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Giant scallop feeding and growth responses to flow

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Abstract: The relationship between ambient seawater flow velocity and growth of the giant scallop *Placopecten magellanicus* Gmelin is shown to be a reverse ramp function with growth inhibition at flow velocities of $>10\text{--}20\text{ cm}\cdot\text{s}^{-1}$. The mechanism of inhibition involves a reduction in ration as velocities around the scallop increase. In ambient flows which are sufficient to cause overloading of the scallop gill, the feeding/filtration rate is reduced by an unknown mechanism, possibly involving the mantle edge closing or a gill bypass mechanism operating. In ambient flows where the pressure at the exhalant opening exceeds the inhalant plus the pressure head created by the gill, as when the scallop is placed dorsal edge to the flow, the tendency for flow reversal is resisted by a similar mechanism involving a reduction in feeding/filtration rate.

Key words: Bay of Fundy; Filtration/feeding; Flow velocity; Growth rate; *Placopecten magellanicus*

INTRODUCTION

Field studies have demonstrated a wide range of effects of flow on animal populations or communities, e.g., in controlling the distribution and behavior of the lobster *Homarus gammarus* (Howard & Nunny, 1983); the occurrence of corals on seamount peaks of the deep sea where topography forces current acceleration (Genin *et al.*, 1986); where epiphytic growths on mussels cause drag and dislodgment at a threshold current speed (Witman & Suchanek, 1984); and see the review by Hiscock (1980). An important controlling effect of flow is on the food supply and hence growth or production of populations of suspension-feeding benthic animals inclusive of polychaetes (Fauchald & Jumars, 1979), bryozoans (Okamura, 1985), and brachiopods (Eshleman & Wilkens, 1979), as well as many species of bivalve mollusc.

It is the purpose here to focus on the trophic and growth responses of suspension-feeding bivalve molluscs. Early workers on bivalves recognized the importance of flow to species composition and production (Belding, 1910; Gutsell, 1931; Kerswill, 1949) but the mechanisms involved remained obscure. Experimental investigation of bivalves

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in pipe flow or flumes (Kirby-Smith, 1972; Wildish & Kristmanson, 1984, 1985) confirmed that population growth (but not necessarily individual growth) was a function of seston supply rates which were determined by flow velocity times the seston concentration (Wildish & Kristmanson, 1979). Field experiments (Frechette & Bourget, 1985) or field observations (Cooper & Marshall, 1963; Buss & Jackson, 1981; Broom, 1982; Officer *et al.*, 1982) also supported the so-called "seston depletion effect" hypothesis. Seston depletion occurs when the benthic boundary layer flow passes over a bivalve bed and seston is removed by active bivalve filtering/feeding or pseudofecal production at a rate much faster than supplied by advection or resuspension from the sediment.

The seston depletion effect is an ecological concept because it applies particularly where populations of suspension-feeders and their living space, in terms of hydrodynamic path length, are specified. Another way in which high flows may influence bivalve trophic ecology is by direct growth inhibition of an individual bivalve and this is a physiological concept. Kirby-Smith (1972) first reported physiological growth inhibition in the bay scallop *Argopecten irradians concentricus* and thought that increasing flow reduced the growth rate in a continuous fashion. By contrast, Walne (1972) claimed that the filtration, heart, and growth rates of five species of bivalve were all positively linked to the flow rates he provided. In order to resolve this apparent conflict, we undertook some experiments with the giant scallop *Placopecten magellanicus* Gmelin in controlled flow conditions to determine its effect on growth physiology and filtering/feeding responses.

METHODS

Adult giant scallops were obtained locally in Passamaquoddy Bay, Bay of Fundy, by scuba diving and held for <2 wk in flowing seawater tanks before use in growth or feeding rate experiments. Scallops used were all in their 5th yr, of 7.4–8.0 cm in shell height and 59.9–74.5 g total wet weight. Each animal was individually tagged with a small plastic tag glued to the left valve.

