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Effects of flow velocity, food concentration and particle flux on growth rates of juvenile bay scallops *Argopecten irradians*

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Abstract: Feeding rates, and hence growth, of suspension-feeding organisms are determined by many interacting factors including efficiency of particle capture, food-particle concentration, and ambient flow regimes. Studies in a recirculating seawater flume were conducted to examine the growth rates of juvenile bay scallops *Argopecten irradians irradians* (L.) (3–10 mm in shell height) in four flow velocities (0, 1, 6, and 15 $cm \cdot s^{-1}$) over a range of food concentrations (0–75 000 cells $\cdot ml^{-1}$) in a four-by-four factorial design. Particle flux (algal cells $\cdot cm^{-2} \cdot s^{-1}$) encountered by the scallops is the product of food concentration (cells $\cdot ml^{-1}$) and flow velocity ($cm \cdot s^{-1}$). The experimental levels of food concentration and flow velocity were chosen to produce a wide range of fluxes. Several treatments with equal flux derived from different flows and food concentrations were used to decouple the effects of each factor. Within a given flux of particles, growth rates were not significantly different between flows or particle concentrations. Growth was only weakly correlated to flux of particles over the range of fluxes tested. The effects of algal concentration were more pronounced than the effects of flow velocity suggesting that differences in growth were a result of differences in algal concentrations. Additional experiments were run to determine the clearance rates of scallops at different food concentrations. These experiments support the findings of the flume experiments; clearance rates were seen to decrease with increasing food concentrations. Flux of food particles is not a predictor of growth, rather it is the combination of the effects due to food concentration and flow velocity which determine the response of the individual juvenile bay scallop.

Key words: *Argopecten*; Bay scallop; Flow; Food concentration; Growth

Introduction

Sessile suspension-feeders are dependent on the physical transport of particles to within range of their feeding apparatus. Ingestion of food particles is then the result of either active pumping by the animal or passive passage of water over sieving structures. Therefore, suspension-feeders, both active and passive, are dependent on water movement to bring food within reach. Water velocity and food concentrations interact to determine the supply of food, rate and efficiency of particle capture, and in some cases, the feeding behavior of suspension-feeders.

Increased flow velocity (and increased food fluxes) increase rates of particle capture

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in passive suspension-feeders (Leversee, 1976; McFadden, 1986). In active suspension-feeders, flow velocity may decrease particle-capture efficiencies (Kirby-Smith, 1972; Jørgensen et al., 1986) despite increased food fluxes. Bryozoans and spionid polychaetes have been shown to change their feeding behavior in response to food fluxes; bryozoans change from filter-feeding to tentacular capture of particles (potentially, a more energy efficient feeding mode at high food availability) with an increase in flow velocity (Okamura, 1987) while spionid polychaetes change from a deposit-feeding to a filter-feeding mode with increases in food fluxes (Taghon et al., 1980). Growth rates within populations of bivalves have been positively correlated to food fluxes in field situations (Wildish & Kristmanson, 1985; Eckman, 1987) although other authors have maintained that flow velocities are a major determinant of growth rates (Kirby-Smith, 1972); high flow velocities inhibiting a bivalve's ability to remove particles from the water (Kirby-Smith, 1972; Jørgensen et al., 1986; Wildish et al., 1987). For some suspension-feeding bivalves, the feeding processes may be facilitated by the local flow regime. By orienting the inhalant opening into the flow, suspension-feeding bivalves can enhance the pressure gradient over the gill area, forcing water through the mantle cavity (Jørgensen et al., 1986). This may represent a semipassive filtration mechanism, especially in those animals which are known to have a preferred orientation (i.e., sea scallops; Wildish et al., 1987). As flows increase, however, volumes of water forced through the mantle by the stronger pressure gradient may exceed the filtration capacity of the gills. At this point, either water is shunted around the gill, pumping rates decrease, the mantle margins may be constricted, or any combination of these responses takes place (Wildish et al., 1987).

Increases in food concentrations (also affecting food fluxes) produce increases in growth only up to a maximal food concentration beyond which growth rates decline (Winter, 1978). At very low food concentrations, bivalves may pump at a reduced rate to meet respiratory demands but not to feed. At very high particle concentrations, ingestion becomes limited by the capacity of gill ctenidia to remove particles from the water, ingestion rates no longer increase with increasing food concentration (Winter, 1978), and growth rates are independent of food concentration (Kirby-Smith & Barber, 1974). Further increases in food-particle concentration may result in decreased pumping rates or increased filtration efficiency (Winter, 1978). Most studies of food-concentration effects have been performed in static water systems, and, therefore, do not take into account interactions between food concentrations and flow velocities (see Wildish et al., 1987, for exception). In general, the effects of food concentration, water velocity, and their product (food × flux) on bivalve growth rates have not been decoupled.

