Marine Biology 113, 219–225 (1992)

Marine Biology
Life in Oceanic and Coastal Waters

Measurement of filtration rates by infaunal bivalves in a recirculating flume

B. E. Cole, J. K. Thompson and J. E. Cloern

U.S. Geological Survey, 345 Middlefield Road, MS-496, Menlo Park, California 94025, USA

Date of final manuscript acceptance: January 24, 1992. Communicated by M. G. Hadfield, Honolulu

Abstract. A flume system and protocol for measuring the filtration rate of infaunal bivalves is described. Assemblages of multi-sized clams, at natural densities and in normal filter-feeding positions, removed phytoplankton suspended in a unidirectional flow of water. The free-stream velocity and friction velocity of the flow, and bottom roughness height were similar to those in natural estuarine waters. Continuous variations in phytoplankton *(Chroomonas salinay)* cell density were used to measure the filtration rate of the suspension-feeding clam *Potamocorbula amurensis* for periods of 2 to *28* h. Filtration rates of P. *amurensis* varied from *100* to *580* liters $(g d)^{-1}$ over a free-stream velocity range of *9* to *25* $cm s^{-1}$. Phytoplankton loss rates were usually constant throughout the experiments. Our results suggest that suspension-feeding by infaunal bivalves is sensitive to flow velocity.

Introduction

A prominent theme of coastal oceanography is "benthic-pelagic coupling", which we interpret to mean the exchange of materials (or energy) between the water column and benthic organisms and bottom sediments. One process of benthic–pelagic coupling, the ingestion of phytoplankton biomass by suspension-feeding infauna, may be a large component of energy flow in shallow coastal waters and estuaries (e.g. Dame et al. *1980,* Cloern *1982,* Nichols *1985,* Peterson and Black *1987).* This hypothesis is, however, largely based on laboratory-measured filtration rates, and thus has not yet been rigorously tested for the soft-bottom infaunal communities that often dominate estuarine benthos (we note that rapid phytoplankton ingestion by dense populations of epibenthic suspension feeders such as *Mytilus edulis* has been documented unequivocally; e.g. Frechette and Bourget *1985,* Fréchette et al. *1989).*

Filtration rates of suspension-feeding benthic invertebrates have traditionally been measured as the removal rate of suspended material (phytoplankton or inorganic particles) by a few bivalves, over short time-periods, in confined experimental vessels, and under static conditions (e.g. Foster-Smith *1975,* Winter *1978,* Møhlenberg and Riisgård *1979,* Shumway et al. *1985,* Riisgård *1988)* or in poorly defined flows (Kirby-Smith *1972,* Møhlenberg and Riisgård *1979,* Bricelj and Malouf *1984,* Doering and Oviatt *1986).* Particle capture by suspension feeders in a static medium may differ substantially from that in the dynamic tidal flows of estuaries (Rubenstein and Koehl *1977,* LaBarbera *1984).* Recent studies (Wildish et al. *1987,* Cahalan et al. *1989,* Eckman et al. *1989,* Wildish and Miyares *1990)* have shown that feeding rates of epibenthic bivalves vary inversely with flow velocity. Filtration rates have also been estimated using individual animals held in artificial settings, rather than assemblages of animals held within natural substrate. These potential limitations led to the design of a flume-based approach for measuring filtration rates of estuarine infauna, which we describe here.

Numerous studies demonstrate that hydrodynamics can control processes important to feeding and growth by the estuarine benthos. Variations in near-bed particle densities (Muschenheim 1987), flow and settlement around bivalve siphonal currents (Ertman and Jumars *1988,* Monismith et al. 1990), and feeding strategies (Vogel *1981)* are affected by hydrodynamics. Particle capture by deposit feeders (Jumars and Nowell *1984)* and suspension feeders (Rubenstein and Koehl *1977,* LaBarbera *1984)* are both dependent on the mechanisms by which water flow delivers particles to the animals' food-gathering apparatus. The effects of flow velocity on feeding rates of suspension-feeding bivalves were ignored in most earlier studies (Winter *1978,* Møhlenberg and Riisgård *1979,* Riisgård *1988).* However, recent studies have shown that for epifaunal bivalves there is an inverse relation between flow velocity and growth as well as feeding rate. Growth of individual scallops (Kirby-Smith *1972,* Wildish et al. *1987,* Cahalan et al. *1989,* Eckman et al. *1989)* and the filtration rate of assemblages of epibenthic mussels (Wildish and Miyares *1990)* decrease

as flow velocity approaches 15 to 20 cm s^{-1}. Wildish et al. and Wildish and Miyares suggested that the reduction in growth as flow velocities increase may be due to reduced feeding rate in response to flow-induced differences in water pressure between inhalant and exhalant siphons. We initiated this project with the assumption that particle capture by infaunal bivalves might also be influenced by hydrodynamic conditions (i.e., free-stream velocity, friction velocity).

The technique described here uses a recirculating flume in which flows can be controlled and quantified and in which infaunal assemblages can be placed in natural substrate. We describe an experimental protocol suitable for measuring filtration rates by an assemblage of organisms under conditions that approximate those of a tidal estuary, such as San Francisco Bay, and then present initial results using that protocol. These results support the hypothesis that phytoplankton removal by infaunal bivalves is sensitive to near-bed hydrodynamics.

