Vol. 141: 37–45, 1996 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published October 3

Growth, filtration and respiration in the mussel *Mytilus edulis*: no evidence for physiological regulation of the filter-pump to nutritional needs

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ABSTRACT: The specific growth rate of blue mussels *Mytilus edulis* fed *Rhodomonas* sp. algal cells in laboratory experiments increased with increasing food concentration to obtain a maximum value of about 9.5% d^{-1}, irrespective of a relatively high concentration of silt (5 mg l^{-1}) added to the water. Likewise, the net growth efficiency increased with the specific growth rate to a maximum value of about 75%. Measurements of the relationship between respiration and growth showed that the energy cost of growth constituted 12% of the growth. The filtration rate of a 100 mg dry wt 'standard' mussel was high and constant (about 30 ml min^{-1}) at algal concentrations below about 6000 cells ml^{-1} when measured in both short-time (5 h) and long-time (9 to 14 d) experiments. High algal concentrations of 1.3 to 2.4 × 10^4 cells ml^{-1} reduced the filtration rate by about 40%. The estimated growth, presuming maximum filtration rate, satisfactorily described the actual growth at algal concentrations <5000 cells ml^{-1}, and the concentration necessary for maximum growth was estimated at 4500 cells ml^{-1} (corresponding to 5.6 µg chlorophyll *a* l^{-1}). The mean specific growth rate in *M. edulis* transferred in net bags to a fjord system (Kertinge Nor/Kerteminde Fjord, Denmark) was about 6% d^{-1}. The results show that there is no physiological regulation of the filtration rate to nutritional needs, and that food uptake in nature (median concentration in Danish waters = 5.1 µg chlorophyll *a* l^{-1}) is characterized by the full exploitation of the capacity of the bivalve filter-pump.

KEY WORDS: Actual and estimated growth · Feeding and effects of silt · Costs of growth · Net growth efficiency · Regulation of filtration rate

INTRODUCTION

It has been claimed by Jørgensen (1990, 1996) that food uptake by mussels is basically an autonomous process which is not regulated at the organismic level according to nutritional needs. This view conflicts with the majority of the bivalve filter-feeding literature which apparently disregards laboratory experiments that have shown the capacity of the bivalve filter-pump to be usually fully exploited in the presence of phytoplankton (Riisgård & Larsen 1995). Adverse environmental conditions, including very low or unnaturally high algal concentrations, may, however, cause reduction of water pumping due to closure of the valves (Riisgård & Randløv 1981, Riisgård 1991). To assess if valve closure may be a consequence of physiological regulation of the filtration rate it is helpful to determine the minimal algal concentration which may lead to maximum growth when the bivalve is utilizing its pump capacity (no regulation). Such knowledge, combined with field data for growth and phytoplankton concentrations, may form the basis for reconsidering the hypothesis for regulation of the filtration rate in filter-feeding bivalves. In the present work such fundamental knowledge is gained through experimental determination of growth, filtration and respiration in *Mytilus edulis*, and the measured values are used as parameters in an energy budget used for estimating the growth rate at different algal concentrations. Further, we have examined whether or not an admixture of silt is a prerequisite for mussels to obtain maximum growth as proposed by Kiørboe et al. (1981), Møhlenberg & Kiørboe (1981) and Jørgensen (1990).

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MATERIALS AND METHODS

Blue mussels *Mytilus edulis* were collected from piers (1 to 2 m water depth; 15‰ S) in Helnæs Bight, southwestern Funen, Denmark, and transported to the Fjord Biological Laboratory, Kerteminde. The locality for collecting mussels was selected because of a low condition index (CI = W/L^3, where W = dry wt of soft parts and L = shell length) which empirically prevented the mussels from spawning during feeding experiments in the laboratory. Mussels in the shell length size range of 25 to 30 mm were selected for both laboratory experiments and field growth experiments.