The early life history of the bay scallop *Argopecten irradians* (L.) makes this species particularly vulnerable to effects of flow and food concentration. Bay scallops have pelagic larvae which remain in the water column 2–3 wk before settling into grass beds (Castagna & Duggan, 1971). The postlarvae often attach to blades of seagrass where they metamorphose into juvenile scallops (Belding, 1910; Gutsell, 1930). Byssate juvenile scallops in the seagrass canopy (elevated off the bottom) are exposed to higher

current velocities and more turbulence than adults in the lower waters of the bed. The juveniles remain bysally attached to grass blades until they reach 1–2 cm in shell height at which point they detach and fall to the bottom (Belding, 1910; Gutsell, 1930; Castagna, 1975). Although flow velocities near the sediment surface may be decreased by the presence of seagrasses, velocities in the canopy, where the juvenile scallops are attached, may be substantially higher (Fonseca et al., 1982). Growth rates of juvenile bay scallops are relatively rapid, e.g., up to 10 mm · month^{-1} (Tettlebach, 1986), 7 mm · month^{-1} (Castagna & Duggan, 1971) and hence growth experiments can be performed with measurable changes in size of animals over short periods (7–10 days).

Decreased flow velocities near the bottom within seagrass beds may increase particle-deposition rates, enhancing fluxes of food particles to the substratum. High growth rates of bivalves in eelgrass beds have been attributed to increases in flow velocity (Marshall, 1960; Eckman, 1987) and to increases in food concentration (Peterson et al., 1984) both of which produce higher food fluxes. The effects of food supply rate, and its individual components, water velocity and particle concentration, on the growth rates of juvenile scallops in these habitats are unknown.

The objectives of the present study were to determine the relative importance of flow velocity, food concentration and particle flux on growth rates of individual *A. irradians*. The effects of flow velocity and food concentration were investigated simultaneously by exposing young scallops to a combination of different flow velocities and food concentrations in a factorial design.

Materials and Methods

GROWTH EXPERIMENTS

To assess the impact of fluid-flow velocities, food concentration and flux of food particles on the growth of juvenile *A. irradians*, long-term growth experiments were run in a recirculating seawater flume (see Cahalan, 1988). The flume consisted of three channels (30 cm wide by 200 cm long, maintained at 11 cm water depth) gravity fed from a single reservoir. Each channel ran at a different flow velocity, controlled by the size of the opening feeding into the channel. Rectifier grids (3 mm honeycomb material, 5 cm thick) were fitted into the head of each channel to breakdown large-scale turbulent eddies. Exit weirs were placed in the tail end of the two slower flow channels to maintain the 11 cm water depth used in all experiments and partially control the flow velocities. Flow in the channels during all experiments was smooth to transitional turbulent (Reynolds numbers of 2×10^3 to 1×10^5; Tritton, 1977).

Flow was measured using a heated bead thermistor flowmeter modified from a design from Vogel (1981) and LaBarbera & Vogel (1976). Thermistor output was recorded on a strip chart recorder with recordings converted to units of flow velocity based on a calibration curve. The flowmeter was calibrated against calculated centerline velocities in a 1-cm i.d. pipe (Vogel, 1981). Measured flow velocities at the working section

(130 cm downstream) revealed a vertical velocity gradient which extended 0.5–1.5 cm above the bed. Above this depth, flow velocity did not change measurably. Free-stream velocities were determined to be 1.2, 6.5 and 15 cm · s^{-1}.

Juvenile bay scallops were raised in the laboratory or were obtained from the Shinnecock Indian Tribal Oyster Hatchery, Southhampton, Long Island, New York, or The Clam Farm, Fisher's Island, New York. Small (3–10 mm) scallops were attached onto rigid pieces of balsa wood (1 × 6 cm × 1 mm wide) using small quantities of epoxy glue. The scallops were all located above regions of the boundary layer characterized by a steep velocity gradient at two heights, 3 and 5 cm above the floor of the flume (Fig. 1). Scallops were attached to the leading edge of the balsa wood

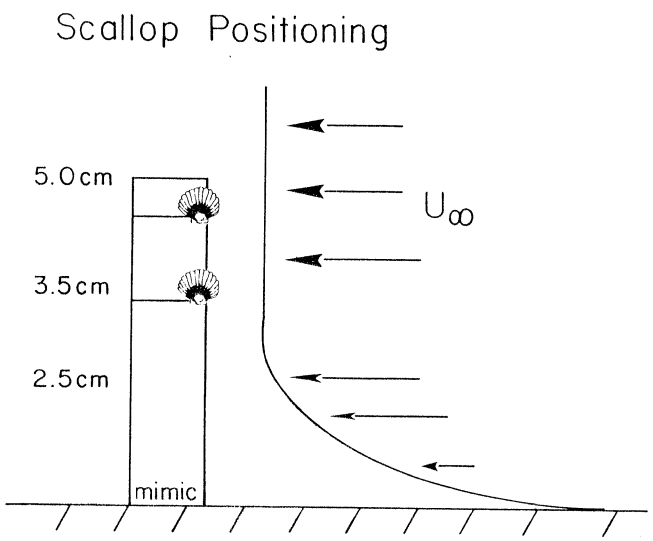


Fig. 1. Position of bay scallops on leading edge of balsa wood supports (seagrass mimics), above boundary layer. All scallops were oriented with anterior margins into flow. Flow direction is from right to left.

(Fig. 1) with their anterior margins oriented into the flow and their hinge facing toward the flume floor since this was observed to be their preferred orientation (pers. obs.; see also Wildish et al., 1987).