Materials and methods

Filtration-rate studies were conducted in a recirculating laboratory flume designed to maintain steady flow conditions and to minimize physiological or mechanical stress on the grazer (the bivalve *Potamocorbula amurensis*) and the food source (Chroomonas salina) held in this system for extended periods. Dense batch-cultures of the phytoplankton were added to the flume filled with water amended with Instant Ocean" salts. Artificial seawater was used because experiments with natural seawater were confounded by the rapid population growth and phytoplankton grazing by ciliates. The flow in the flume was adjusted to the desired velocity, and then changes in phytoplankton fluorescence were monitored continuously throughout an experiment. Discrete water samples were collected periodically for microscopic enumerations that were used to relate changes in fluorescence to changes in phytoplankton cell density. The ability to accurately relate fluorescence to phytoplankton cell density enabled us to continuously monitor fluctuations in infaunal filtration rates for periods of up to 5 d. After that period of time, phytoplankton mortality increased in the flume. Background phytoplankton losses, in the absence of clams, were used as experimental controls, while losses when the clams were present were used to estimate filtration rates.

The flume

The flume (Fig. 1), based on design criteria of Nowell and Jumars (1987), allows continual recirculation of water over a test section where grazers and their particle capture are localized. The flume has a 350 cm-long channel located between a headbox and tailbox which are connected by a 20 cm-diam return pipe. The channel is 38 cm wide, with the test section 250 cm from the head of the flume. The test section accommodates a 20 x 30 cm (0.06 m^2) tray of sediment into which the clams bury. The edges of the test section are 9 cm from the sidewalls, so that sidewall boundary effects over the test section are small (Nowell and Jumars 1987). A variable-height weir, 40 cm downstream of the test section, allows for water depths of up to 8 cm without significant upstream-flow reflection. Flume capacity is 400 liters, and flow is maintained by a three-blade propeller in the return pipe below the tailbox (Vogel 1981). A propeller-driven system was used because it provided adequate flow velocity but imparted relatively little shear (compared to impeller and centrifugal pumps), allowing the algae to survive for prolonged times with only a slow loss rate. A speed controller is connected to the propeller drive motor to regulate flow velocity. Flows of 3 to > 50 cm s^{-1} have been obtained with this system, but above ~30 cm s^{-1} air is entrained, flow becomes unsteady, and there is excessive sediment scour from the test section.

A portion of the flume water and suspended algae are continuously withdrawn from the tailbox using a peristaltic pump, passed through a fluorometer, and then directed back into the flume. The fluorescence signal is monitored continuously and 5 min averages of the continuous fluorescence data are stored with a data-logger.

Proper simulation of hydrodynamic conditions in the flume is essential to maintain flow conditions for the clams. Several flow parameters might be critical (Nowell and Jumars 1984), but Monismith et al. (1990) note that only the friction velocity (u_*, a measure of turbulence) and roughness height (z_o, in this case clam siphon-height) need to match field conditions to represent the natural flow environment of benthic infauna. Vertical profiles of the flow velocity (Fig. 2) confirm the presence of a well-formed boundary layer over the test section. Velocity profiles were measured with a single-component, tracker-based laser-Doppler anemometer as described by Monismith et al. Friction velocities of 0.5, 0.8, and 1.1 cm s^{-1} were measured at free-stream velocities (U_∞) of 10, 15, and 24 cm s^{-1}, respectively, over a smooth plate in the test section. When clams were present ($z_o \simeq 0.5$ to 0.7 cm), friction velocities of 0.3, 0.8, and 1.0 cm s^{-1} at U_∞ of 5, 15, and 17 cm s^{-1}, respectively, were measured over the tray containing the clams. These values of u_* are within the range of friction velocities reported for tidal estuaries (0 to 5 cm s^{-1}; see Dyer 1980, Knight 1981, Gross and Nowell 1983, and Sternberg et al. 1986).

Phytoplankton cultures

Eight-liter batch cultures of Chroomonas salina (Wislouch) Butcher (Clone CCMP 1319), a cryptomonad flagellate about 7 x 10 μm in size, were grown in aerated artificial seawater (15‰ S) made with Instant Oceans salts and amended with *f*/2 nutrients (Guillard 1975). Cultures were grown under continuous light and harvested in the log-phase of growth when they reached a density of about 1 x 10^6 cells ml^{-1}.

This flagellate was selected as a representative food source because microflagellates, including cryptophytes, are ubiquitous and often dominant components of estuarine phytoplankton assemblages (Patten et al. 1963, Gardiner and Dawes 1987, Orive 1989), they have higher nutritional quality than other algae (Shumway et al. 1985, Stewart and Wetzel 1986, Klaveness 1991), because their sinking rates are slow (Pedros-Alio et al. 1989), so that losses to the

