Retention efficiency and pumping rate of *Ostrea edulis* in suspensions of *Isochrysis galbana*

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ABSTRACT: Retention efficiency, E, of *Isochrysis galbana* and pumping rate, R_p, were measured in *Ostrea edulis* using a direct method in short-term (4 to 5 h) and long-term (54 to 56 h) experiments. E and R_p varied in all experiments. In the short-term experiments E and R_p were positively correlated in 44.4 % of the experiments and negatively correlated in 5.6 %. Long-term experiments showed that the relationship between E and R_p changed during the course of each experiment. E and R_p were related to the concentration of flagellate cells between concentrations of 1.74 and 487.5 cells μl^{-1}. E declined exponentially with concentration, while R_p reached a maximum rate at 23.81 cells μl^{-1} before declining at higher concentrations.

INTRODUCTION

This paper reports results of experiments on pumping rates and retention efficiencies of adult *Ostrea edulis* using the modified direct method of Hildreth (1976). Pumping rate or rate of water transport, R_p, is defined as the volume of water passing through the gills per unit time. Retention or filtration efficiency, E, represents the percentage of particles of a specified size removed from supension in a single passage through the gills.

The literature on suspension feeding of *Ostrea edulis* contains one brief report on pumping rate (Drinnan, 1964) and one on retention efficiency (Møhlenberg and Riisgård, 1978). The majority of studies have used indirect methods to measure filtration rates of *O. edulis* (Allen, 1962; Walne, 1972; Mathers, 1974; Newell et al., 1977; Rodhouse, 1978). Filtration or clearance rate, F, is defined as the volume of water filtered completely free of particles of specified size per unit time. However, Winter (1969 and 1976) has emphasized that conclusions drawn regarding either pumping rate or retention efficiency on the basis of results obtained using the indirect method are purely speculative in nature. E, in particular, has frequently been confused with relative retention efficiency, E_r, which is the efficiency of retention of a specific size-class of particles expressed as a percentage of the maximum retention efficiency for the particle-size classes filtered by the bivalve, e.g. Haven and Morales-Alamo (1970), Vahl (1972a, b, 1973a, b), Palmer and Williams (1980) and Williams (1982). Indirect methods can be used to measure E_r but not E.

The objective of the present investigation was twofold; firstly to measure R_p and E of the flagellate *Isochrysis galbana* by *Ostrea edulis*; secondly to determine if R_p and E were related to each other or to the algal concentration of the medium being filtered.

MATERIALS AND METHODS

Sublittoral specimens of *Ostrea edulis* were collected in Kilkieran Bay, Co. Galway by SCUBA, and cleaned of epibiotic growth and prismatic scales. A rubber balloon was cut into the form of a sleeve, fitted over the exhalant aperture of each oyster and glued in place with cyanoacrylate adhesive. Two small cubes of plastic sponge were placed between the shell margins and the edges of the sleeve to reduce leaks when the valves were open.

Oysters which had been fitted with sleeves were kept in a holding system for a minimum of 10 d at 20 °C and fed a suspension of 150–200 cells μl^{-1} *Isochrysis galbana* before being used. Each oyster was attached to the direct measurements apparatus at least 24 h before measurements were begun. The sleeve attachment was periodically tested for leaks using a fine jet of milk.
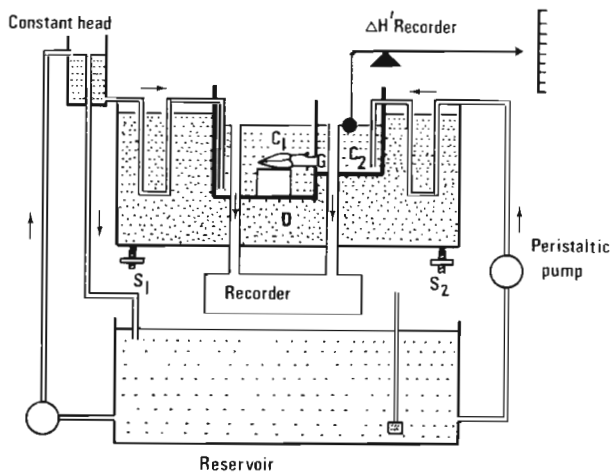
Fig. 1 *Ostrea edulis*. Apparatus for direct measurement of retention efficiency and pumping rate. For lettering see text