For each experimental run, 16 scallops were placed into each flume channel, four scallops (two at 3 cm and two at 5 cm off the flume floor) attached to each of four pieces of balsa wood. These were then mounted onto the bottom of seawater-filled flume channels (oriented parallel to flow) using stainless steel pins which held the wood pieces steady at all flow velocities. Flow rates were slowly increased over a 2-h period until treatment levels (see below) were obtained. Phytoplankton (*Isochrysis galbana*, Tahitian strain) harvested from exponential-phase laboratory cultures was then added to the tail tank and allowed to mix, bringing the flume to experimental cell concentrations. All experiments were performed at 18–23 °C and under a photoperiod 10 light:14 dark.

A series of 1–2-wk experiments was performed using four flow velocities and four food concentrations in a full factorial design (Fig. 2). This allowed comparisons to be made among flow velocities, food concentration, and the interaction of the two (flux).

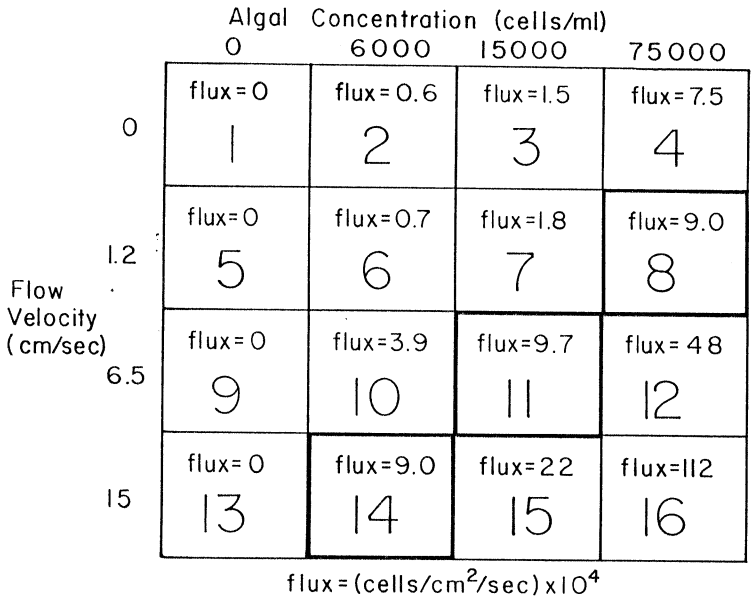


Fig. 2. Matrix of 16 experimental treatments. Treatment numbers and flux values are presented in each cell of experimental design. Treatment combinations producing statistically equivalent fluxes for analysis of effects of flux are outlined in bold.

Food concentrations of 0, 6000, 15 000, and 75 000 cells · ml^{-1} were used together with flow velocities of 1.2 ($Re = 1.2 \times 10^3$), 6.5 ($Re = 6.5 \times 10^3$), and 15 ($Re = 1.5 \times 10^4$) cm · s^{-1}, as well as a static water (0 cm · s^{-1}) control, to generate a wide range of fluxes (0–112 cells · $cm^{-2} \cdot s^{-1}$). The no-flow treatment was located in a glass finger-bowl (50 cm diameter, 15 cm tall) on top of the tail tank. Water from the head tank (feeding the other flume channels) was siphoned slowly into this bowl (overflowing into the tail tank) to provide an exchange of water without the creation of a flow. The scallops in this treatment were mounted and spaced identically to those in the flume channels. In addition, these scallops were exposed to the same light regime, flume vibrations, and temperature as those scallops in the flume. Although the spatial restrictions of the laboratory precluded the use of another channel to house this treatment, the spatial scale of the control container allows the inclusion of this treatment in the analysis. The 15 000 cells · ml^{-1} treatment was replicated in two separate experiments. A single-flux treatment of $9.0–9.7 \times 10^4$ cells · $cm^{-2} \cdot s^{-1}$ (statistically similar) was produced from three different combinations of flow rate and cell concentrations (Fig. 2). This flux treatment permitted analysis of growth rates of scallops exposed to a similar flux of food particles but differing flow velocities and food concentrations.

Drained wet weights of the animals were determined before and after each experiment by gently draining the mantle cavity of the scallop before weighing it. Drained wet weights were measured (to the nearest 0.01 mg) on a Cahn Model 26 electrobalance or a Mettler balance.

Growth rate was computed for each scallop according to Ricker (1975):

$$\text{growth rate} = \frac{\text{final weight} - \text{initial weight}}{\text{initial weight}} \times \frac{24}{\text{h}} \times 100.$$

Shell dimensions (height and width) were measured to the nearest 0.1 mm using vernier calipers, however, changes in shell growth rate lag behind changes in rate of weight gain (Kirby-Smith, 1972; Lucas & Benninger, 1985). Because change in tissue weight is a more sensitive measure of the individual's growth than change in shell dimensions, only whole wet weights were used in the calculation of growth rates.

CELL-CONCENTRATION MEASUREMENTS

The flume was filled with 1-μm-filtered seawater from Flax Pond, Stony Brook, New York. The phytoplankton used to stock the flume was grown in the laboratory using standard culture techniques (Guillard, 1975). Cell counts of stock cultures and flume dilutions were obtained using a Coulter counter (Model TA II using a 100-μm aperture tube and a 1 : 5 sample dilution). Background particle counts from filtered seawater were subtracted from flume-particle counts to account for the presence of some small particles (<5 μm) in the filtered seawater.