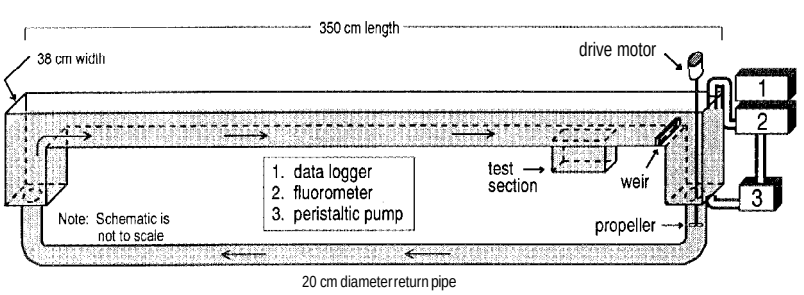

Fig. 1. Schematic diagram of the flume. Water containing suspended phytoplankton circulates through flume and flows over clams located in test section while changes in phytoplankton fluorescence are recorded by data-logger

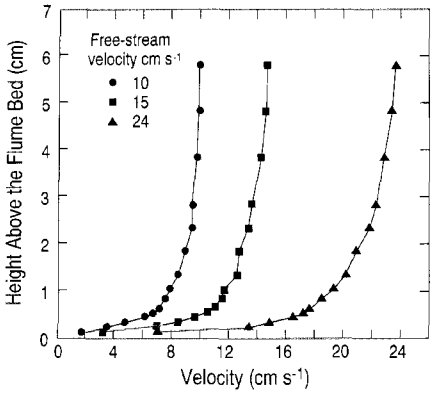

Fig. 2. Profiles of streamwise velocity above flume bed. Velocity profiles made at upstream edge of test section show presence of well-formed boundary layers and, depending on free-stream velocity, markedly different flow rates in layer < 0.5 cm above bed, i.e., layer from which the clams feed

flume bed are small and because they grow rapidly in culture over a wide range of salinities and temperatures. The cultures were dark-acclimated since flume experiments were conducted in the dark to eliminate phytoplankton growth and because a stable relation between fluorescence and phytoplankton density was necessary to accurately monitor changes in phytoplankton abundance from in-vivo fluorescence. A dark-adaptation period of about 18 h is required to ensure a stable ratio between fluorescence and cell density. Otherwise, after a culture is placed in the dark the phytoplankton continue to divide (increase in cell numbers) for a period of hours even though fluorescence decreases immediately (data not shown).

Clams

An assemblage of multi-sized (5.5 to 20.5 mm shell length) *Potamocorbula amurensis*, a siphonate bivalve, were collected from San Francisco Bay, separated from the bottom sediment and other animals, and then placed in a tray containing medium-grained sand devoid of other infauna. The clams were allowed to burrow into the sediment and were then maintained in tanks covered with aerated water for 1 to 3 d prior to the experiments. The clams were fed periodically during the holding period with cultures of *Chroomonas salina*.

Potamocorbula amurensis, a member of the Corbulidae family, is well adapted to suspension-feeding (Yonge 1946) and varying environmental conditions. This clam lives in diverse habitats throughout San Francisco Bay, ranges in length from 0.5 to 31 mm, and typically occurs in densities of 5000 to 10000 m^{-2} (Carlton et al. 1990). Such densities are equivalent to 300 to 600 clams per 0.06 m^{-2}, the surface area of the sediment tray.

Experimental protocol

The flume was filled with about 350 liters of artifical seawater which was aerated and aged at least 24 h to insure that the inorganic salts had reached chemical equilibrium. Temperature in the flume was 15 °C ± 1.5 C°. The flow in the flume was adjusted to the desired velocity; then a dark-adapted *Chroomonas salina* culture was added until the phytoplankton density in the flume was about 15000 cells ml^{-1}, a density typical of phytoplankton blooms in San Francisco Bay (Wong and Cloern 1982). Fluorescence was monitored continuously with a Turner Designs® Model 10 fluorometer in conjunction with the collection of 5 to 17 discrete samples for calibration of the fluorescence to cell density. The initial 6 to 18 h of each experiment were usually conducted without clams in the flume and with a coverplate over the test section. Loss rates during this initial control period, presumably a result of settling and mortality caused by mechanical forces, were subtracted from loss rates measured during the experimental periods when clams were present. After the control period, the flow was stopped, the coverplate removed, and the tray of sediment and clams lowered into place. A thin layer of fresh sand was added to the sediment tray so that the sediment surface was flush with the flume bed. Water flow in the flume was then resumed and monitoring of fluorescence and collection of discrete water samples continued. At the end of an experiment, the clams were removed from the sediment and their shell lengths (cm) measured. The soft-tissue biomass of the clams (g ash-free dry wt, AFDW) was estimated from shell lengths using the equation:

$$\ln (\text{AFDW}) = -4.81 + 2.81 \ln (\text{shell length}), \quad (1)$$

which has been found to be valid for individuals collected in both April and December (JKT, unpublished data).

Calculation of filtration rate

Traditional measures of bivalve filtration rate in a closed static system have been based on the difference between an initial and final cell density of phytoplankton (end-points) during a grazing experiment (see Coughlan 1969). The limitations and possible errors associated with this approach are discussed by McClatchie and Lewis (1986), who argue that time-series data are preferable to end-point measurements because significant errors result if the feeding rate varies or ceases during the course of an experiment. Continuous measurement of fluorescence can be used to obtain a time-series of estimated phytoplankton cell density throughout the course of an experiment. Estimates of cell density were derived from correlation of discrete measures of cell density (from microscopic enumeration) with in-vivo fluorescence (Table 1). Cell densities were measured by microscopic enumeration of the algae in 25 µl aliquots of sample using a Palmer-Maloney plankton counting chamber. The number of cells counted ranged from 15 to 530 cells 25 μl^{-1} sample.