Laboratory experiments. ***Growth:*** Growth experiments were conducted in 14 l aquaria with through-flowing bio-filtered seawater (about 15°C and 15 to 18‰ S) (Fig. 1). A dosing pump supplied the growth aquaria holding the experimental mussels with suspensions of pure algae (A-experiments) or algae plus silt (AS-experiments), which were kept homogeneous by strong aeration. The growth experiments were carried out as 3 series (I, II, III) of 5 replicates supplied by the same source tank (I: A_0, A_2, A_3, A_2S, A_4S; II: A_0S, A_1, A_4, A_1S, A_4S; III: A_5, A_6, A_7, A_8, A_9; cf. Table 1). The flagellate *Rhodomonas* sp. from a continous culture (constant pH and dilution rate) was used as food. The algal concentration was measured by means of an electronic particle counter (Elzone 80 XY). Silt suspensions were made of industrially manufactured 'moler powder' (GM-2, Damolin) consisting of a pure mixture of inorganic clay particles and shells of diatoms from an Eocaenian deposit (Fur, Denmark). The silt used consisted of particles of different sizes (2 to 6 µm: 50% of weight; 2 to 30 µm: 90% of weight; from data-sheet specifications given by Damolin) and with a low carbon content (0.4% of weight). The actual content of silt in the different experiments (about 5 mg l^{-1}) was checked by filtering a known volume of water through pre-combusted GF/C filters, which were afterwards rinsed with distilled water to remove salt, and dried (105°C, 23 h) before weighing and subsequent burning (450°C, 24 h) and reweighing to determine the ash-free dry weight. In AS-experiments the fluorescence (Sequia-Turner, model 450) in water samples (10 ml) was used to determine the algal concentration. Shell length and flesh dry weight (24 h, 105°C) were determined for a representative group of mussels (n = 15) on Day 0 and for all remaining mussels (n = 25) at the end of the growth period on Day t. The specific growth rate was determined according to Eq. (1) (see later).

Filtration: The filtration rate was measured as the volume of water cleared by *Rhodomonas* sp. (almost spherical cells, about 6.2 µm in diameter). The particle size for 100% retention efficiency is about 4 µm in *Mytilus edulis* (Møhlenberg & Riisgård 1978). Flagellate cells were added to strongly aerated aquaria (volume, V = 14 l) each containing a group of 25 mussels, which was sufficient to limit individual variation. The reduction in the number of algal cells as a function of time was followed by taking samples every 5 min and measuring the algal concentration. The filtration rate (F) was determined from the exponential reduction in algal concentration using the formula: $F = (V/nt)\ln(C_0/C_t)$, where C_0 and C_t are the algal concentrations at time 0 and time t, respectively, and n = number of mussels. The filtration rate was measured in 2 types of experiments: (1) short-time (5 h) exposure experiments in which the same group of mussels were exposed to 4 different algal concentrations (about 2.5, 8.5, 13 and 24 × 10^3 cells ml^{-1}) with or without about 5 mg silt l^{-1}; (2) long-time (9 to 14 d) exposure experiments with steady-state concentrations of algae and silt, as described for the growth experiments (A- and AS-experiments). In the long-time experiments the dosing pump and water through-flow were stopped at time 0 on different days and the exponential reduction in algal concentration measured (verified as a straight line in a semi-log plot made by hand during the experiment) The slope of the line was used to estimate the filtration rate (no sedimentation was recorded in a control aquarium).

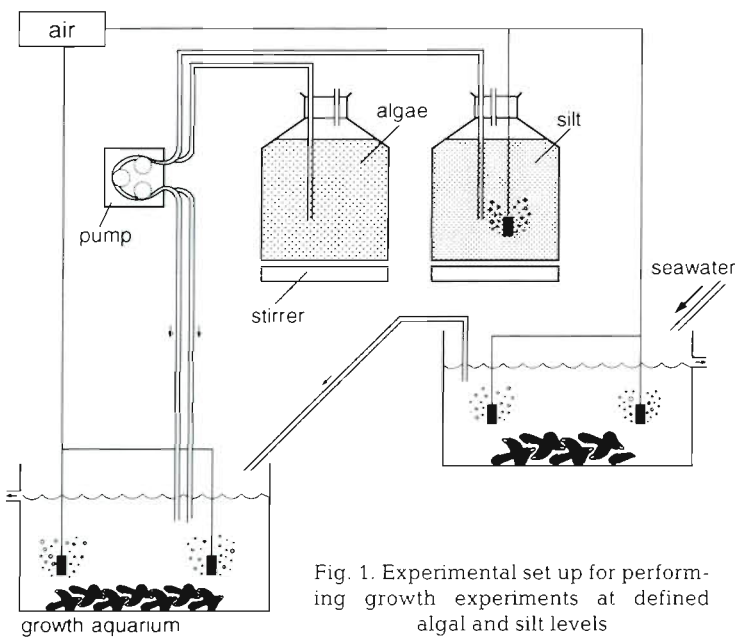

Fig. 1. Experimental set up for performing growth experiments at defined algal and silt levels

Respiration: On the last day of the growth period mussels (8 to 10 individuals) were transferred directly from each growth aquarium to a respiration chamber with 250 ml seawater and an algal concentration of 3 × 10^3 algal cells l^{-1}. The respiration chamber was made of a plexi-