Direct measurement technique

The direct measurement apparatus used in the present investigation is shown in Fig. 1. The oyster was constantly illuminated, while water bath D was maintained at 20 °C for all experiments. The constant head described by Hildreth (1976) to supply chamber C_2 was replaced by a peristaltic pump to give a more precise control of water flow into C_2. The flow rates into C_1 and C_2 were maintained at 500 ml min^{-1} and 25 ml min^{-1} respectively unless otherwise specified.

The pre-adjustments described by Hildreth (1976) were employed to ensure that ΔH, the hydrostatic pressure difference between C_1 and C_2, was zero before the oyster was attached.

Measurement of R_p

R_p was measured during short-term experiments by collecting and measuring the total outflow from C_2 over 30 min periods, and subtracting from each volume of water collected the volume contributed by H_2 during that period (750 ml). In long-term experiments a 120 ml capacity dumping device (Loosanoff and Engle, 1947) connected to a chart recorder was used to record the outflow from C_2.

Pumping rates were weight-normalised for an ash-free dry tissue weight, A.F.D.W., of 1 g using the weight exponent of 0.74 (Winter, 1973).

Correction of R_p

An oyster in the direct measurement apparatus must do work by raising the water level in C_2 in order to increase R_p. If it is assumed that the gravitational potential energy of the water removed from the surface

around the lip of the standpipe is converted to kinetic energy in the flow over the lip then:

$$Q \cong 0.613 \, \pi \, d \, g^{\frac{1}{2}} \, h^{\frac{3}{2}} \qquad (1)$$

where Q = flow rate (ml min^{-1}); 0.613 = typical value for the discharge coefficient; d = internal diameter of the pipe; g = gravitational constant; h = height of water level above the lip. If $d = 14$ mm $g = 9.81$ m s^{-2} then:

$$Q \cong 501.5 \, h^{\frac{3}{2}} \qquad (2)$$

This theoretical model does not, however, take into account the influences of surface tension, viscosity, turbulence and geometric imperfections of the lip of the standpipe. Further analysis indicates that surface tension and geometric imperfections have a potentially greater influence than viscosity and turbulence, but both these factors are difficult to measure in the experimental system.

An alternative empirical approach was to measure the position of the water level in C_2 for various flow rates from the deflection of a lever and float system suspended in C_2 with G closed. A glass standpipe of 14 mm internal diameter was used. The observed pressure difference, $\Delta H'$, was assigned the arbitrary value of zero when water overflowed from C_2 at a minimal sustainable rate of 1.5 ml min^{-1}.

It was found that within a flow rate range of 1.5 to 173.0 ml min^{-1}

$$\log\Delta H' = 0.528\log Q - 1.352$$
$$(r = 0.984; \; n = 10). \qquad (3)$$

Thus the theoretical model (2) predicts that, for example, a flow rate of 150 ml min^{-1} will produce a pressure difference of approximately 0.45 mm, while the empirical model (3) predicts a pressure difference of approximately 0.63 mm. The difference is mainly attributable to the influences of surface tension and the imperfections on the lip of the pipe as previously stated.

The relationship between observed pumping rate, R_p' and $\Delta H'$ was found using the method of Hildreth (1976), but in the present study $\Delta H'$ was again taken as zero at a flow rate of 1.5 ml min^{-1}. Experiments were made with 7 oysters (mean A.F.D.W. $= 1.51 \pm 0.17$ g) for values of $\Delta H'$ between -1.20 and 1.22 mm. Analysis of covariance (ANCOVA) indicated that in all 7 experiments a common regression existed between R_p' and $\Delta H'$ ($F_{(6,37)} = 0.504$; $P > 0.05$) namely:

$$R_p' = 53.602 \, \Delta H' + 131.924 \qquad (4)$$

Hence the relationship between percentage change in R_p', $R_p'\%$, with $\Delta H'$ is given by:

$$R_p'\% = 40.631 \, \Delta H' \qquad (5)$$

In the experimental system the pressure difference

produced by the oyster is the difference between $\Delta H'$ at $(R_p' + 25)$ ml min^{-1} and H' at 25 ml min^{-1} or from (3) and (5):

$$R_p'\% = 1.808 \cdot 3.726^{\log (R_p' + 25)} - 9.892 \quad (6)$$

However, the arbitrary zero $\Delta H'$ is equivalent to a flow rate of 1.5 ml min^{-1}, which from (3) and (5) is an $R_p\%$ of 0.208 %. Therefore, the resultant correction factor, $R_p\%$, is given by:

$$R_p\% = 1.808 \cdot 3.726^{\log (R_p' + 25)} - 9.684 \quad (7)$$

Hence, for example, an R_p' of 150 ml min^{-1} will have a correction factor of 24.871 % giving a corrected R_p of 187.307 ml min^{-1}.

Measurement of E

The flagellate *Isochrysis galbana* was used because of its acceptability as a food to *Ostrea edulis*, its regular shape and size of 3.5 to 4.0 μm diameter and its low bioseston levels when fed (see below). Healthy cultures in the exponential growth phase were used to avoid depression of filtering by the oyster (Wilson, 1979; Griffiths, 1980). Sea water was filtered free of particles >1 to 2 μm by sand and cartridge filtration prior to the addition of algae.

Algal numbers were counted with a model B Coulter Counter with a 70 μm aperture tube. E was calculated using the formula of Hildreth and Mallet (1980). Retention of *Isochrysis galbana* did not have an obvious relationship with $\Delta H'$ and no correction factor was applied.

In short-term experiments E was calculated from duplicate 0.5 ml counts in samples taken from the total volume of water collected from C_2 during each 30 min period. In long-term experiments E was based on counts made on discrete 30 ml samples taken at hourly intervals.

The production of bioseston (Hildreth, 1980) by oysters fed *Isochrysis galbana* was examined in a series of 8 experiments. In each experiment the algal concentration of the inflowing water was kept constant. The size-frequency distribution of particles between 2 and 8 μm diameter in the inhaled and exhaled water was plotted using a J-plotter every 30 min over a 4 h period. E for each particle-size class varied with time, but did so in unison with E for other size classes. There was no evidence that bioseston was produced in significant quantities within the particle-size range examined or at concentrations of *I. galbana* between 14 and 350 cells μl^{-1}. Similar experiments with *Platymonas suecica* showed that high levels of bioseston even at low concentrations precluded accurate measurement of E (see also Hildreth, 1980).

Relationship between E and R_p

E and R_p were measured in 18 short-term experiments using 6 *Ostrea edulis* (mean A.F.D.W. = 1.34 ± 0.22 g). Each oyster was used in 3 experiments. In the first the oyster was subjected to 10 to 50 cells μl^{-1}, in the second to 150 to 200 cells μl^{-1} and to 300 to 350 cells μl^{-1} in the third. Each experiment lasted 5 h, following a 2 h adjustment period, during which the algal concentration was set at a value within one of the stipulated ranges.

E and R_p were also measured in five 54 to 56 h experiments. Five oysters (mean A.F.D.W. = 0.95 ± 0.098) were used. Concentrations of *Isochrysis galbana* were maintained at 100 cells μl^{-1}.

Relationship between algal concentration and E and R_p

Eight *Ostrea edulis* (mean A.F.D.W. = 1.25 ± 0.61 g) were used to determine the relationship between R_p and concentration of *Isochrysis galbana*, C, while 10 oysters (mean A.F.D.W. = 1.12 ± 0.56 g) were used in similar experiments for E and C. Each oyster was tested at 6 algal concentrations. Mean values for E and R_p were calculated for each value of C from readings made every hour over 4–5 h periods.