Clam filtration rates were calculated from incremental decreases in phytoplankton concentration as represented by the curve e^{-x}, where x is the specific loss rate due to bivalve filtration (Coughlan 1969). The specific loss rate for a time-series of cell density (fluorescence) measurements is given by the slope of a linear regression of ln (estimated cell density) against time. Hence, the filtration rate [liters $(g\ d)^{-1}$] is given by:

$$\text{filtration rate} = (x - x') \cdot \frac{V}{B}, \quad (2)$$

where x' is the specific loss rate (d^{-1}) during the control period, V is the volume (liters) of water in the flume, and B is bivalve biomass (g AFDW). Because a change in filtration rate is easily detected using a closely sampled series of measurements, there is a greater degree of confidence in the accuracy of filtration rates measured using time-series data than in those derived from end-point data. For a closely timed series of measurements, fluctuations in the filtration rate or cessation of feeding during the course of an experiment are readily apparent.

Results and discussion

Fig. 3 illustrates a typical time course of variation in cell density of *Chroomonas salina* (as estimated from changes in fluorescence) for extended periods and over a range of flow velocities. During the initial 6 h control period, the phytoplankton loss rate was 0.22 d^{-1} as phytoplankton density decreased from 12300 to 11500 ml^{-1}. Repeated experiments (data not shown) show that loss rates during

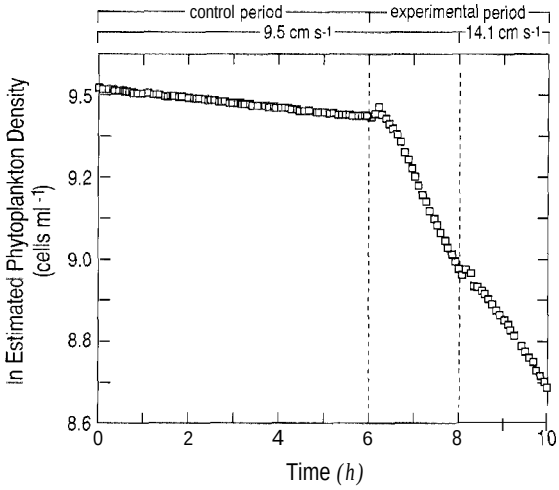

Fig. 3. *Chroomonas salina.* Variation in estimated phytoplankton abundance with time. Rate of decrease in cell density increased dramatically when clams *(Potamocorbula amurensis)* were added to system at Hour 6 and then slowed when flow velocity was increased to *14.1* cm s^{-1} at Hour 8. Each data point represents average cell density for a *5* min interval, based on continuous measurement of in-vivo fluorescence

Table 1. *Chroomonas salina.* Regression parameters from linear regressions of cell density (cells ml^{-1}), measured by microscopic enumeration of preserved samples, against fluorescence. *A:* regression intercept; *B:* regression slope; r^2: coefficient of determination; S_{yx} (cells ml^{-1}): standard error of estimate of cell density; *n:* number of samples in data set; Range: range of cell densities (cells ml^{-1}) used in regression

Date	A	B	r^2	S_{yx}	(n)	Range
Nov. *1989*						
17	*−2413*	*205 556*	*1.00*	*317*	*(9)*	*12 920– 240*
23	*−3535*	*194 404*	*0.96*	*869*	*(6)*	*12 000– 760*
Dec. *1989*						
2	*− 1887*	*176 639*	*0.98*	*262*	*(15)*	*6 500–1 640*
5	*−4547*	*213 582*	*0.84*	*713*	*(17)*	*10 800–6400*
Apr. *1990*						
2	*−5472*	*228 033*	*0.99*	*650*	*(7)*	*21 000– 600*
4	*−1 373*	*168 775*	*0.99*	*631*	*(5)*	*15 400– 240*
6	*−1 738*	*168 451*	*0.99*	*704*	*(5)*	*14 560– 480*

control runs remain constant for periods of 24 h. At the end of the control period, Potamocorbula amurensis were added to the flume and flow was maintained at 9.5 cm s^{-1}. Within 15 min, the phytoplankton loss rate increased to 5.5 d^{-1} and remained constant while flow was maintained at that velocity. After 2 h, the flow rate was increased to 14.1 cm s^{-1} and the phytoplankton loss rate decreased to a constant 3.8 d^{-1}.

The phytoplankton loss rate was generally constant during each experimental period over a range of cell densities (Table 2). However, following a change in flow velocity or immediately after the clams were added to the flume at the end of the control period, there was a short period of about 15 to 30 min when the fluorescence signal was erratic (e.g. Fig. 3). Transitory periods of variable fluorescence may have been caused by: the temporary disruption of clam filtration after disturbance; increases in fluorescence when bed material was resuspended as the tray was placed in the flume; and the resuspension of bed material after the flow rate was increased. The resuspension of fluorescent material (phytoplankton, pseudofeces, and feces) that had apparently settled to the surface of the sediment tray or flume bed was most pronounced when the flow rate was increased following experiments at low velocities (data from other experiments, not shown). Data collected during such transitory changes in fluorescence during the initial acclimation period-were not used to calculate clam filtration-rates. Casual observations made during the experiments suggest that settling to the bed increased as flow velocity decreased or the concentration of suspended material increased. Settling-out of the phytoplankton within the flume system is corrected for in the control loss-rate, but resuspension of previously ingested fluorescent material may result in underestimates of filtration rates at high flow velocities. The effect of resuspended feces and pseudofeces on measured filtration rates will be examined in future studies.