Table 1 *Mytilus edulis*. Shell length (L), shell growth (ΔL), condition index (CI), soft tissue dry weight (W) and specific growth rate (μ) for blue mussels in laboratory experiments. Subscript 0 and t refer to start and end of experiment, respectively. Experiments performed with pure algae or algae + silt are indicated by A_x and A_xS, respectively. Standard deviation (± SD) is indicated

Expt	Shell length (mm)		Shell growth (mm mo^{-1})	Condition index CI = W/L^3 (mg cm^{-3})		Soft tissue dry weight (mg)		Specific growth rate (% d^{-1})
	L_0	L_t	ΔL	CI_0	CI_t	W_0	W_t	μ
A_0	29.86 ± 0.39	31.47 ± 1.06	2.01	6.07	3.69	161.8 ± 20.9	115.1 ± 16.5	−1.4
A_1	27.68 ± 0.18	28.09 ± 0.50	0.95	2.12	3.49	44.9 ± 12.8	80.5 ± 16.0	4.5
A_2	28.47 ± 0.16	29.86 ± 0.39	3.09	2.78	6.07	64.3 ± 21.5	161.8 ± 20.9	6.8
A_3	28.47 ± 0.16	29.54 ± 0.63	2.38	2.78	7.02	64.3 ± 21.5	186.2 ± 29.8	7.9
A_4	27.68 ± 0.18	27.71 ± 0.32	0.10	2.12	4.58	44.9 ± 12.8	102.2 ± 13.4	9.1
A_0S	27.68 ± 0.18	27.59 ± 0.26	0.00	2.12	1.79	44.9 ± 12.8	37.6 ± 9.9	−1.4
A_1S	27.68 ± 0.18	27.69 ± 0.34	0.02	2.12	3.35	44.9 ± 12.8	72.3 ± 8.7	3.7
A_2S	28.47 ± 0.16	29.66 ± 0.51	2.64	2.78	6.21	64.3 ± 21.5	162.2 ± 21.6	6.9
A_3S	28.47 ± 0.16	29.79 ± 0.94	2.93	2.78	7.37	64.3 ± 21.5	195.7 ± 31.0	8.2
A_4S	27.67 ± 0.18	27.73 ± 0.41	0.17	2.12	5.03	44.9 ± 12.8	107.4 ± 16.0	9.7
A_5	27.00 ± 0.70	28.20 ± 0.80	3.35	3.89	3.84	77.0 ± 12.0	87.0 ± 15.0	1.1
A_6	26.60 ± 0.80	31.80 ± 1.10	4.73	4.02	4.56	77.0 ± 21.0	146.0 ± 20.0	1.9
A_7	27.40 ± 0.30	29.03 ± 0.60	2.15	3.00	4.79	61.5 ± 11.6	117.3 ± 14.3	2.8
A_8	28.40 ± 0.20	29.70 ± 0.60	2.79	3.58	5.25	81.7 ± 14.2	137.3 ± 24.1	3.7
A_9	31.60 ± 0.90	34.70 ± 1.10	3.88	3.66	5.47	116.0 ± 23.9	229.1 ± 29.1	2.8

glass tube (inner diameter = 60 mm) with one end closed and the other end tightened with a plexiglass collar through which an oxygen electrode was inserted into the chamber This electrode was connected to an oxygen monitor (WTW, microprocessor-based oximeter, OXI 196) and recorder (Servogor S). A magnetic stirrer (Oximeter-RZ 90) was mounted close to the membrane of the electrode and coupled to an outside rotating magnet. The temperature was held constant (15°C) by placing the respiration chamber in a water bath. All measurements were made about 20 min after transfer of mussels to the respiration chamber. The decreasing dissolved oxygen tension was continously monitored over 20 to 30 min. Two respiration measurements were carried out in series on each group of mussels. Control measurements without mussels were performed at the start and end of each series of respiration measurements. The oxygen uptake rate was calculated from the decrease of dissolved oxygen tension taking temperature, salinity and pressure into consideration.

Field growth experiments. Blue mussels for field growth experiments were transferred to commercially manufactured cylinder-shaped net bags (n = 30 individuals) made of polypropylene fibers with a mask width of 0.5 to 1.0 cm (Riisgård & Poulsen 1981). The bags were placed 1 m below the water's surface at 5 stations in the fjord system consisting of Kerteminde Fjord/Kertinge Nor. The fjord has a sill at its mouth to the Great Belt. The discharge over the sill is forced by the diurnal tide (± 20 cm) and the salinity varies typically between 14 and 22‰ over the year (fresh water input is negligible) (Jürgensen 1995). Growth experiments were conducted during 3 periods: (I) May 28 to June 14, 1994 (mean temperature = 15.0 ± 0.4°C), (II) April 28 to May 25, 1992 (8.5 ± 0.7°C), and (III) June 1 to July 28, 1992 (19.5 ± 1.1°C). During the growth periods water samples (5 l) for measurement of chlorophyll *a* were taken frequently (period I: 9 times; II: 10; III: 5) at each station. The water samples were filtered (Whatman GF/C, 0.3 bar) and the chlorophyll extracted into 10 ml of 96% ethanol and placed in the dark for 24 h. Chlorophyll *a* content was measured according to standard procedures (Arvola 1981) by measuring the absorption at 665 nm on a Perkin-Elmer model 554 spectrophotometer. Shell length and flesh dry weight (24 h, 105°C) were determined for a representative group of mussels (n = 30) on Day 0 and for all the remaining mussels in the net bags (n = 30) at the end of the growth period on Day t. The specific growth rate was determined according to Eq. (1) (see below).