RESULTS

Relationship between E and R_p

E and R_p varied during all 18 5h experiments. The coefficient of variation of E ranged from 1.35 to 46.34 % with a mean of 15.19 %, while that of R_p ranged from 7.14 to 75.92 % with a mean of 27.82 % There was no significant correlation (P > 0.05) between

Table 1. *Ostrea edulis*. Significant regression equations (P > 0.01) of retention efficiency, E, on pumping rate, R_p, (l h^{-1}) for short-term experiments

Experiment number	Algal concentration (cells μl^{-1})	Regression equation	r	n
1	22	E = 4.40 R_p + 69.39	0.89	12
2	39	E = 3.37 R_p + 30.91	0.61	12
3	47	E = 19.82 R_p + 6.77	0.86	10
4	50	E = 0.74 R_p + 67.20	0.85	11
5	151	E = −5.87 R_p + 70.91	−0.56	11
6	194	E = 3.02 R_p + 56.71	0.58	10
7	200	E = 6.54 R_p + 47.47	0.75	10
8	301	E = 7.05 R_p + 32.09	0.78	10
9	350	E = 8.73 R_p + 32.23	0.72	11

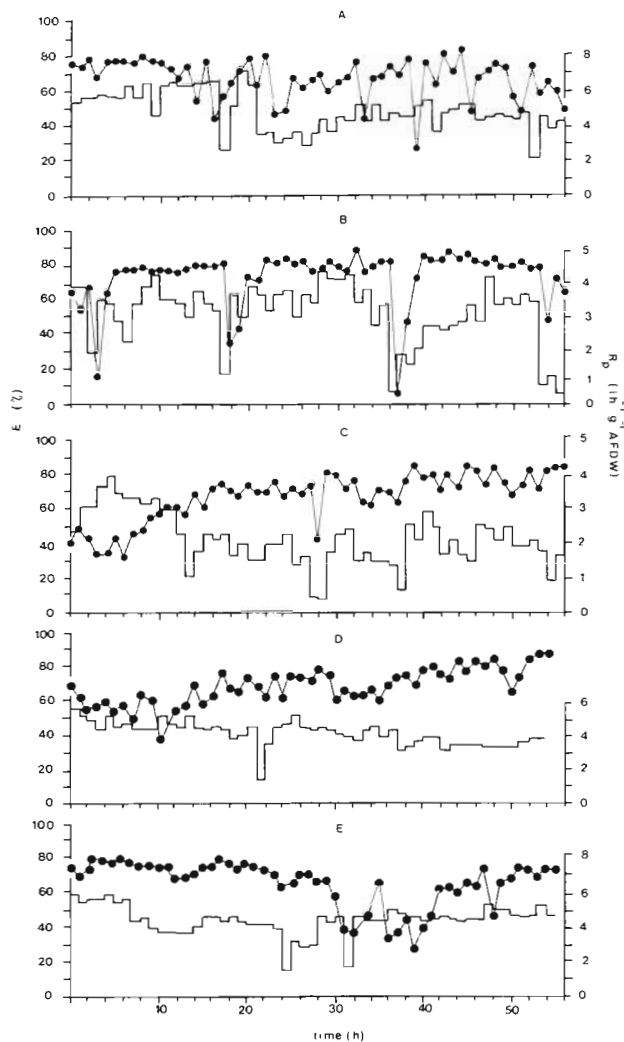'r' = correlation coefficient; 'n' = number of readings

Fig. 2. *Ostrea edulis*. Histograms of pumping rate, R_p ($1\,h^{-1}\,g^{-1}$ A.F.D.W.) with retention efficiency, E, (solid circles) over 54 to 56 h periods for 5 oysters (A to E) at 100 cells μl^{-1} *Isochrysis galbana*

the coefficients of variation of E and R_p and C. Regressions of E on R_p were significant ($P > 0.05$) in 9 experiments (Table 1). There was a $-$ve correlation between E and R_p in only 1 experiment (no. 5; Table 1), while there were $+$ve correlations in the remaining 8 experiments. Pair-wise comparisons of regression coefficients for the 8 $+$ve relationships by ANCOVA showed that Experiment nos. 2, 7, 8 and 9 were related by a common regression line ($P > 0.01$):

$$E = 4.933\ R_p + 35.407 \qquad (r = 0.680)$$

No conclusions could be made as to the effect of C on the relationship between E and R_p.