We also truncated the fluorescence time-series at the end of a grazing experiment if the fluorescence signal approached the "background" value seen in the absence of phytoplankton cells. The total fluorescence signal includes contributions from phytoplankton, dissolved organic constituents, feces, and pseudofeces produced during the course of an experiment. Because phytoplankton fluorescence is only part of the total fluorescence signal and because there are relatively large errors (>10%) in cell counts based on microscopic enumerations, the estimated cell abundances from fluorescence become less precise as cell density approaches zero. Consequently, we truncated the fluorescence time-series at that point where the 95% confidence interval of estimated phytoplankton abundance, $2 \cdot S_{yx}$ (where S_{yx} is the standard error of the estimate of cell density), first included zero cells ml^{-1} (i.e., where estimated cell density $= 2 \cdot S_{yx}$).

For example, Fig. 4 shows changes in estimated cell density during a 3 d experiment. For the first 15 h, the loss rate was constant at about 3.4 d^{-1}. However, after Hour 15, the density dropped below 1400 cells ml^{-1}, and the rate of decrease in estimated cell density (fluorescence) slowed and departed from the initial experimental loss rate. Inclusion of data from this later portion of the experiment resulted in 95% confidence limits that included estimated cell densities of <0 cells ml^{-1}. Therefore, data from the later portion of the experiment were not used to estimate clam filtration-rates. Non-linearity of decreases in ln (cell density) with time (Fig. 4, Hours 15 to 70) is common when the fluorescence approaches background (low and non-varying) levels. Consequently, although experiments typically ran for periods of I to 3 d, filtration rates were usually calculated using data collected over periods of 2 to 24 h.

For most experiments, the loss rate was constant over a range of 2000 to 15000 cells ml^{-1} (Fig. 5 and Table 2). However, during the experiment begun on 2 April 1990, the rate of fluorescence decline varied (Fig. 5d). The

Table 2. Summary of conditions and results from filtration-rate experiments with clams (Potamocorbula amurensis) filtering phytoplankton (Chroomonas salina). Values for phytoplankton loss rates are specific loss rates, as measured by slope of regression of ln (estimated cell density) against time, ±95% confidence interval for regression. n: number of clams; AFDW: ash-free dry wt

Date	Density range (cells ml^{-1})	Period (h)	Flow rate (cm s^{-1})	Phytoplankton loss rate		Flume vol. (l)	(n)	AFDW (g)	Filtration rate	
				control (d^{-1})	clams (d^{-1})				per clam (l d^{-1})	per gram (l d^{-1})
Nov. 1989										
17	12 300–2 400	25.8	15.4	0.28	1.58 ± 0.14	337	(489)	4.26	0.90	103
23	4 600– 620	11.2	25.3	0.27	4.10 ± 0.06	337	(489)	4.26	2.64	303
Dec. 1989										
5	11 600–8 000	1.7	9.5	0.22	5.48 ± 0.10	365	(473)	4.12	4.02	462
2	5 800–3 400	2.0	10.3	0.27	4.64 ± 0.08	365	(473)	4.12	3.37	387
5	7 900–6 000	1.6	14.1	0.22	3.76 ± 0.08	365	(473)	4.12	2.69	309
Apr. 1990										
4	13700–1940	14.7	10.5	0.30	3.18 ± 0.04	360	(236)	1.94	4.39	534
2	18800–1700	27.8	15.6	0.30	1.95 ± 0.08	360	(236)	1.94	2.52	306
6	15000–2400	13.6	24.0	0.30	3.40 ± 0.02	360	(236)	1.94	4.73	575

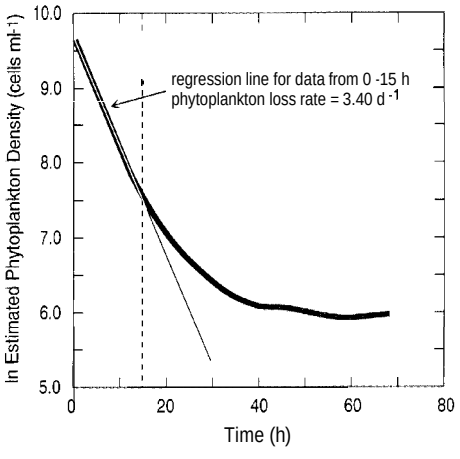

Fig. 4. Chroomonas salina. Variation in estimated phytoplankton density during 70 h experiment. Rate of decrease in estimated phytoplankton density was constant for 15 h, but then slowed. By Hour 40, fluorescence had declined to background levels; consequently, estimates of cell density stabilized. Change in rate of decrease at Hour 15 coincided with time when estimates of cell density could not be distinguished (at 95% confidence level) from 0 cells ml^{-1}