GROWTH EXPERIMENTS

The maximum distance from umbo to ventral edge of each animal was determined, with the aid of callipers, as the shell height in cm (L). Specific daily growth rate during each experiment was calculated by

$$\left[\frac{L_1 - L_0}{L_0 N} \right] \cdot 100,$$

where the subscripts 0 and 1 indicate initial and final shell heights and N is the duration of the experiment in days.

Total wet weight in g (W) was also determined for each animal after draining the pallial cavity and gently blotting the valves. Specific daily wet weight growth is

$$\left[\frac{W_1 - W_0}{W_0 N} \right] \cdot 100 .$$

Growth experiments were conducted in a multiple channel flume (Wildish & Kristmanson, unpubl.). The working section of the flume was 5 m long and divided by plywood walls into four equal channels of 15 cm width flaring to 20 cm at the downstream end. A small shed protected the flume from the weather and unfiltered seawater taken from near the bottom of the St. Andrews Biological Station tidepool was pumped to a calming section upstream of the working section. The seawater contained natural seston from the mouth of the St. Croix estuary in Passamaquoddy Bay, Bay of Fundy. After passage through the flume, the seawater was allowed to go to waste. Tagged scallops (16–24) were placed in each channel of the flume directly on the wooden floor, after the flow had been adjusted to that required. In Expt. 6, the scallops were glued to thin Plexiglas plates before placing in the flume so they had a particular orientation with respect to flow. In another experiment, medium fine sand or dead blue mussel shells were placed on the channel floors to influence roughness and hence height of the flume boundary layer. Growth experiments were of 25–33 days duration and were arranged during 1983–85 (Table I) so that seasonal growth patterns could be observed.

Seston uptake rates at controlled flow velocities were measured by observing the uptake rate of a unialgal culture in a Blažka respirometer (see Beamish, 1978). The respirometer is a closed system consisting of an inner and outer tube with flow induced in the inner tube and returning in the outer tube. Flow is induced by a propeller connected to a sealed shaft operated by a DC motor and adjusted by means of a variable rheostat controller. The total volume of seawater used in the respirometer was 41 l. An experiment was begun by adding a known volume of stock culture of *Chroomonas salina* (Wislouch) Butcher (Clone 36), a species known to be filtered and assimilated by the giant scallop (Shumway *et al.*, 1985), to filtered seawater so that 10 000 cells ml⁻¹ were present initially in the respirometer. Stock cultures of *C. salina* were batch cultured at laboratory temperatures according to the method of Guillard (1984). Three types of replicated experiment were run as follows:

- controls from which scallops were omitted;
- adult giant scallops (five) glued by their right valve to a Plexiglas plate were slid into the respirometer \approx 5 min before addition of the algal stock cultures. In this treatment, the pallial gape faced into the flow; that is at 90 °C with respect to the giant scallop's orientation;
- similar to the previous treatment except the position of the scallop was changed by gluing the right valve at different positions including one treatment at 225° where the exhalant opening was directed towards the oncoming flow.

TABLE I
Seawater temperature, seston concentration and initial scallop size ($\bar{x} \pm SE$) during growth experiments.

Expt.	Start	Duration (d)	Temperature ($^{\circ}C$)	Seston concentration		Initial scallop size	
				Chlorophyll <i>a</i> ($\mu g/l$)	ATP (ng/l)	Length (cm)	Wet weight (g)
1	23.09.1983	32	12.2 \pm 0.18	2.7 \pm 0.37	1.6 \pm 0.2	7.5 \pm 0.1	73.5 \pm 1.0
2	02.05.1985	32	6.3 \pm 0.16	2.5 \pm 0.41	3.5 \pm 0.4	7.8 \pm 0.1	65.7 \pm 1.6
3	11.07.1984	27	11.6 \pm 0.20	2.5 \pm 0.29	0.8 \pm 0.1	7.4 \pm 0.1	59.9 \pm 1.6
4	01.03.1985	30	1.8 \pm 0.11	0.3 \pm 0.01	1.2 \pm 0.2	7.8 \pm 0.1	68.4 \pm 2.3
5	29.10.1983	25	8.8 \pm 0.20	2.9 \pm 0.35	2.2 \pm 0.8	8.0 \pm 0.1	74.5 \pm 1.4
6	23.10.1984	33	9.7 \pm 0.20	1.3 \pm 0.95	—	8.0 \pm 0.06	76.5 \pm 1.7

TABLE II

The effects of scallop orientation to flow and inlet/outlet position on growth responses in the multiple channel flume, presented as the average wet weight increase (g) and shell height increment (mm) for the 33-days growth period. Average daily growth responses can be calculated by dividing the quoted results by 33. Density of 27 scallops $\cdot m^{-2}$ and velocity of each orientation of $\sim 5 cm \cdot s^{-1}$.