Temporal variations in E and R_p occurred in all five 54 to 56 h experiments (Fig. 2), but no pattern of fluctuation in E or R_p with time was evident from ANCOVA.

When each of the 5 long-term experiments was subdivided into eight 6 h periods and 1 concluding 6 to 8 h period, a significant linear relationship ($P > 0.05$) existed between E and R_p during 9 of the 45 periods (Table 2). The relationship was $-$ve in only 1 period ($C_{7-12\,h}$, Table 2), while pair-wise comparisons of regression coefficients for the remaining 8 $+$ve relationships by ANCOVA showed that, except for 2 periods ($B_{37-42\,h}$ and $D_{43-48\,h}$; Table 2), the relationship between E and R_p shared a common regression line ($P > 0.05$):

$$E = 9.317\ R_p + 42.823 \qquad (r = 0.785)$$

Relationship between C and E and R_p

In Figs. 3 and 4 relative retention efficiency, %E, and relative pumping rate, %R_p, percentages of the maximum values recorded for each oyster in the ranges of C tested, are plotted against C. For %E and C the exponential curve

Table 2. *Ostrea edulis*. Significant regression equations ($P > 0.05$) of retention efficiency, E, on pumping rate, R_p, ($1\,h^{-1}$) for long-term experiments

Experiment	Interval (h)	Regression equation	r	n
B	13–18	$E = 20.17\ R_p + 20.33$	0.95	6
B	37–42	$E = 24.17\ R_p + 26.85$	0.82	6
B	49–56	$E = 7.50\ R_p + 56.57$	0.84	8
C	7–12	$E = -6.33\ R_p + 72.87$	−0.80	6
C	37–42	$E = 7.67\ R_p + 60.26$	0.83	6
D	43–48	$E = 39.67\ R_p - 52.24$	0.85	6
E	7–12	$E = 4.17\ R_p + 54.99$	0.70	6
E	13–18	$E = 7.83\ R_p + 40.37$	0.87	6
E	19–24	$E = 14.17\ R_p + 11.10$	0.61	6

'r' = correlation coefficient; 'n' = number of readings

$$\%E = 100 \, e^{-0.0021C}$$

gives the best fit ($r = -0.849$: $P > 0.001$). The parabola:

$$\%R_p = 29.75 + 44.32 \ln C - 6.99 \, (\ln C)^2$$

is the best fit for $\%R_p$ and C ($r^2 = 0.62$: $P > 0.001$). This curve is valid only for concentrations between 1.74 and 487.50 cells μl^{-1}. There was considerable scatter of data points in both plots. The standard error of estimate for $\%E$ on C was $\pm 16.94 \%$, while for $\%R_p$ on C it was $\pm 21.34 \%$.

DISCUSSION

Drinnan (1964) recorded an average pumping rate for *Ostrea edulis* of unspecified weight of 3.39 $l \, h^{-1}$ at a temperature of 18.5 °C, while in the absence of shell movements a steady rate of almost 41 h^{-1} was achieved. The mean weight-specific pumping rate recorded in the present investigation for 12 oysters for periods in excess of 5 h at a temperature of 20 °C and an algal concentration of 100 cells μl^{-1} *Isochrysis galbana* was $4.99 \pm 1.691 \, h^{-1} \, g^{-1}$ A.F.D.W. Mean retention efficiency for the same oysters was $65.90 \pm 11.21 \%$ Møhlenberg and Riisgård (1978) measured E as 62 to 80 % for *O. edulis* filtering low concentrations (< 10 particles μl^{-1}) of 3.5 to 4.0 μm diameter particles (assuming a maximum E of 86–98 % within the particle sizes examined). This is equivalent to approximately 51 to 66 % at 100 cells μl^{-1} *I. galbana* (assuming $\%E = 100 \, e^{-0.0021C}$).