Calculations of specific growth and energetic parameters. The specific growth rate (μ, d^{-1}) of *Mytilus edulis* was calculated according to:

$$\mu = \ln(W_t/W_0)t^{-1} \quad (1)$$

where W_0 and W_t are the mean body masses of the mussels on Day 0 and Day t, respectively.

By simultaneous measurements of respiration and growth in animals with body mass, W, the relationship between total respiration rate (R_t) and growth rate ($\mu \times W$) may be described according to Kiørboe et al. (1987): $R_t = R_m + n\mu W$ or

$$R_t/W^b = a + n\mu W^{1-b} \quad (2)$$

where R_m (= aW^b where a and b are constants) is the metabolic maintenance (measured as starvation

respiration rate) and n is the energy cost per unit of growth, also termed 'net cost of growth' (Wieser 1994). In the present work the energy cost of growth was estimated by using $b = 0.67$ (Hamburger et al. 1983) and experimentally determined values of R_t and μ, which enables the identification of n (i.e. M = the slope of regression line for R_t/W^b, referred to as the 'scaled' specific respiration rate, as a function of μW^{1-b}, the 'scaled' specific growth rate).

The energy balance of a mussel can be expressed as:

$$I = G + R_t + E \quad (3)$$

where I is ingestion; G is growth (production); R_t is total respiration (sum of maintenance respiration, R_m, and respiratory cost of growth, R_g); and E is excretion. Further, assimilation, $A = G + R_t$, and the net growth efficiency, $NGE = G/A$ or:

$$NGE = G/(G + R_t) \quad (4)$$

In the present work the growth was described as: $G = I \times AE - (R_m + R_g)$ or:

$$G = (F \times C \times AE) - (R_m + R_g) \quad (5)$$

where AE is assimilation efficiency, F is filtration rate, and C is algal concentration.

Conversion factors. The following conversion factors were used for estimating growth of *Mytilus edulis* according to Eq. (5) and Riisgård (1991): (1) algal cells, *Rhodomonas* sp., equivalent to 1.75 µJ cell^{-1} (Kiørboe et al. 1985); (2) maintenance respiration rate (R_m, ml O_2 h^{-1}) as a function of size (W, g dry wt) in *M. edulis*: $R_m = 0.475 W^{0.663}$ (Hamburger et al. 1983); (3) 1 ml O_2 h^{-1} = 19.88 J h^{-1} = 5522 µJ s^{-1} (or microwatts, µW); (4) 1 mg dry wt of soft parts of *M. edulis* = 20.51 J = 0.43 mg C. The relationship between chlorophyll *a* concentration (µg chl *a* l^{-1}) and concentration of *Rhodomonas* sp. (C, $\times 10^3$ cells ml^{-1}) was determined by triple determination of samples of filtered seawater added to different algal concentrations (0.2 to 3×10^4 cells ml^{-1}): chl *a* = $1.251 \times C$ (n = 5, $r^2 = 0.999$).

RESULTS

Growth and filtration rates

The specific growth rate in laboratory experiments with *Mytilus edulis* increased with increasing food concentration to obtain a maximum value of about 9.5% d^{-1}, irrespective of a relatively high concentration of silt (5 mg l^{-1}) added to the water (Fig. 2). Likewise, the net growth efficiency (Table 2) increased with the specific growth rate to obtain a maximum value of about 75% for $\mu > 6\%$ d^{-1} (Fig. 3).