Orientation ($^{\circ}$)	Initial wet wt (g)	Inlet		Outlet		<i>n</i>
		Wet wt ($\bar{x} \pm SD$)	Shell height ($\bar{x} \pm SD$)	Wet wt ($\bar{x} \pm SD$)	Shell height ($\bar{x} \pm SD$)	
0	75.16	9.40 \pm 1.56	2.67 \pm 0.7012	8.72 \pm 2.02	2.66 \pm 0.73	11
90	79.09	8.99 \pm 1.60	2.99 \pm 0.7012	8.44 \pm 1.57	2.42 \pm 0.92	11
180	75.69	10.10 \pm 1.50	3.11 \pm 0.7512	10.20 \pm 1.40	2.97 \pm 1.01	11
270	76.03	9.74 \pm 3.04	3.04 \pm 0.7112	8.89 \pm 1.83	2.51 \pm 1.20	12

The filtration/feeding rate experiments lasted for 1–2 h with a water sample being taken at the beginning and end of each experimental run.

FLOW MEASUREMENTS

The free stream velocity flow at the midline above the flume boundary layer was measured in each channel of the multiple channel flume by observing the passage time of a nearly neutrally buoyant plastic cylinder over a 1 m distance. In operating the Blažka respirometer, the DC volts of the controller were calibrated to the inner tube flow as determined by a small propeller type current meter positioned where the scallops were placed. Flow in the respirometer was also measured at the outflow end by inserting a Nixon 403 stream flow probe (Nixon Instrumentation, U.K.) through a small hole in the cylinder. The 40 cm long probe with an 11.6-mm rotor was used to profile the flow of the experimental cylinder. Typical tube flow profiles were obtained with flows being greatest at the midpoint of the inner tube where the scallops were placed during experiments.

SESTON CONCENTRATION

Particulate chlorophyll *a* was determined from a 600-ml sample in the case of flume growth studies and a 150-ml sample in the case of feeding studies in the Blažka respirometer by the method of Strickland and Parsons (1968).

RESULTS

EFFECT OF FLUME FLOW ON GROWTH

Six separate growth experiments with giant scallops were completed (Table I). A maximum of four treatments was possible for each experiment with the four channels of the multiple channel flume. For each of these treatments, the seston concentration and quality supplied was the same. At a scallop density in each channel of ≤ 27 scallops \cdot m⁻² and a flow of ≈ 5 cm \cdot s⁻¹ (Table II, Expt. 6), ANOVA showed that there was no significant difference ($P > 0.05$) in growth between inlet and outlet ends of the flume. Because the scallops were glued in place, it suggests that at this density, or lower, no seston depletion effects were likely. At this optimum current speed, comparisons of growth for different orientations show that there was no significant difference ($P > 0.05$) due to scallop orientation.

Considerable growth variation was observed between each run of the five other experiments (Fig. 1) due to seasonal effects. For both shell height and wet weight growth, velocities of 2–10 cm \cdot s⁻¹ were maximal in all experiments, but > 10 cm \cdot s⁻¹ was inhibitory. Free hand lines drawn to connect the treatments within each experiment suggest a reverse ramp function between flow velocity and growth. Thus, extrapolation of the line to 0 wet weight growth suggests that this occurs at