Water samples were taken immediately upstream (within 5 mm) and at the same depth as the individual scallops using a Pasteur pipette. Water samples were counted within 30 min and the cell concentration of the flume was then adjusted to the desired experimental level. Samples were taken every 4–10 h throughout the 1–2-wk experimental periods. Phytoplankton concentrations in the flume were maintained to within 10% of their experimental values. Time-averaged cell counts, obtained from the cell concentration and the number of hours the flume spent at that concentration, were used in the calculation of final food concentration in each experiment.

CLEARANCE EXPERIMENTS

Experiments were performed to determine effects of phytoplankton cell concentrations on clearance rate of scallops. Individual juvenile scallops (3–6 mm shell height, 10–35 mg whole wet weight) were placed in separate 250-ml beakers with 150 ml 1-μm-filtered seawater and a predetermined amount of *I. galbana*. The scallops were allowed to acclimate for 1-2 h. The water was then slowly siphoned out of each beaker and replaced with fresh seawater of the same concentration of *I. galbana*. This water was then sampled and initial algal cell counts determined. Beakers were aerated very gently from a common air source and experiments run at 20–23 °C, the same tempera-

ture at which all the juvenile scallops were maintained in the laboratory. Scallops were left in the dark to feed for 2–8 h. Algal counts from terminal samples were obtained using Coulter counter techniques described earlier. The time period of the experiment was chosen to insure that final algal concentrations were $\leqslant 30\%$ lower than the initial concentrations. This provided a measurable change in concentration and prevented changes in ingestion rate due to decreased cell counts.

Clearance rates were calculated as the volume of water cleared of algal cells · unit time^{-1} · wet weight scallop^{-1} using the formula:

$$CR = \frac{V[\ln(C_i) - \ln(C_f)]}{W},$$

where CR is the clearance rate, V is the volume of water in the experimental chamber, C_i and C_f are the initial and final concentrations of algae and W is the weight of the scallop (Coughlan, 1969).

Controls for these experiments consisted of beakers containing seawater at the proper algal concentration but without a scallop. Algal reproduction measured in these controls was subtracted from changes in cell concentration measured in experimental beakers.

Results

GROWTH EXPERIMENTS

Growth rates varied from -0.50% ($\pm 0.22\%$ SE, $n = 12$) weight · day^{-1} in the 15-cm · s^{-1} and no-food treatment to 19.45% ($\pm 1.65\%$ SE, $n = 14$) weight · day^{-1} in the 6.5-cm · s^{-1} and 6000-cells · ml^{-1} treatment. There were no significant differences in growth within the common flux group ($9.0–9.7 \times 10^4$ cells · cm^{-2} · s^{-1}) (Kruskal–Wallis ranked test, $\chi^2 = 2.29$, $P = 0.32$, df = 2; Sokal & Rohlf, 1981). A weak but significant correlation was seen between growth rates and flux values (Kendall's $t = 0.118$, $P = 0.05$, $n = 242$). Growth rates based on changes in shell height (0.00–0.24 mm · day^{-1}) were consistent with growth rates calculated in other experimental systems (0.01–0.46 mm · day^{-1}; Kirby-Smith & Barber, 1974).

Nonparametric statistical tests were used in all analyses because treatment variances were heteroscedastic and could not be transformed. Since replication should be used at the level where the greatest variation is expected (in this case individual scallops) (Green, 1979), individual scallops were designated as replicates. Hurlbert (1984) has defined psuedoreplication in field experiments as "the testing of treatment effects with an error term inappropriate to the hypothesis being considered"; using this definition this statistical design is not psueodoreplicated. In field experiments, such as those discussed by Hurlbert, single experimental units (such as cages) are exposed to a variety of uncontrolled factors which is not the case in laboratory studies. The variation here clearly lies at the level of individual scallops (experimental units) not at the level of the

experiment. The assumption that scallop-growth rates vary more between individual scallops than between experimental methods was tested by ANOVA using growth rates of scallops in the two replicated 15 000-cells · ml^{-1} experiments. The error mean square (from variance among scallops) was 55.97 (df = 85) while the mean square due to main effects (between experiments) was 1.79 (df = 1). There was no significant difference between experiments ($P > 0.86$, df = 86, $F = 0.03$) using ANOVA. This data failed a Cochran's test for homogeneity of variance ($C = 0.193$, $P > 0.05$), and, therefore, an approximate t test assuming heterogeneity of variance was performed and growth rates between experiments were not significantly different ($P > 0.05$). To test the independence of replicates, a runs test for dichotomized data (testing the independence of observations: Sokal & Rohlf, 1981) also was performed. The distribution of scallop growth rates within a flume channel (ordered from right to left) was compared to a binomial distribution. Growth rates of scallops were distributed randomly ($P < 0.05$; except in one channel where $P = 0.05$), and so independence of observations was assumed.