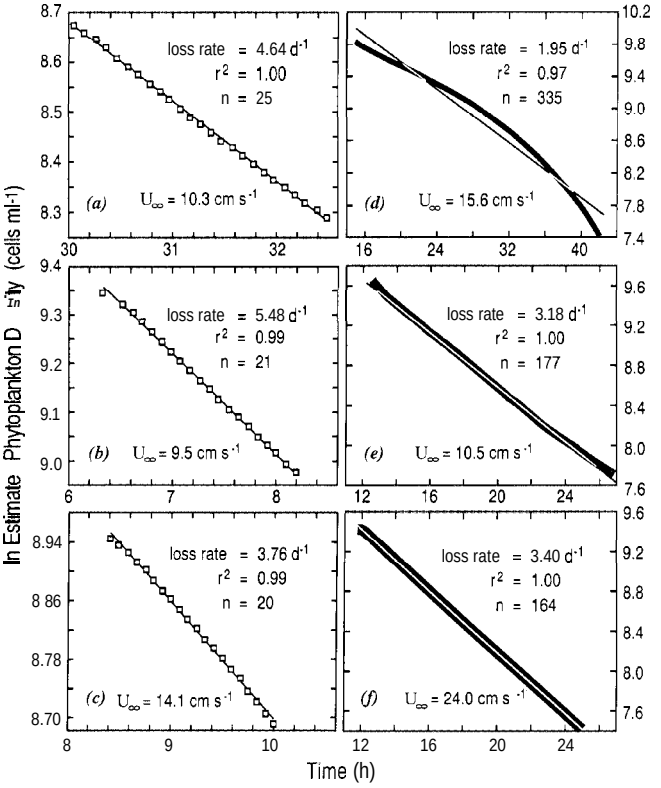

Fig. 5. Chroomonas salina. Variation in estimated phytoplankton density. Rate of decrease in cell density was constant over grazing periods of 2 to 15 h (a–c; e, *f)* but varied over course of the 28 h experiment (d). Each data point represents cell density for 5 min interval. Because of density of data in (d)–(f), individual data points for the extended-duration experiments cannot be distinguished. Thin line is regression slope of ln (estimated cell density) against time, which is equivalent to phytoplankton loss rate. U_∞: free-stream velocity, (a): 2 Dec.; (b): 5 Dec. at 9.5 cm s-'; (c): 5 Dec. at 14.1 cm s^{-1}; (d) 2 Apr.; (e): 4 Apr.; *(f):* 6 Apr.

specific loss rate derived from data collected between Hours 14 and 42 (1.9 d^{-1}; r^2=0.97) is an average loss rate for the 28 h experimental period. But, the filtration rate was not constant during this experiment. The significance of this variation is not clear. Previous studies have reported variations in filtration rate in response to changes in food flux (Fréchette et al. 1989), but not in response to food concentration (Hildreth and Crisp 1976). Both food flux and concentration vary during an

experiment in the flume system described here. But, the range in phytoplankton density during the experiment on 2 April was not greater than the range encountered during the other experiments (Fig. 5a–c, e, f), when there was no variation in loss rate as the concentration and flux of algae declined.

The change in loss rate observed during the 28 h experiment conducted on 2 April may indicate that uptake during short experimental periods does not reflect sustained filtration rates. Other measurements of filtration rate in this and previous studies were conducted over shorter time periods. So, the gradual change in loss rate we observed during the 28 h experiment may simply reflect a natural rhythm not seen in short experimental periods. Regression analysis of 2 h subsets of the data result in exponential losses that are each highly significant (data not shown), suggesting that over short time-periods the filtration rate was constant. However, analysis of the entire data set clearly shows that the filtration rate changed during the course of the experiment. Previously published filtration rates for clams have generally been based on end-points from short-term (0.5 to 2 h) experiments (e.g. Foster-Smith 1975, Winter 1978, Shumway et al. 1985, Wildish et al. 1987). Consequently, it is not known if bivalve filtration rates typically vary as in Fig. 5d, or are constant over long periods as in Fig. 5e and f.

Three common trends were revealed by the results of our initial experiments. First, the phytoplankton loss rate during control periods was $\sim 0.27\ d^{-1}$ (± 0.06; 2 SD) over a range of flow velocities and cell densities (Table 2). This value presumably represents the inherent loss rate of this phytoplankter in the flume due to natural mortality, settling to the bed, and mortality from mechanical stress created in the flume system. Second, our initial results suggest that the filtration rate of a siphonate clam varies in response to free-stream velocity. Among different experiments, while the bivalve population and environmental conditions remained the same, significant variations ($p < 0.05$) in filtration rate coincided with changes in flow velocity (Table 2). During experiments conducted in November 1989, there was a threefold increase in filtration rate with an increase in velocity from about 15.4 to 25.3 cm s^{-1}. In the December experiments, filtration rate decreased from 460 to 310 liters $(g\ d)^{-1}$ when velocities increased from 9.5 to 14.1 cm s^{-1}. And finally, in the April experiments, filtration rates were similar at free-stream velocities of 10.5 and 24.0 cm s-', but were significantly lower at 15.6 cm s^{-1}. The third trend we observed was constant loss rate during the course of an experiment (Fig. 5). In all but one case, filtration rate was constant over a range of cell densities (Table 2). The duration of the experiments varied, however, so we cannot generalize about how long bivalves maintain a constant filtration rate.