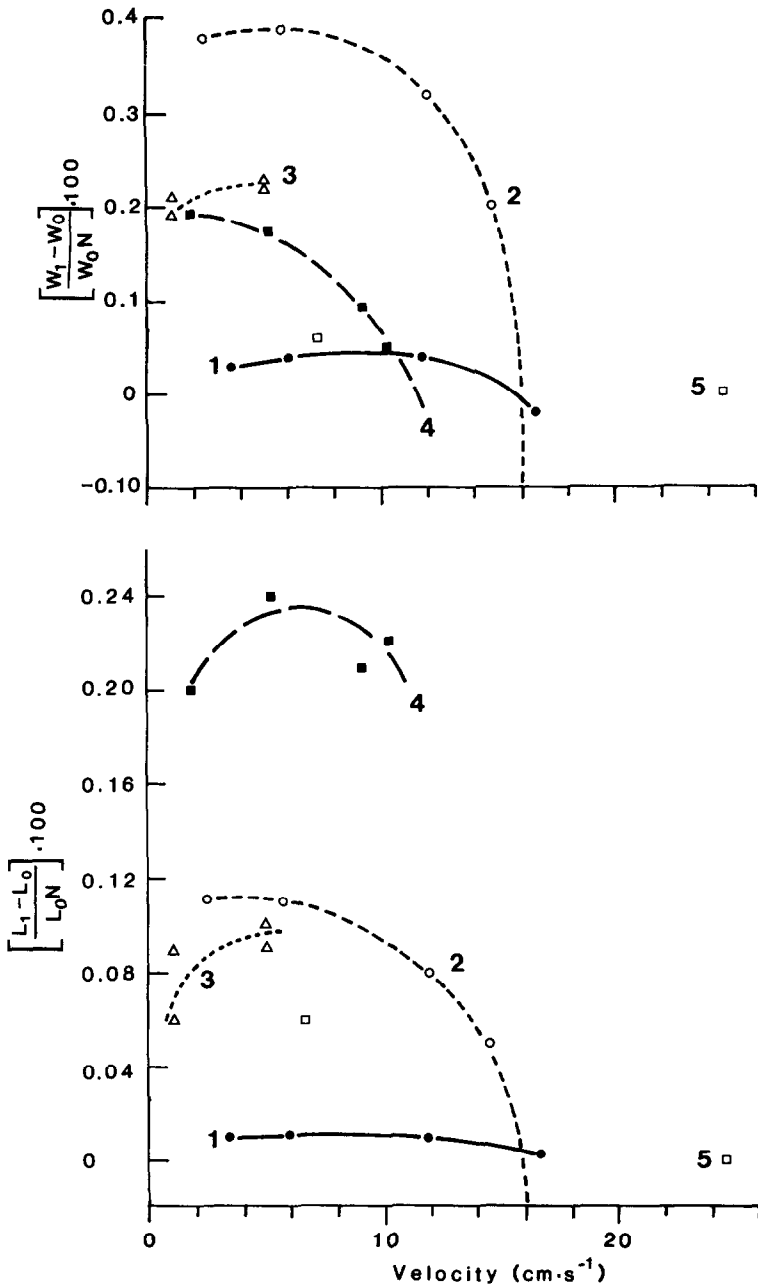


Fig. 1. Specific daily growth rates of adult giant scallops in unfiltered seawater from Passamaquoddy Bay, Bay of Fundy, in flume flows. Lines connecting the points are drawn freehand and the number on each curve indicates the seasonal timing as given in Table I.

$\approx 12 \text{ cm} \cdot \text{s}^{-1}$ in Expt. 4 and at $\approx 16 \text{ cm} \cdot \text{s}^{-1}$ in Expts. 1 and 2. Similar extrapolation for shell height growth suggests that in Expt. 1 the 0 growth occurs at $18\text{--}20 \text{ cm} \cdot \text{s}^{-1}$ and in Expt. 2 at $16 \text{ cm} \cdot \text{s}^{-1}$.

SEASONAL EFFECTS ON FLUME GROWTH

Maximal growths at velocities of $2\text{--}10 \text{ cm} \cdot \text{s}^{-1}$ for Expts. 1–5 in Table I, when flow was not limiting, were used to plot the specific seasonal growth patterns. The results show (Fig. 2) a spring peak in wet weight and fall peak in shell height growth which are unrelated to each other. During the winter months from December to March/April, there was little positive growth either of the shell or wet biomass.