Fig. 3a shows the effect of flow velocity on growth coefficients for each food concentration. Growth was lower in the no-food treatment than in the high-food. There was no significant effect of flow velocity at the low ($\chi^2 = 25.47$, $P < 0.001$, df = 3) and high ($\chi^2 = 18.13$, $P < 0.001$, df = 3) food concentrations while at the two intermediate

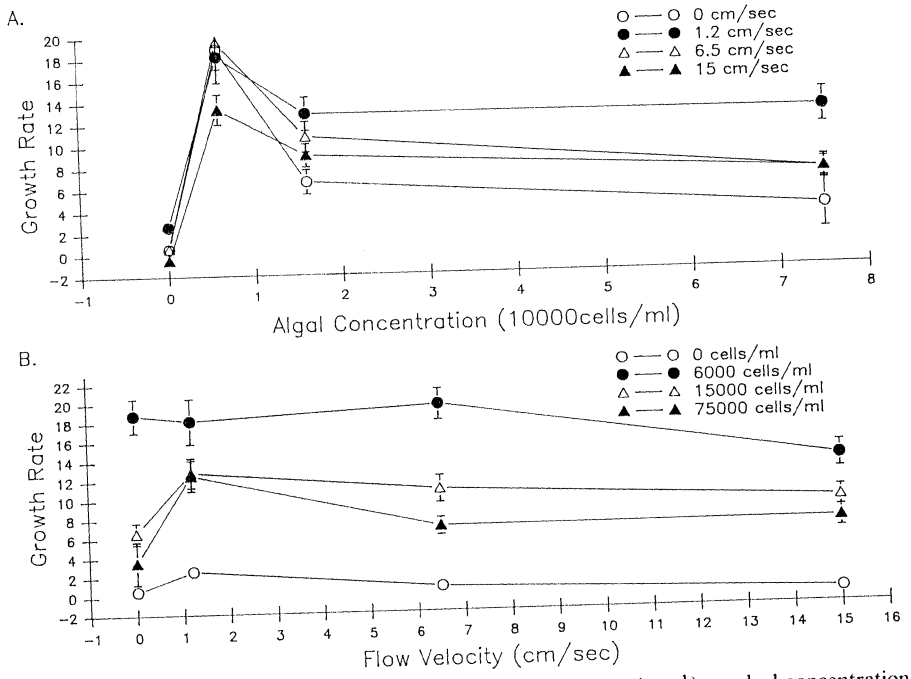


Fig. 3. Scallop growth rates (% relative increase in whole wet weight · day^{-1}) vs. algal concentration (a) and flow velocity (b). Lines in plot (a) represent different flow velocities; lines in plot (b) represent different algal concentrations. Error bars are SE of $\bar{x}$.

concentrations, flow velocity had no effect on growth (6000 cells · ml^{-1}: $\chi^2 = 7.68$, $P = 0.053$, df = 3; 15000 cells · ml^{-1}: $\chi^2 = 5.34$, $P = 0.149$, df = 3). Flow velocity has a significant effect on growth only within the two extreme concentrations.

The effects of food concentration were examined in a similar manner. Growth coefficients were plotted against flow velocity for each of the cell concentrations (Fig. 3b). Growth rates were significantly different between cell concentrations within each flow velocity (Kruskal–Wallis tests, df = 3, $P < 0.001$ for all tests). At all flow velocities, the highest growth rates were achieved at 6000 cells · ml^{-1} and the lowest growth was seen at 0 cells · ml^{-1}.

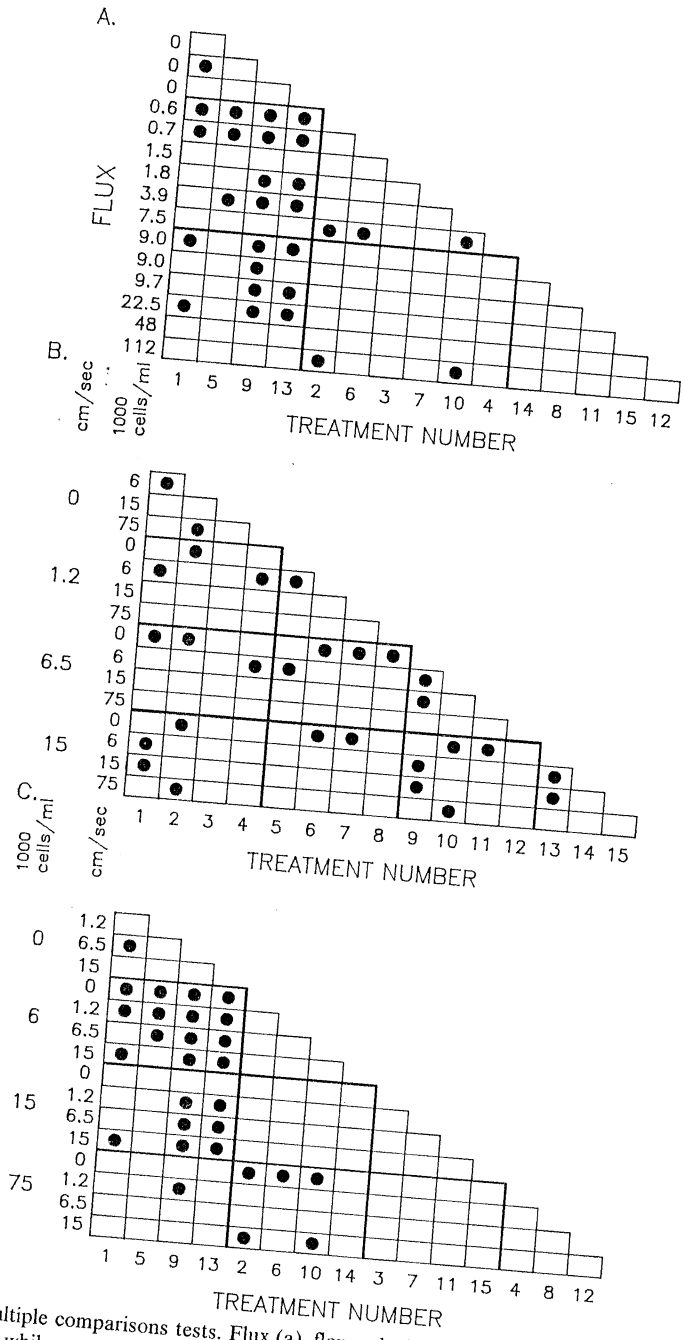
To verify these findings, a one-way Kruskal–Wallis test of growth rates on flux values was performed (Sokal & Rohlf, 1981), followed by a simultaneous multiple comparison test based on the overall Kruskal–Wallis ranks (Hollander & Wolfe, 1973). This allowed the effects of flux on scallop-growth rates to be analyzed. Growth in each flux treatment was compared with growth in every other flux treatment in a 16 × 16 matrix of all possible comparisons. These comparisons are arranged by increasing flux values and each cell represents a comparison between growth rates of scallops exposed to two different treatments (Fig. 4). Filled circles indicate significantly different scallop growth rates (at an experiment-wise error rate of 0.05).