The mean weight specific filtration rate calculated from R_p and E values measured in the present study was $3.3 \pm 1.7 \, l \, h^{-1} \, g^{-1}$ A.F.D.W. at a concentration of 100 cells μl^{-1} *Isochrysis galbana*. F values for adult *Ostrea edulis* have been recorded by Allen (1962), Walne (1972), Mathers (1974), Newell et al. (1977) and Rodhouse (1978). The different types and concentrations of suspensions used in these studies made comparisons with F recorded in the present investigation difficult. Some estimates can be made, however, from the available information.

Allen (1962) used small oysters of 80 mg mean A.F.D.W. When F measured by Allen is weight normalised (using a weight exponent of 0.74) the resulting value is $3.51 \, l \, h^{-1} \, g^{-1}$ A.F.D.W. for concentrations of 30–60 cells μl^{-1} *Phaeodactylum tricornutum*. E is presumably higher for *P. tricornutum* than for *Isochrysis galbana* because of its greater size. Walne (1972) recorded an F value of $11.422 \, l \, h^{-1} \, g^{-1}$ A.F.D.W. at a flow rate of 400 ml min^{-1} for oysters of 0.884 g mean A.F.D.W. Oysters of 1.250 g mean A.F.D.W., however, had an F of $8.804 \, l \, h^{-1} \, g^{-1}$ A.F.D.W. at the same flow rate. It should also be noted that Walne (1972) rejected low F values. The lack of detailed information on
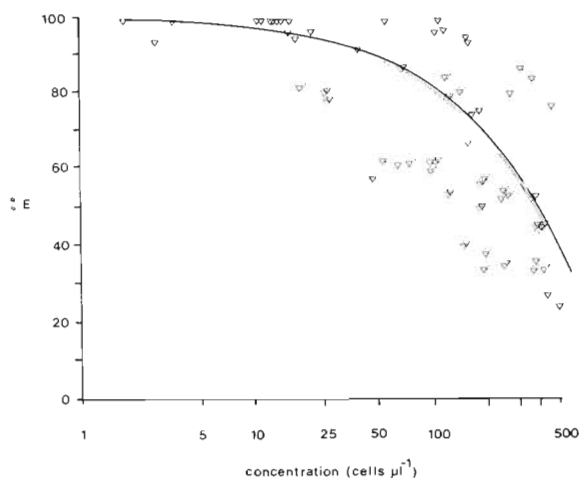

Fig. 3. *Ostrea edulis*. Relative retention efficiency, $\%E$, against *Isochrysis galbana* concentration, C, (cells μl^{-1}). The results for 10 oysters, each tested at 6 concentrations, have been pooled (mean A.F.D.W. = 1.12 ± 0.56 g). The curve, $\%E = 100 \, e^{-0.0021C}$, was fitted by the method of least squares ($r = 0.849$)

particle concentrations and sizes used by Walne (1972) make adjustments of his F values for comparative purposes impossible. Mathers (1974), Newell et al. (1977) and Rodhouse (1978) quote relatively low F values for *Ostrea edulis* of 60 ml h^{-1} wet weight (300 ml $h^{-1} \, g^{-1}$ A.F.D.W. assuming a water content of 80 %), 495 ml h^{-1} per 285 mg A.F.D.W. ($1.27 \, l \, h^{-1} \, g^{-1}$ A.F.D.W. normalised with a weight exponent of 0.74) and $1.63 \, l \, h^{-1}$ g^{-1} A.F.D.W. respectively. Particle concentrations used by Mathers (1974) and Rodhouse (1978) are not given. Newell et al. (1977) used 50 cells μl^{-1} *P. tricor-*
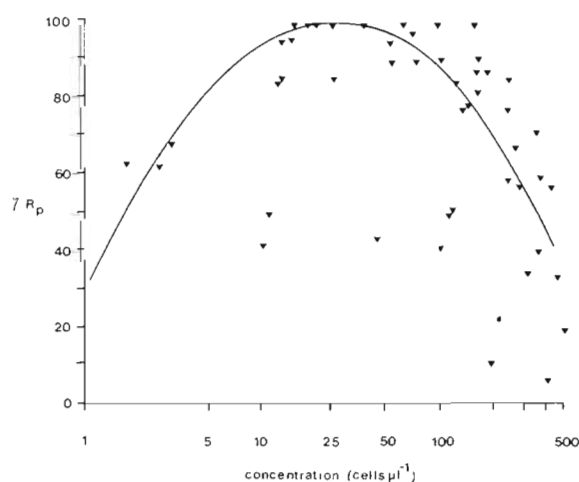

