rate over a wide range of ambient seawater flows. Consequently increased filtration, ingestion or assimilation rates as a function of current speed need not be considered as an explana-

tion for the increased production at higher current speeds that we observed. Wildish & Peer (1983) found that horse mussel production in the Bay of Fundy was related to current speed. Many reports on cultured blue mussel production suggest that production is greater where current speeds are higher. Thus Loo & Rosenberg (1983) found that individual mussel growth was slower in densely populated, higher current speed areas of western Sweden due to competition for available seston, although overall production in these areas was higher than in areas of lower current speed. Whether the results obtained by Walne (1972) can be explained by a seston depletion effect or apply specifically to recently settled spat is not yet clear.

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