Based on the diagram (Fig. 4a), three groups of flux values were selected; a low-(no)-flux group, an intermediate-flux group and a high-flux group. These groups are outlined by slightly darker divisions.

Within low-flux group, there are no significantly different treatments and only 20% of the comparisons within the intermediate fluxes were between significantly different groups. Most of the significant differences were found in comparisons between low-(no)- and either intermediate- or high-flux treatments.

This same set of comparisons was then rearranged into two other 16 × 16 matrices to show growth rates resulting from flow velocity and food concentration (Fig. 4b,c). These are the same comparisons ordered by either flow velocity or food concentration. In Fig. 4b, comparisons are ordered by increasing flow velocities with cell concentrations arranged within each velocity. This tested the effects of flow velocity, taking into account food concentration, and interaction terms. Within any given flow velocity, 17–33% of the comparisons are significantly different. Among different flow velocities, 13–25% of the comparisons revealed significantly different growth rates. There was no discernible pattern to these results, significantly different treatments being seen within as well as among flow velocities.

When these same comparisons were rearranged by increasing cell concentrations with flow velocity nested within each concentration (Fig. 4c), there were no significantly different comparisons within any of the concentrations (with the exception of one significant comparison in the no-food treatments), nor between the low- and intermediate-food treatments or between the intermediate- and high-food treatments. Comparisons between the no-food treatments and the intermediate- and low-treatments revealed a high percentage of significantly different growth rates. This pattern indicates



ig. 4. Results of multiple comparisons tests. Flux (a), flow velocities (b), or algal concentrations (c) are sted on left margin while corresponding treatment numbers are listed on bottom margin. Solid circles enote comparisons between treatments with significantly different (experiment-wise error rate $P < 0.05$) owth rates. Flux groupings in (a), flow groupings in (b), and cell concentration groupings in (c) are outlined in bold.

an effect on growth rate due to concentration. Treatments at 0 cells · ml^{-1} were different from the fed treatments and low-food treatments were different from the high-food treatments. This is not a linear relationship, however, since only a few of the no-food treatments were different from the high-food treatments.

CLEARANCE EXPERIMENTS

Clearance rates (volume of water cleared of particles · unit time^{-1}) ranged from 0.096 ml cleared · min^{-1} · mg scallop^{-1} at 7500 cells · ml^{-1} to 0.042 ml · min · mg scallop^{-1} at 69000 cells · ml^{-1} (Fig. 5). Clearance rates varied with particle concentrations (ANOVA, $F = 16.58$, $P < 0.001$). Clearance rates at 7500 cells · ml^{-1} differed

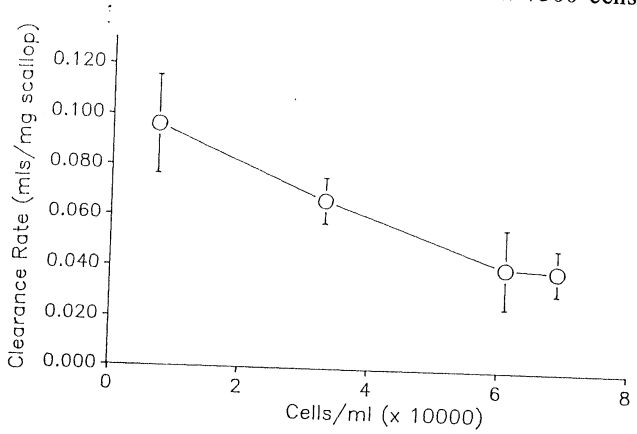


Fig. 5. Juvenile bay scallop clearance rates (cells removed · min^{-1} · mg whole wet weight^{-1}). Error bars are SE of $\bar{x}$.

significantly at an experiment-wise error rate of 0.01 from clearance rates at 60000 and 69000 cells · ml^{-1}. Regression of log-transformed clearance rates on algal concentration was significant with $r^2 = 0.99$.