Fig. 4. *Ostrea edulis*. Relative pumping rate, $\%R_p$, against *Isochrysis galbana* concentration, C, (cells μl^{-1}). The results for 8 oysters, each tested at 6 concentrations, have been pooled (mean A.F.D.W. = 1.25 ± 0.61 g). The curve, $\%R_p = 29.75 + 44.32 \ln C - 6.99 \, (\ln C)^2$, was fitted by the method of least squares ($r^2 = 0.62$)

nutum, which would again be retained more efficiently.

The differences between published values of F for *Ostrea edulis* may be attributable in part to the indirect methods used. Hildreth and Crisp (1976) and Riisgård (1977) have shown that recirculation of exhaled water may cause underestimation of F. Thompson and Bayne (1972), Wilson and Seed (1974) and Griffiths (1980) showed that feeding after starvation may be atypical. Hildreth (1980) has also shown that some algae, including *Platymonas suecica* and *Phaeodactylum tricornutum*, are potential sources of bioseston leading to underestimates of filtering.

The direct method has also been criticised by various authors. The problem of pressure differences has already been discussed by Hildreth (1976) and in the present paper. Jørgensen (1966), Walne (1972) and Bayne et al. (1976) have suggested that the rubber sleeve attached to the bivalve causes an atypical pumping rate. No supporting evidence, however, is offered by these authors. Vahl (1972a) and Jørgensen (1976) also suggest that low retention efficiencies in some direct studies are due to disturbance of the bivalve by the sleeve. They erroneously support this contention by comparisons of E recorded by direct methods and relative retention efficiencies, E_r, measured indirectly.

Relationships between E and R_p have been examined by Tammes and Dral (1955), Davids (1964), Wilson and Seed (1974), Bayne et al. (1976) and Hildreth and Mallet (1980). In the 3 earliest reports an inverse relationship between E and R_p was observed. Bayne et al. (1976) proposed on theoretical grounds that there could be no relation between the 2 parameters. Hildreth and Mallet (1980) identified 3 relationships between the 2 parameters. The commonest was a Type *a* behaviour; the maintenance of a constant E while R_p varied. Type *b* behaviour (+ ve correlation) and Type *c* (− ve correlation) were less common. In the present investigation E and R_p were correlated in 50 % of 18 short-term experiments, but no Type *a* behaviour was evident. Type *b* behaviour was recorded in 44.4 % of the experiments, while Type *c* behaviour was present in 5.6 % of the experiments. Furthermore, only half of the Type *b* relationships shared a common regression. In the 5 long-term experiments, where E was not recorded continuously, there was a linear relationship between E and R_p in only 20 % of the 45 6- to 8-h periods; 17.7 % being Type *b* and 2.2 % Type *c*. Only 13.3 % of the Type *b* relationship shared a common regression line.

Hildreth and Mallet (1980) explained the 3 types of behaviour in terms of the synchrony of groups of laterofrontal cirri and the resultant effect on the dimensions of the gill-filter meshwork. The mechanics of

suspension feeding at low Reynold's number have been discussed by Strathmann (1971), Fenchel (1980), Jørgensen (1981) and Koehl and Strickler (1981) amongst others. Jørgensen (1981) stated that 'instead of acting as filters, the laterofrontal cirri seem to move water', and that particle retention by the gill 'depends primarily upon the size of the particle, and upon the steepness and height of the gradients within the boundary zone between the surface current and the through current'. In the light of these studies theories regarding the function of the laterofrontal cirri as proposed by Hildreth and Mallet (1980) may not be valid. The results of the present paper indicate that relationships between E and R_p for *Ostrea edulis* are only partially explained by the mechanism described by Hildreth and Mallet (1980) for *Mytilus edulis*.