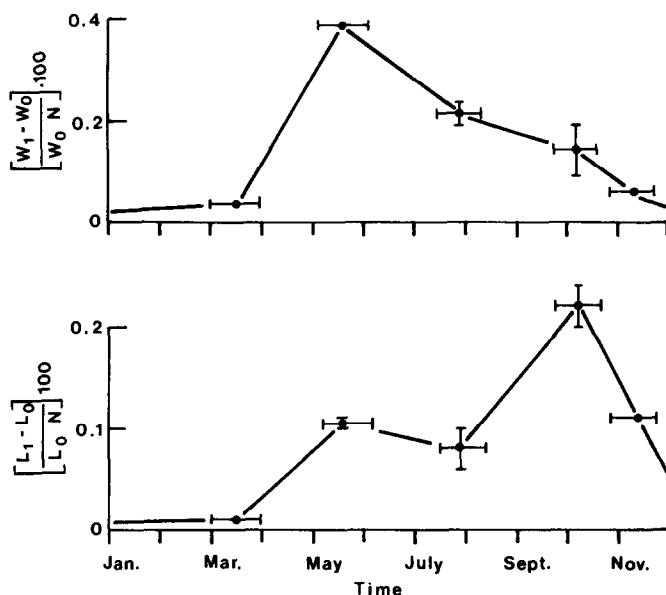


Fig. 2. Specific daily growth rates of adult giant scallops. Same data as Fig. 1 except only nonlimited flow growth at $2\text{--}10 \text{ cm} \cdot \text{s}^{-1}$ is included as a function of season. Points are mean growth, horizontal bars indicate the growth period and vertical bars the growth range.

FEEDING RATE EXPERIMENTS

Numerous control experiments in which scallops were omitted showed that there was no significant difference between the initial and final concentration of chlorophyll *a* in the respirometer. This suggested there was no significant mortality of *C. salina* caused by the respirometer propeller or that significant cell division took place during the experimental period.

Results of experiments in which giant scallops were glued so that the pallial gape and ventral edge faced directly into the respirometer flow, that is at 90° with respect to the

scallop's own orientation, are shown in Fig. 3. This is the usual position that *P. magellanicus* (Caddy, 1968) adopts with respect to currents in its natural environment. Two patterns of feeding response by the giant scallop are evident from Fig. 3. At flows of $> 10\text{--}15\text{ cm}\cdot\text{s}^{-1}$, the scallop either slows or stops feeding (slashed line, Fig. 3),

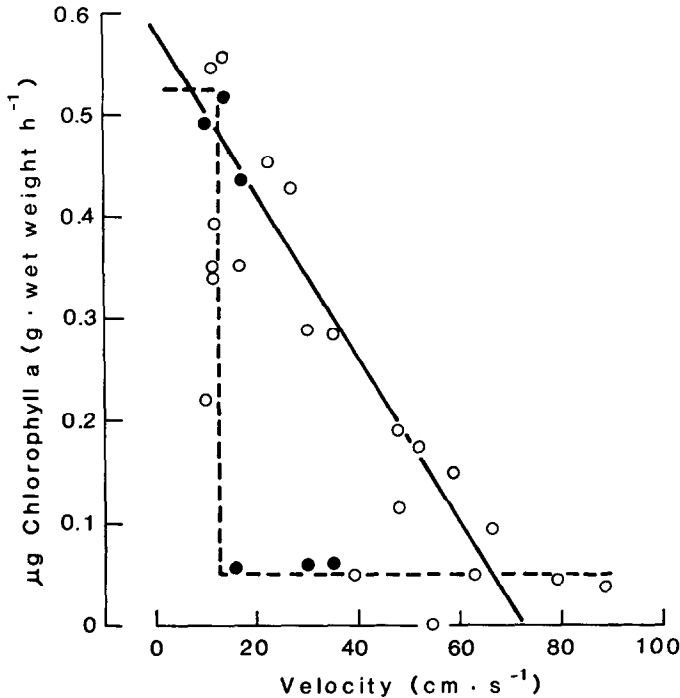


Fig. 3. Filtration rates of adult giant scallops as a function of ambient flow velocity. The initial cell concentration for each experiment shown is $10000\text{ }C. salina\text{ cells}\cdot\text{ml}^{-1}$. ○ culture < 8 days old, ● > 8 days old. Temperature range during experiments $3\text{--}8^\circ\text{C}$.