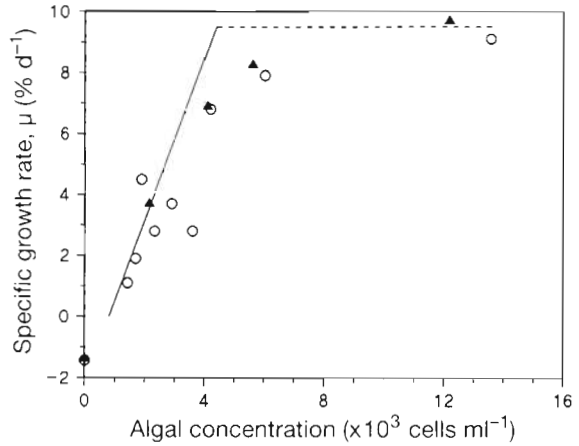

Fig. 2. *Mytilus edulis*. Specific growth rate (μ) as a function of algal concentration in laboratory experiments. (○) Growth experiments without silt (A-experiments); (▲) results from growth experiments with about 5 mg l^{-1} silt added to the water (AS-experiments; Table 1). The actual experimentally determined specific growth rates may be compared with the theoretically estimated growth rate shown by the inserted line which is based on Eq. (5), assuming cost of growth = 12% of growth, and μ_{max} = 9.5% d^{-1} Dotted line indicates maximum possible growth

Fig 4 shows laboratory measurements of the relationship between scaled specific respiration rate and scaled specific growth rate. As the slope of the regression line expresses the energy cost per unit of growth (cf. Eq. 2), it can be seen that the energy cost of growth constituted $[118.5 \times (19.88/20.51)/1000] \times 100 \approx 12\%$ of the growth, irrespective of silt added to the water.

Fig. 5A shows the results from a typical filtration experiment. The reduction in algal concentration between new additions of algal cells is fast and constant (i.e. constant slope of line fitted for the algal reduction in a semi-log plot) The estimated filtration rates for all time inter-

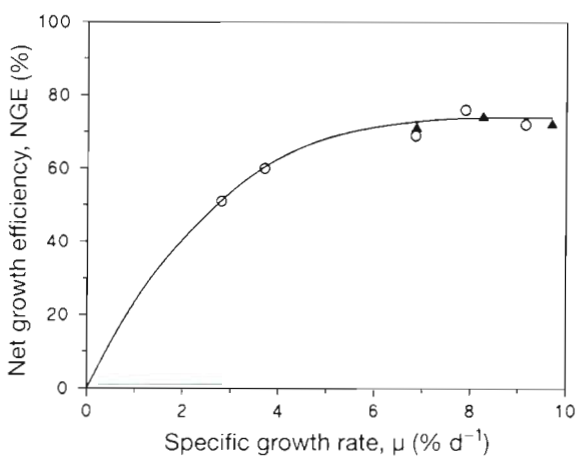

Fig. 3. *Mytilus edulis*. Net growth efficiency (*NGE*) as a function of specific growth rate (μ) in laboratory experiments. Symbols as in Fig. 2

vals between new algal additions are shown in Fig. 5B together with a parallel experiment with silt added to the water. The results of this and similar short-time experiments performed at higher algal concentrations are shown in Table 3, together with the results obtained from the long-time experiments. It is seen that the individual filtration rate is high (about 30 ml min^{-1}) at algal concentrations below about 6000 cells ml^{-1}, and unaffected (or slightly stimulated in the short-time experiments) by silt in the water. At high algal concentrations of 13 to 24 $\times 10^3$ cells ml^{-1} the filtration rate is considerably reduced. Observations made during the experiments confirmed that the mussels partly closed their valves and reduced the opening of the exhalant siphon at the high algal concentrations. Production of pseudofaeces was observed in all experiments with silt and in pure algal experiments with concentrations $\geq 8.5 \times 10^3$ cells ml^{-1} (Table 3).

Table 2. *Mytilus edulis*. Food concentration, carbon specific growth (G) and respiration (R) rate, and net growth efficiency [$NGE = G/(G+R)$]. Experiments performed with pure algae or algae + silt are indicated by A_x and A_xS, respectively

Expt	Algal concentration ($\times 10^3$ cells ml^{-1})	Food concentration (µg C l^{-1})	G (µg C mg^{-1} C d^{-1})	R (µg C mg^{-1} C d^{-1})	NGE (%)
A_0	0 ± 0	0	−14	21	−193
A_1	1.9 ± 0.4	89	45	–	–
A_2	4.1 ± 0.8	196	68	30	69
A_3	6.0 ± 1.5	284	79	25	76
A_4	13.6 ± 7.0	640	91	36	72
A_0S	0 ± 0	0	−14	34	−71
A_1S	2.1 ± 0.5	101	37	–	–
A_2S	4.1 ± 1.4	195	69	29	71
A_3S	5.6 ± 1.8	265	82	29	74
A_4S	12.1 ± 4.3	574	97	37	72
A_5	1.4 ± 0.4	67	–	–	–
A_6	1.7 ± 0.5	80	–	–	–
A_7	2.3 ± 0.8	110	28	27	51
A_8	3.0 ± 0.6	137	37	25	60
A_9	3.6 ± 0.5	170	–	–	–

Field growth experiments

The condition index and specific growth rate measured in *Mytilus edulis* transferred in net bags to the Kertinge Nor/Kerteminde Fjord are shown in Table 4 together with data for chlorophyll *a* content of the surrounding water. There was a marked increase in the condition index in all cases. The mean specific growth rate was about 6% d^{-1} for the 3 periods and no distinct differences in growth rate were seen between the stations in the same period.