DISCUSSION

While food supply (flux of particles) has been reported as an important factor controlling growth rates in field populations (Wildish & Kristmanson, 1985; McFadden, 1986; Eckman, 1987; Okamura, 1987; Wildish et al., 1987), this was not the case for individuals tested in these experiments. In this study, the effects of food concentration on scallop-growth rates were more pronounced than those of either flow velocity or food flux. Flow velocity affects growth rates only when food concentration was extremely high or low, and therefore, possibly stressful to the animal. Effects of food fluxes on individuals are less obvious than effects due to the individual components of flux (food concentration and flow velocity). The correlation between growth rates and fluxes of food particles may result solely from the effects of food concentration on growth rates.

EFFECTS OF FOOD FLUXES

Fluxes of food particles did not have a strong influence on growth rates of individual scallops. There is a slight correlation between food fluxes and growth rates but this may be attributed to effects of food concentration. Within a given flux of food particles, there were no differences in growth rates for bay scallops.

Many studies have shown that food fluxes limit growth rates in field populations of suspension-feeders (e.g., Buss & Jackson, 1981; Peterson et al., 1984; Frechette & Bourget, 1985; Wildish & Kristmanson, 1985; Eckman, 1987). A shadow of food-depleted water has been observed on the downstream edges of large beds of bivalves (e.g., Wildish & Kristmanson, 1985) and other suspension-feeders (Frechett & Bourget, 1985). Depletion in the boundary layer can also be found in other systems of suspension-feeders (i.e., Leversee, 1976; Buss & Jackson, 1981; McFadden, 1986). The extent of this depletion is related to flow velocities; higher flows allow more mixing and higher total volume of water (and food) moving over the suspension-feeders (Peterson et al., 1984; Wildish & Kristmanson, 1985; Eckman, 1987).

The effect of flux on individuals (as in this study) is not necessarily a proper measure of food supply to an individual. Individuals sample the particle concentration around them when they filter the water, hence instantaneous food concentration may be the pertinent parameter of interest, not flux. Some populations of suspension-feeders are able, through depletion, to decrease the average particle concentration of the water over the area which they occupy. In this case (populations of suspension-feeders), flux may be the parameter of interest. For an individual in the present experiment, growth was highest at an intermediate concentration and decreased at concentrations above an optimal level. For a population, growth will be highest when the concentration over all the individuals in the population is high enough to result in high, mean individual growth rates. In other words, when the flux of food particles over the population is large enough for the animals at the trailing edges to be exposed to a nongrowth-limiting food concentration, the population as a whole will have a higher growth rate.

Based on the clearance rate results presented in this study, food depletion by upstream scallops may not be a mechanism limiting growth of juvenile scallops. Assuming a clearance rate of 0.1 $ml \cdot min^{-1} \cdot mg\ scallop^{-1}$ (at algal concentrations of 6000 $cells \cdot ml^{-1}$), a 20-mg scallop is able to clear 0.033 $ml \cdot s^{-1}$. At a flow rate of 1 $cm \cdot s^{-1}$, a density of 3300 $scallops \cdot m^{-2}$ would be required to remove 25% of the food particles from the water (a 1 cm thick layer) at a distance of 0.25 m into the patch. For juvenile hard clams *Mercenaria mercenaria*, a reduction of 25% of the phytoplankton in the water is sufficient to cause decreases in growth rates (Malinowski & Siddall, in press). Thus, juvenile scallops present at this very high density may deplete the food supply at low flow velocities in as little as 0.25 m, however, these calculations assume that water containing food is not mixed into the water passing the scallops. This is unlikely to be the case. If a mixing rate of 25% is added to these calculations, a substantial decrease in food-particle concentration will occur at 0.5 m into the patch. Juvenile scallops, however, occur in the eelgrass canopy where mixing is likely to be

$>25\%$, thereby increasing the distance into the patch where depletion would occur. Additionally, these calculations assume very high densities of juvenile scallops which are not likely to be maintained for any period of time as scallops emigrate and predation lowers the population densities. Also, the clearance rate used is at the high end of the range of those found in this study. Lower clearance rates or higher flow rates will also tend to decrease the effects of food depletion effect on the scallops. However, adult scallops have a much higher clearance rate and live on the floor of the seagrass beds, and hence there remains a strong possibility of depletion under some circumstances.

Flux, in and of itself, is a complex measure of food availability. This study presents data which indicate that although it does have an effect on growth rates, it is very slight, and at best, flux can only weakly predict growth rates of individuals. It is perhaps more appropriate to decouple the components of flux, flow velocity and food concentration, in order to predict growth rates. The effects of these components have much more profound effects on growth rates than flux and they may interact to produce results which cannot be incorporated into a single number such as flux.