or maintains filtration with increasing velocity but at a decreasing rate (solid line, Fig. 3). For the latter case, there was an inverse relationship between filtration (Y) and velocity (X): $Y = 0.59 - 0.01X$; $r^2 = 0.90$, $n = 11$ (dashed-line points in Fig. 3 omitted in the regression analysis), so that filtration had declined to background levels at $\approx 66\text{ cm}\cdot\text{s}^{-1}$ and completely stopped at $72.6\text{ cm}\cdot\text{s}^{-1}$. It is possible that age of the cultured *Chroomonas* cells influenced stoppage of feeding by the giant scallop. Cells older than 8 days are in the early senescent stage of growth and thus may be less attractive as food, although in at least two of the experiments at $\approx 15\text{ cm}\cdot\text{s}^{-1}$ scallop feeding remained high with early senescent cells as food.

The effect of repositioning the scallop with respect to the flow was examined in an experiment with the scallop at four different positions during the feeding rate observations (Table III) and at three different velocities. Giant scallops with their exhalant opening directly into the flow at 225° showed a significant reduction in filtration rate

at 18 and 31 $\text{cm} \cdot \text{s}^{-1}$ (Duncan's multiple range test at $P < 0.05$). A similar test showed that at 31 $\text{cm} \cdot \text{s}^{-1}$ filtration/feeding for all orientations was significantly less than at lower velocities.

TABLE III

Mean seston uptake rates as μg chlorophyll *a* $\cdot \text{g}$ wet scallop $\cdot \text{h}^{-1}$ in two replicated Blažka respirometer experiments. Initial food cell density is 10000 *C. salina* cells $\cdot \text{ml}^{-1}$, in log phase. Temperature = 9.5 ± 0.2 °C (\pm SE).

Scallop orientation with respect to the flow	Velocity ($\text{cm} \cdot \text{s}^{-1}$)		
	10	18	31
45	0.7725	0.7769	0.2358
135	0.9554	0.7603	0.4906
225	0.5367	0.2717	0.0695
315	0.7663	1.4428	0.5339

Assuming 100% filtering efficiency by the scallop, the seston uptake rate data at optimum ambient flows can be converted to pumping rates using the formula of Coughlan (1969) for enclosed systems. The maximum pumping rate calculated by this method was $\approx 10 \text{ l} \cdot \text{h}^{-1}$ for the adult-sized scallops used in this study.

DISCUSSION

Natural growth of adult giant scallops in the Bay of Fundy is shown by our data to be seasonal in nature. An unrelated pattern of tissue and shell growth is present similar to that recognized in the blue mussel by Kautsky (1982) and Hillbish (1986). The seasonal pattern of growth reported here also fits the spawning and reproductive cycle described for the giant scallop in the Bay of Fundy by Bourne (1964) and Beninger (1987). Thus, the gonosomatic index indicates reproductive growth from May to September which coincides with a strong pulse of wet weight growth and little shell growth. The major spawning is from August to September, although spawning may occur throughout the winter. Immediately following the main spawning peak, there is a major spurt of shell growth and correspondingly little wet weight growth in October. Within the Bay of Fundy, the growth of the giant scallop occurs in the period from May to November with peaks in May and October. We suggest that it is the availability of suitable phytoplankton species that is the driving force for the seasonal growth patterns observed. Shumway *et al.* (1985) have shown that the giant scallop selects and utilizes only some of the species it filters. We do not yet know which are the natural algal species preferred by the giant scallop in the Bay of Fundy.