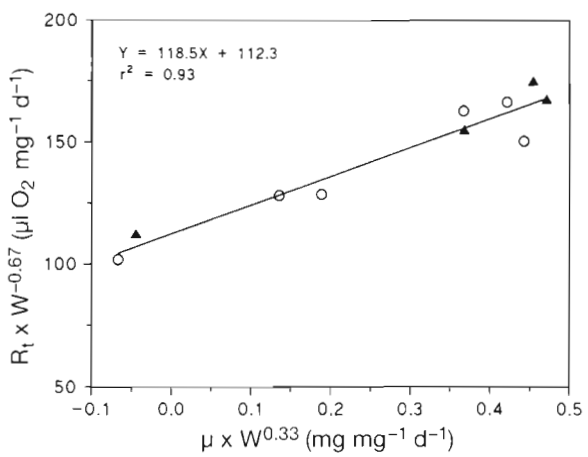

Fig. 4. *Mytilus edulis*. 'Scaled' specific respiration rate ($RW^{-0.67}$) as a function of 'scaled' specific growth rate ($\mu W^{0.33}$). The slope of the line expresses the energy cost of growth. Symbols as in Fig. 2

Estimated growth

In this section the algae concentration needed to cover maintenance and maximum growth of a 100 mg dry wt (W_t) 'standard' *Mytilus edulis* is estimated according to Eq. (5), taking into account experimentally determined values for maximum specific growth rate, energetic cost of growth and filtration rate.

The maximum specific growth rate of a standard mussel was approximately μ_{max} = 9.5% d^{-1} (Table 1) corresponding to a maximum growth rate G_{max} = $\mu_{max} \times W_t$ = 0.95 × 100 = 9.5 mg d^{-1} = 2255 µW. The maintenance metabolism (R_m) was estimated at 0.103 ml O_2 h^{-1} = 570 µW, and the filtration rate measured to F = 30 ml min^{-1} (Fig. 5B, Table 3). The energetic cost of growth was found to be 12% of the growth (Fig. 4), i.e. $R_g = 0.12G$. Thus, the growth rate may be expressed as: $G = A - R_m - 0.12G$ or $G = (A - R_m)/1.12$. Assuming AE = 80% the estimated actual growth rate (G) as a function of algal concentration (C) may now be expressed by the equation: $G = [(F \times AE \times C) - R_m]/1.12 = (30 \times 0.8 \times C \times 1.75)/(1.12 \times 60) - (570/1.12) = 0.625 \times C - 509 = b \times C - a$. The algal concentration needed to cover the energy cost of maintenance ($\mu = 0$) is thus found to be: a/b = 509/0.625 = 814 cells ml^{-1}, and the algal concentration necessary for maximum growth is: $(G_{max} + a)/b$ = (2255 + 509)/0.625 = 4422 cells ml^{-1}. The estimated values have been used to construct the 'growth line'