That flow velocity affects the filtration rate of a suspension-feeding infaunal bivalve is not surprising. Wildish and Miyares (1990), in the only other study that has measured clam filtration-rates over a range of flow velocities, showed that the percentage of phytoplankton consumed by epibenthic mussels is inhibited at high current speeds. However, Wildish and Miyares did not provide actual measures of filtration rate, so comparisons with the filtration rates seen in the present study cannot be made. The observation in the present study that filtration rate varies with flow also agrees with reports that growth of clams is generally inhibited when flows exceed 15 cm s^{-1} (Wildish et al. 1987, Eckman et al. 1989). It is not surprising that the process of drawing water and suspended phytoplankton from the cross-flowing water into a clam's mantle cavity would be affected by the flow velocity and turbulence of the flow past the inhalant siphon (Rubenstein and Koehl 1977, Vogel 1981, LaBarbera 1984, Monismith et al. 1990). Our preliminary results support this hypothesis, but the experiments conducted so far are insufficient to determine whether there are consistent patterns to the effect of flow on filtration rate. How the effects of flow on bivalve filtration-rate vary among clam communities, physiological and reproductive state of the organisms, food concentration and type, bottom roughness, and physical factors (e.g. temperature) and whether the clams vary their orientation and behavior to flow are questions amenable to analysis with the flume system and protocol described here, and will be addressed in future studies.

Acknowledgements. We thank J. Koseff, S. Monismith, and C. O'Riordan for their advice in design of the flume, measurement of flows. and encouragement throughout the development of the experimental system. J. Slack and A. Jassby provided valuable assistance in determining the proper statistical procedures for evaluating the data. We also appreciate assistance from and discussions with F. Nichols regarding collection and handling of the clams. We appreciate the generosity of D. Fontaine and the staff of the California Academy of Sciences, San Francisco, who provided seawater used in preliminary experiments. *Chroomonas salina* (Clone CCMP 1319, formerly Clone 3C) was obtained from the Provasoli-Guillard Center for Culture of Marine Phytoplankton, Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, Maine, USA. The paper benefitted from critical reviews by E. Irlandi, G. Skilleter, D. Wildish, and an anonymous reviewer.

Literature cited

Bricelj, V. M., Malouf, R. E. (1984). Influence of algal and suspended sediment concentrations on the feeding physiology of the hard clam *Mercenaria mercenaria*. Mar. Biol. 84: 155–165

Cahalan, J. A., Siddall, S. E., Lukenbach, M. W. (1989). The effects of flow velocity, food concentration, and particle fluxes on the growth rates of juvenile bay scallops, *Argopecten irradians*. J. exp. mar. Biol. Ecol. 129: 45–60

Carlton, J. T., Thompson, J. K., Schemel, L. E., Nichols. F. H. (1990). The remarkable invasion of San Francisco Bay, California (USA) by the Asian clam *Potamocorbula amurensis*. I. Introduction and dispersal. Mar. Ecol. Prog. Ser. 66: 81–94

Cloern, J. E. (1982). Does the benthos control the phytoplankton biomass in South San Francisco Bay? Mar. Ecol. Prog. Ser. 9: 191–202

Coughlan. J. (1969). The estimation of filtering rate from the clearance of suspensions. Mar. Biol. 2: 356–358

Dame, R.. Zingmark, R., Stevenson, H., Nelson, D. (1980). Filter feeder coupling between the water column and benthic subsystem. In: Kennedy, V. S. (ed.) Estuarine perspectives. Academic Press, New York, p. 521–526

Doering, P. H., Oviatt, C. A. (1986). Application of filtration rate models to field populations of bivalves: an assessment using experimental mesocosms. Mar. Ecol. Prog. Ser. 31: 265–275

Dyer, K. R. (1980). Velocity profiles over a rippled bed and the threshold of movement of sand. Estuar. cstl mar. Sci. 10: 181–199

Eckman, J. E., Peterson. C. H.. Cahalan, J. A. (1989). Effects of flow speed, turbulence and orientation on growth of juvenile bay scallops Argopecren irradians concentricus (Say). J. exp. mar. Biol. Ecol. 132: 123–140

Ertman, S. C., Jumars. P. A. (1988). Effects of bivalve siphonal currents on the settlement of inert particles and larvae. J. mar. Res. 46: 797–813

Foster-Smith, R. L. (1975). The effect of concentration of suspension on the filtration rates and pseudofaecal production for *Mytilus* edulis L., Cerasroderma edule (L.), and Venerupis *pullastra* (Montagu). J. exp. mar. Biol. Ecol. 17: 1–22

Frechette, M., Bourget, E. (1985). Energy flow between the pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed. Can. J. Fish. aquat. Sciences 42: 1158–1165

Frechette, M., Butman, C. A., Geyer, W. R. (1989). The importance of boundary-layer flow in supplying phytoplankton to the benthic suspension feeder, *Mytilus* edulis L. Limnol. Oceanogr. 34: 19–36

Gardiner, W. E., Dawes, C. J. (1987). Seasonal variation of nannoplankton flagellate densities in Tampa Bay, Florida. Bull. mar. Sci. 40: 231–239

Gross, T. F., Nowell, A. R. M. (1983). Mean flow and turbulence scaling in a tidal boundary layer. Contin. Shelf Res. 2: 109–126