The results presented here also show that free stream flow velocities of $> 10\text{--}20 \text{ cm} \cdot \text{s}^{-1}$ are inhibitory to the adult growth of giant scallops. These results are

in substantial agreement with those obtained by Kirby-Smith (1972) for the bay scallop, although we believe that his data can be reinterpreted as a reverse ramp function of flow (Fig. 4), with inhibitory flows of $> 5 \text{ cm} \cdot \text{s}^{-1}$. Differences in the critical flows above

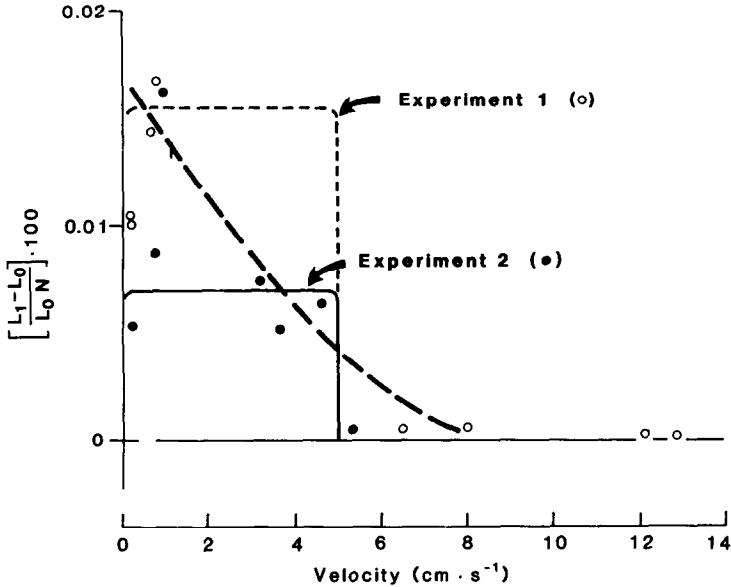


Fig. 4. Specific daily growth rates of the shell height in the bay scallop, *A. concentricus* (Say) in Expt. 1 (○ at 25–28 °C) and Expt. 2 (● at 9–19 °C) of Kirby-Smith (1972). Heavy dashed line is the analysis suggested by Kirby-Smith (1972). Other lines represent the reverse ramp function relationship suggested by the present authors.

which growth is affected can be expected in different bivalve species, although the volumetric flow estimates made by Kirby-Smith, crude flow measurements used in our work, and differences in pipe vs. flume boundary layer flow (Wildish & Kristmanson, unpubl.) should be accounted for in assessing these differences. Both of the above results are in disagreement with the growth data of Walne (1972) obtained with *Mytilus edulis*, *Ostrea edulis* and *Crassostrea gigas*. Walne used a single animal in a polystyrene box of 0.9- or 2.4-l capacity and tested flow rates of 68–74 and 183 ml · min⁻¹. The mixing characteristics within the boxes were not discussed by Walne (1972) although we suspect that mixing was incomplete and that some seawater was not available to the bivalves before overflowing to waste. We believe that both flows did not provide sufficient unfiltered seawater for the bivalves to sustain maximum growth and that the hydrodynamic conditions were unlike those of a natural benthic boundary layer. Differences in mean filtration rates reported by Walne (1972) during his growth experiments were shown by Hildreth & Crisp (1976) to be erroneous due to the use of an inappropriate formula. Average pumping rates of the 8.9–9.1 g live weight blue mussels used by Walne should be of the order of 0.21 × g live weight (Hildreth, 1976), that is

1.87–1.91 l · h⁻¹ per mussel. This compares with flows in the experiment of 4.08–4.44 or 10.98 l · h⁻¹, which would be sufficient provided there was adequate mixing within the box. Growth differences at the two flows found by Walne we suggest to be due to differences in localized seston depletion around the bivalve: less at the higher flow due to the better mixing at this treatment. We conclude that for scallops, at least, there is a limiting flow above which growth inhibition is likely.