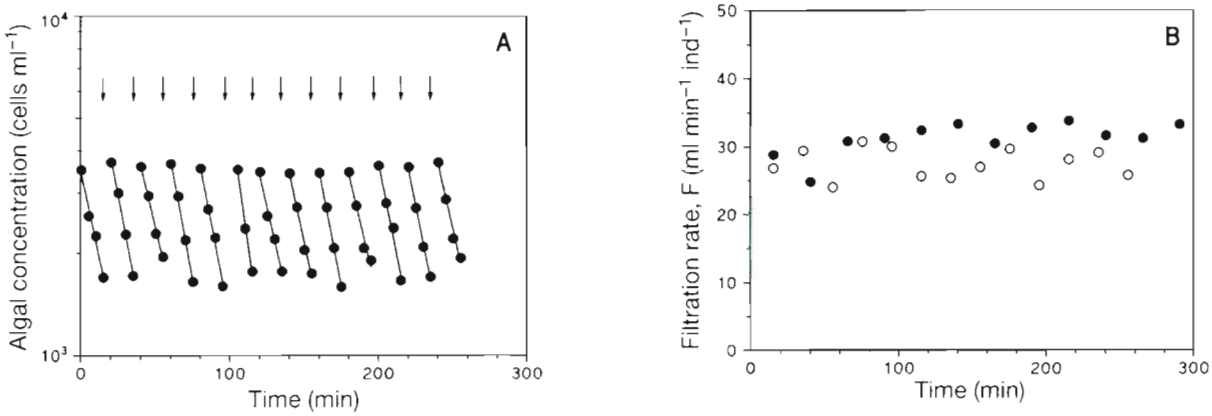

Fig. 5. *Mytilus edulis*. (A) Reduction of algal cell concentration due to filter-feeding by 25 mussels (28.4 ± 0.3 mm shell length) in an aerated aquarium (14 l). Arrows indicate additions of algal cells. The slopes of the regression lines express the mussels' filtration rate. (B) Filtration rate in the same group of mussels as a function of time in 2 series of experiments performed at a mean algal concentration of 2500 ± 100 cells ml^{-1} either without silt (○) or with 5.5 mg l^{-1} silt (●) added to the aquarium

shown in Fig. 2. The growth model expressed by the line satisfactorily describes the growth at algal concentrations <5000 cells ml^{-1}. High algal concentrations of about 1.2×10^4 cells ml^{-1} also result in exploitation of the growth potential, but the deviation from the 'growth model line' shows that the filtration rate and/or the assimilation efficiency must be considerably reduced compared to the values used in the growth model. The first assumption is supported by the reduced filtration rates observed at high algal concentrations (Table 3).

Table 3. *Mytilus edulis*. Mean (± SD) filtration rates in short-time (5 h) and long-time (9 to 14 d) experiments with groups of 25 mussels exposed to different concentrations of pure algae or algae + silt. Number of measurements given in parentheses and production of pseudofaeces shown by asterisks

Algal concentration ($\times 10^3$ cells ml^{-1})	Silt concentration (mg l^{-1})	Filtration rate (ml min^{-1} ind.$^{-1}$)
Short-time (5 h)		
2.7 ± 0.1		27.8 ± 1.7 (3)
2.3 ± 0.1	6.5 ± 0.1	32.2 ± 1.1 (3)*
8.5 ± 1.6		29.7 ± 2.5 (3)*
8.7 ± 0.6	4.0 ± 1.2	33.3 ± 4.2 (3)*
13.7 ± 3.2		12.1 ± 1.7 (3)*
13.0 ± 1.3	4.9 ± 1.2	26.1 ± 0.9 (3)*
24.0 ± 3.4		11.7 ± 3.6 (3)*
21.3 ± 2.1	4.9 ± 1.0	20.1 ± 1.7 (3)*
Long-time (9 to 14 d)		
4.1 ± 0.8		31.9 ± 5.3 (10)
4.1 ± 1.4	2.9 ± 0.5	31.2 ± 6.2 (9)*
6.0 ± 1.5		27.9 ± 4.3 (9)*
5.6 ± 1.8	2.9 ± 0.8	27.9 ± 3.2 (8)*
13.6 ± 7.0		14.7 ± 3.4 (5)*
12.2 ± 4.3	4.8 ± 1.5	13.1 ± 2.8 (9)*

DISCUSSION

In the present laboratory feeding experiments the specific growth rate and net growth efficiency of *Mytilus edulis* increased with increasing algal concentration to attain maximum values of about 9.5% d^{-1} and 70%, respectively, regardless of silt added to the water (Figs. 2 & 3). This shows that silt (or suspended bottom material) is not a prerequisite for mussels to achieve maximum growth as proposed by Kiørboe et al. (1981), Møhlenberg & Kiørboe (1981) and Jørgensen (1990). The estimated growth, according to Eq. (5), using the present value for energetic cost of growth (i.e. 12% of the growth) and a constant filtration rate of 30 ml min^{-1} ind.$^{-1}$ (Fig. 5B) is in satisfactory agreement with the experimental values found at concentrations below about 4000 to 5000 cells ml^{-1} (see growth line in Fig. 2). At higher algal concentrations (1.2 to 2.4 $\times$ 10^3 cells ml^{-1}) the filtration rate was considerably reduced (Table 2). The present filtration rate of 30 ml min^{-1} for the standard *M. edulis* is representative of low algal concentrations and in agreement with earlier measurements made by Riisgård (1991); it may also be compared with the rate of 27 ml min^{-1} predicted from the relationship between body weight and filtration rate capacity found by Møhlenberg & Riisgård (1979). Besides methodical problems, difficulties in creating optimal conditions in the laboratory, including establishing a proper food regime to which the mussels are adapted, have resulted in a vast number of generally low filtration rate measurements which have caused controversies in the literature (Jørgensen 1990, Riisgård 1991, Riisgård & Larsen 1995).