Guillard, R. R. L. (1975). Culture of phytoplankton for feeding marine invertebrates. In: Smith, W. L., Chanley, M. H. (eds.) Culture of marine invertebrate animals. Plenum Press, New York, p. 26–60

Hildreth, D. I., Crisp, D. J. (1976). A corrected formula for calculation of filtration rate of bivalve molluscs in an experimental system. J. mar. biol. Ass. U.K. 56: 111–120

Jumars, P. A., Nowell, A. R. M. (1984). Fluid and sediment dynamic effects on marine benthic community structure. Am. Zool. 24: 45–55

Kirby-Smith, W. W. (1972). Growth of the bay scallop: the influence of experimental water currents. J. exp. mar. Biol. Ecol. 8: 7–18

Klaveness. D. (1991). Biology and ecology of the Cryptophyceae: status and challenges. Biol. Oceanogr. 6: 257–270

Knight, D. W. (1981). Some field measurements concerned with the behavior of resistance coefficients in a tidal channel. Estuar., cstl Shelf Sci. 12: 303–322

LaBarbera, M. (1984). Feeding currents and particle capture mechanisms in suspension feeding animals. Am. Zool. 24: 71–84

McClatchie, S., Lewis, M. R. (1986). Limitation of grazing rate equations: the case for time-series measurements. Mar. Biol. 92: 135–140

Møhlenberg, F., Riisgård, H. U. (1979). Filtration rate, using a new indirect technique, in thirteen species of suspension-feeding bivalves. Mar. Biol. 54: 143–147

Monismith, S. G., Koseff, J. R., I'hompson, J. K.. O'Riordan, C. A., Nepf, H. M. (1990). A study of model bivalve siphonal currents. Limnol. Oceanogr. 35: 376–392

Muschenheim: D. K. (1987). The dynamics of near-bed seston flux and suspension-feeding benthos. J. mar. Res. 45: 473–496

Nichols, F. H. (1985). Increased benthic grazing: an alternative explanation for low phytoplankton biomass in northern San Francisco Bay during the 1976–1977 drought. Estuar., cstl Shelf Sci. 21: 379–388

Nowell, A. R. M., Jumars. P. A. (1984). Flow environments of aquatic benthos. A. Rev. Ecol. Syst. 15: 303–328

Nowell, A. R. M., Jumars, P. A. (1987). Flumes: theoretical and experimental considerations for simulation of benthic environments. Oceanogr. mar. Biol. A. Rev. 25: 91–112

Orive. E. (1989). Differences in phytoplankton abundance and distribution between the Abra of Bilbao and the adjacent shelf waters. Hydrobiologia 182: 121–135

Pattcn, B. C., Mulford, R. A., Warinner, J. E. (1963). An annual phytoplankton cycle in the lower Chesapeake Bay. Chesapeake Sci. 4: 1–20

Pedros-Alio, C., Mas, J., Gasol, J. M., Guerrero, R. (1989). Sinking speeds of free-living phototrophic bacteria determined with covered and uncovered traps. J. Plankton Res. 11: 887–905

Peterson, C. H., Black, R. (1987). Resource depletion by active suspension feeders on tidal flats: influence of local density and tidal elevation. Limnol. Oceanogr. 32: 143–166

Riisgård, H. U. (1988). Efficiency of particle retention and filtration rate in 6 species of Northeast American bivalves. Mar. Ecol. Prog. Ser. 45: 217–223

Rubenstein, D. I., Koehl, M. A. R. (1977). The mechanisms of filter feeding: some theoretical considerations. Am. Nat. 111: 981–994

Shumway, S. E., Cucci, T. L., Newell, R. C., Yentsch, C. M. (1985). Particle selection, ingestion, and absorption in filter-feeding bivalves. J. exp. mar. Biol. Ecol. 91: 77–92

Sternberg. R. W., Cacchione, D. A., Drake. D. E., Kranck, K. (1986). Suspended sediment transport in an estuarine tidal channel within San Francisco Bay, California. Mar. Geol. 71: 237–258

Stewart. A. J., Wetzel, R. G. (1986). Cryptophyceae and other microflagellates as couplers in planktonic community dynamics. Arch. Hydrobiol. 106: 1–19

Vogel, S. (1981). Life in moving fluids. the physical biology of flow. Willard Grant Press, Boston

Wildish, D. J., Kristmanson, D. D., Hoar, R. L., DeCoste, A. M., McCormick, S. D., White, A. W. (1987). Giant scallop feeding and growth responses to flow. J. exp. mar. Biol. Ecol. 113: 207–220

Wildish, D. J.. Miyares, M. P. (1990). Filtration rate of blue mussels as a function of flow velocity: preliminary experiments. J. exp. mar. Biol. Ecol. 142: 213–219

Winter, J. E. (1978). A review on the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. Aquaculture, Amsterdam 13: 1–33

Wong, R. L., Cloern, J. E. (1982). Plankton studies in San Francisco Bay. IV. Phytoplankton abundance and species composition. January 1980–February 1981. U.S. Geological Survey, Menlo Park (Open-File Report 82-443)

Yonge, C. M. (1946). On the habits and adaptations of Aloidis (Corbula) *gibba*. J. mar. biol. Ass. U.K. 26: 358–376