We also considered the question of the mechanism involved in growth inhibition of the giant scallop at flows of > 10–20 cm · s⁻¹. We hypothesize that it is a direct physical result of ambient seawater pressure differences between the inhalant and exhalant openings which cause the feeding rate to slow or stop. Where the ambient seawater pressure at the inhalant exceeds the ambient pressure at the exhalant by an amount greater than the pressure head developed by the scallop's own ciliary pump, it responds by reducing or stopping filtering. In other short siphon bivalves, Foster-Smith (1976a) reported the ciliary pump pressure generated to be of the order of 0.1–2 mm of water. Reduced filtration may be achieved by periodic closure of the inhalant aperture, restriction to a small size and rapidly repeated closures of the exhalant aperture (Foster-Smith, 1976b), or by shunting inhalant seawater between the inner demibranchs as found in blue mussels (Famme & Kofoed, 1983; Famme *et al.*, 1986), thereby bypassing filtration. Either of these mechanisms would reduce the pressure differential and thus avoid overloading the capacity of the filter to capture seston and each would result in the concomitant reduction of the filtering/feeding rate. To test the pressure differential hypothesis, we measured feeding rate as a function of flow in a Blažka respirometer where flow could be controlled. The results show that at > 15 cm · s⁻¹ feeding is either stopped completely or continues but at a reduced rate. Our results do not allow us to decide how the scallop does this and further experimental observations are needed for this purpose. Reduction or stoppage of feeding at > 15 cm · s⁻¹ by the giant scallop is consistent with the growth observations made in separate experiments. Under the particular conditions of our feeding experiments, the filtering/feeding rate is reduced to 50% of the optimum at a flow of ≈ 40 cm · s⁻¹, yet the growth data show that there is no growth with natural food resources at > 18–20 cm · s⁻¹. This discrepancy may be due to one or more of the following:

- the short-term nature of our feeding experiments overestimates the feeding rate if averaged over the duration of a growth experiment;
- when feeding is 50% efficient, growth is in negative balance with energetic requirements being below the ration maintenance requirements of the scallop;
- the artificially high concentration of cells of an alga species known to be favored by the giant scallop may result in continued feeding at the physically caused lower filtering/feeding rate. The rate at this flow may still be enough to keep growth in positive balance with overall requirements and highlights the differences in seston quality and concentration between our feeding and growth experiments.

Current thinking is that bivalve feeding rates are responsive to changes in seston quantity, with ingestion reaching an optimum level at a low unicellular algal concen-

tration (Winter, 1978), but not responsive to changes in flow (Hildreth, 1976). The latter conclusion was based on Expt. 2 in boxes in which flows to the animal were quite unlike those occurring in a natural benthic boundary layer. Bivalves probably also respond to seston quality since it has been shown by Bayne & Newell (1983) in blue mussels that growth efficiency steadily increases when the ration is natural seston but, after a quick rise, is followed by a sharp decline when algal monocultures are presented as food.

Placing scallops with the exhalant opening directly into the ambient flow produced the expected response of reduced filtering and feeding rates at lower flows than for other orientations. This is because there is a tendency for flow reversal when the ambient pressure at the exhalant opening exceeds the combined ambient inhalant and ciliary pump pressure, and the scallop responds by closing its mantle openings. These experiments suggest that the scallop is an "active suspension feeder" in the sense of LaBarbera (1984); they support the pressure difference hypothesis and suggest that the observed growth responses to increasing flow can be explained simply by ration reductions caused by variations in ambient seawater flows.

One implication of our results for the natural trophic ecology of the giant scallop is that there may be a forced periodicity of feeding including times when the scallop is prevented from feeding by high ambient flows. In view of our suggestion that there may be an interactive effect between flow and seston quality and concentration, we cannot exactly specify limiting flows; in natural seawater conditions of the Bay of Fundy it appears to be $\approx 10\text{--}20 \text{ cm} \cdot \text{s}^{-1}$ for adult scallops, although positive growth is predicted to occur at up to $60 \text{ cm} \cdot \text{s}^{-1}$ if the seston quality and concentration is sufficiently high. The relatively low inhibitory velocities determined for natural growth of Bay of Fundy scallops seems anomalous because of the generally high velocities within the Bay. Thus, mean depth-integrated velocities of $> 100 \text{ cm} \cdot \text{s}^{-1}$ are present over the Digby scallop beds in the Bay of Fundy (Wildish & Peer, 1983). Obviously, this requires further investigation, although we point out that velocity within the benthic boundary layer will be lower than the depth-integrated velocity and that giant scallops have been reported (Caddy, 1968) to excavate pits within the sediment and hence avoid high flows.

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