EFFECTS OF FOOD CONCENTRATION

The effects of food concentration were much more pronounced than the effects of flow velocity. Normal variations of phytoplankton concentration (in natural field populations) do not influence growth in scallops (Kirby-Smith & Barber, 1974), however, in this study the experimental food concentrations spanned a larger range than those that might normally be encountered in the field. Growth rates varied with food concentration (Fig. 3b). They did not increase monotonically with increasing food levels, however. Although highest food concentrations resulted in lower growth rates than in the lower food concentrations, the lowest growth rates were observed in the no-food treatments. The results of the clearance experiments support this trend. At food concentrations >7500 cells $\cdot$ ml^{-1}, clearance rates of scallops decreased. This agrees with Winter (1978) who found decreased growth at higher food concentrations.

The data suggest that there is an optimal food concentration, above which the scallops do not increase their ingestion rate. Ingestion rates in other studies have shown that above some limiting concentration, a constant amount of food is ingested in a given unit of time, independent of concentration (Winter, 1978; Riisgård et al., 1980). Growth rates seen in this study, however, do not necessarily agree with the results of Riisgård et al. (1980). At high particle concentrations, increased production of pseudofeces may represent a significant energy loss and account for decreased growth.

EFFECTS OF FLOW VELOCITY

Growth rates of scallops placed in the flume did not vary significantly with flow velocity (Fig. 3a) although growth rates showed a trend toward decreasing at higher flow velocities. At 6000 cells $\cdot$ ml^{-1} algal concentration, growth rates of the scallops peaked at 6.5 cm $\cdot$ s^{-1}, an intermediate flow velocity.

Some studies have shown that growth rates of adult scallops tend to decrease with increasing flow velocity (Kirby-Smith, 1972; Wildish et al., 1987), while others report increased growth in areas of increased flows (Marshall, 1960; Wildish & Kristmanson, 1985; Eckman, 1987). These latter studies have focused on the responses of field populations to flow velocities. The discrepancies between these studies may be explained by investigating the mechanisms of particle capture and other factors affecting growth rates in field situations.

Decreased ingestion rates in individuals might be expected at higher flow velocities due to the mechanical constraints of particle capture from flowing water. Most bivalves are active filter-feeders which means they remove particles from the surrounding water by pumping water through their mantle cavity and over their gill filaments. Bivalve gill filaments do not appear to act as sieves when removing particles from the water (Jørgensen, 1981). At high flow velocities, pressure gradients over the gills may be high enough to inhibit particle capture (Jørgensen et al., 1986).

Scallops may also employ behavioral responses to relieve stresses caused by high flow velocities. In high flow velocities the filtering capacity of the gill filaments may be overwhelmed by high pressure differences across the gills. Wildish et al. (1987) reported decreased pumping by sea scallops *Placopecten magellanicus* exposed to high flow velocities, resulting in decreased growth. A behavioral response of scallops exposed to high flow velocities results in less time spent feeding. The trend in the present study toward decreases in growth rates with increasing flow velocities is consistent with those of Kirby-Smith (1972) and Wildish et al. (1987) who suggested that particle-capture rates are inhibited by high flow velocities. The lack of statistical significance of this result may have resulted from the conservative nature of the statistical test used or the low power of the statistical design.

There is evidence supporting increased growth rates in areas of increased flow velocities. Eckman (1987), Wildish & Kristmanson (1985), and Frechette & Bourget (1985) all observed increased growth of bivalves under field conditions of high flow velocities. These enhanced growth rates may be a result of increased food supplies to the population (food fluxes), or increased feeding efficiency. Scallops tend to orient themselves with their inhalant margins facing into the flow which may facilitate the passage of water through the mantle cavity and thus represent an energy savings. Wildish et al. (1987) showed increased growth rates in sea scallops held with anterior margins facing into oncoming water while scallops held at other orientations did not show the same trend. At flow velocities $> 10\ \mathrm{cm} \cdot \mathrm{s}^{-1}$, growth rates were depressed at all orientations.

The data presented here show differences in growth only at extreme concentration treatments. At the highest and lowest concentrations, the no-flow and the high-flow treatments were different from the two intermediate-flow treatments (and from each other). This may indicate the presence of a compensatory mechanism where at low food levels a slightly higher flow rate will provide sufficient food (increased flux) for the scallop to continue to grow. At supraoptimal food levels, the scallop may not be able

to compensate for the stressful flow velocity and hence growth rates are depressed. At intermediate levels of both flow velocity and food concentration, this mechanism is not in effect. In those situations, the effects of flow velocity may be masked due to the compensating effects of food concentration.

In conclusion, growth of individual scallops observed in this study varies with flow velocity and food concentration and not with food supply rates (flux). The response of individuals to flow regimes may be the result of behavioral changes which decrease stresses imposed on the individual by flow. Responses of populations may vary with these two parameters integrated over the area occupied by the population. The responses of the population to these parameters do not necessarily reflect the physical constraints placed on the individual by the environment; it may be more appropriate to report flow velocities and food concentrations rather than flux values or, at a minimum, report how food supply values were altered, for instance through increased velocity. Populations respond to food fluxes, that is, the concentration of food over time and space occupied by the population. While population studies give insights to the effects of the environment on community dynamics and population structure, they do not reflect the physiological responses of the individual to these same parameters. Individuals respond to food concentration as a result of the mechanics involved with particle capture. The response of individuals to flow regimes may be the result of behavioral changes which decrease stresses imposed on the individual by flow.

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