In general it has been found that F decreases as particle concentration increases (see review by Winter, 1976). In Fig. 5, F as calculated from results of the
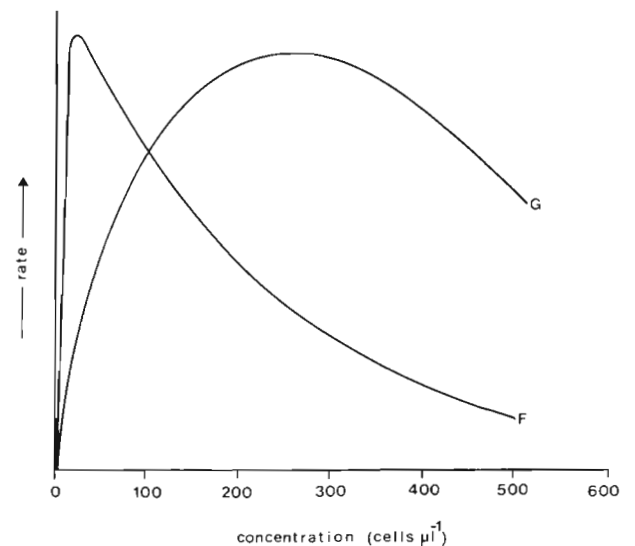

Fig. 5. *Ostrea edulis*. Relationship between filtration rate, F, grazing rate, G, and *Isochrysis galbana* concentration (cells μl^{-1})

present investigation is plotted against C. After rising to an initial peak at 18.2 cells μl^{-1}, F declines steadily with concentration. Grazing rate, G, the rate of cell uptake by the oyster, increases with concentration to a maximum at 235.3 cells μl^{-1} and declines thereafter. The general form of the curves corresponds with Winter's schematic representation of food concentration and filtration rate (Fig. 11: Winter, 1976), although no plateaux in the curves as described by Winter are apparent.

Studies on the effects of particle concentration on E and R_p have been limited to *Mytilus edulis* and *Crassostrea virginica* (Loosanoff and Engle, 1947;

Loosanoff and Tommers, 1948; Tammes and Dral, 1955; Davids, 1964; Wilson and Seed, 1974, and Hildreth and Mallet, 1980). In all these studies it was found that R_p decreased with increasing particle concentration. Loosanoff and Engle (1947) and Davids (1964) suggested tentatively that E decreased with increased particle concentration in *C. virginica* and *M. edulis* respectively. Hildreth and Mallet (1980) found that E of 5μ diatoms by *M. edulis* was independent of concentration up to 110 cells μl^{-1}. It is interesting that Davids (1964) recorded E values of 25 and 31 % at 400 cells μl^{-1} *Isochrysis galbana* compared with 83 and 87 % at 100 cells μl^{-1} *I. galbana*. The much larger *Phaeodactylum tricornutum* did not produce a marked decline in an E of 86 to 98 % until concentrations of 900 cells μl^{-1} or more were reached. The indirect studies of Wilson (1980) and Palmer and Williams (1980) of particle-size selection and retention by larvae and spat of *Ostrea edulis* and adult *Argopecten irradians* and *C. virginica* respectively indicate that the retention/concentration response may be governed by particle size.

The concentrations of cells used in the present study are representative of those that may be encountered in maricultural systems. Similar concentrations of particles probably occur on oyster beds. Rodhouse (1978) measured maximum total particulate matter concentrations of almost 50 mg A. F. D. W. l^{-1} at the Beaulieu oyster beds in England, while high seston levels have been recorded in other oyster growing areas (Jørgensen, 1966). It would seem therefore, that adjustments of E and R_p by *Ostrea edulis* do occur in some natural situations.

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