The respiration at zero growth, i.e. the value of *a* (112 µl O_2 mg dry wt^{-1} d^{-1}) for the regression equation in Fig. 4 may be compared with the rate of 117 µl O_2 mg^{-1}

Table 4. *Mytilus edulis*. Concentration of chlorophyll *a*, condition index (CI), soft tissue dry weight (W) and specific growth rate (μ) in field growth experiments during 3 different periods (I, II and II) performed at different stations (Stn). Subscript 0 and t refer to start and end of experiment, respectively. Standard deviation (± SD) is indicated

Period	Stn	Chlorophyll *a* ($\mu g\ l^{-1}$)	Condition index $CI = W/L^3$ ($mg\ cm^{-3}$) CI_0	CI_t	Soft tissue dry weight (mg) W_0	W_t	Specific growth rate ($\% \ d^{-1}$) μ
I	1	2.8 ± 0.5	1.36	2.87	29.0 ± 11.6	63.7 ± 12.7	4.6
	2	2.5 ± 1.0	1.36	4.17	29.0 ± 11.6	92.1 ± 19.4	6.8
	3	3.3 ± 0.8	1.32	4.60	30.9 ± 9.8	114.3 ± 29.9	7.7
	5	2.2 ± 0.3	1.32	3.12	30.9 ± 9.8	74.7 ± 20.4	5.2
II	1	2.7 ± 0.8	2.28	6.73	47.5 ± 9.1	169.8 ± 39.0	4.7
	2	2.5 ± 0.7	2.24	7.42	51.9 ± 16.4	218.0 ± 19.0	5.3
	3	3.8 ± 0.7	2.28	8.29	47.5 ± 9.1	219.0 ± 30.7	5.7
	4	3.8 ± 0.8	2.44	8.40	45.6 ± 6.9	223.1 ± 27.9	5.9
III	1	7.4 ± 1.5	2.71	5.88	50.9 ± 15.3	170.9 ± 44.4	4.5
	2	4.3 ± 1.0	2.69	5.96	44.6 ± 10.9	160.8 ± 41.6	4.7
	3	5.3 ± 0.7	2.82	7.67	36.9 ± 7.3	159.1 ± 26.5	5.4
	4	3.8 ± 1.5	3.06	9.27	44.5 ± 12.2	186.7 ± 28.2	5.3

d^{-1} predicted from the relationship between body mass and maintenance respiration found by Hamburger et al. (1983). The agreement is encouraging and supports the present finding that the energy cost of growth is about 12% of the growth, which may be compared to 17% as estimated by Jørgensen (1990; Fig. 27 therein) and 20% of the absorbed ration as measured by Bayne et al. (1989). These values of cost of growth for *Mytilus edulis* may be compared with those reported for other marine invertebrates: 20 to 26% of the growth in *Nereis diversicolor* and *N. virens* (Nielsen et al. 1995), 21 to 23% in the ascidian *Ciona intestinalis* (Petersen et al. 1995), 19% in the copepod *Acartia tonsa* (Kiørboe et al. 1985), 40% in the sea star *Asterias rubens* (Vahl 1984), and >100% in the sponge *Halichondria panicea* (Thomassen & Riisgård 1995). *H. panicea* differs from other invertebrates by having high energy demands for growth which may be comprehensible if the sponge is considered to be a colony of heterotrophic microorganisms as pointed out by Thomassen & Riisgård (1995); however, for a recent review dealing with the cost of growth in cells and organisms, including fish and endotherms, see Wieser (1994).

Specific growth rates obtained in nature in the present work (about 5% d^{-1}, Table 4) are shown in Fig 6 as a function of the mean phytoplankton concentration measured in the surrounding water, and compared with data from similar field growth experiments with mussels raised above the bottom in net bags. By converting the chlorophyll *a* concentrations to *Rhodomonas* sp. algal equivalents (Fig. 6: upper abscissa), it can be seen that (assuming that the above conversion is generally valid) the available phytoplankton biomasses in nature, even in the eutrophic Limfjord (Riisgård & Poulsen 1981), usually does not exceed the concentration level at which the maximum filtration rate of the mussels is affected. This is inconsistent with the frequently reiterated supposition of 'regulation' of the bivalve filter-pump (e.g. Winter 1973, Navarro & Winter 1982, Bayne et al. 1987, 1988, 1989, 1993, Hawkins & Bayne 1992, Stenton-Dozey & Brown 1992, Willows 1992, Navarro et al. 1994, Kreeger et al. 1995). Earlier contradictions to the theory of 'physiological control' or 'regulation of filtration rate' have in particular been advanced by Jørgensen (1990) in his book on bivalve filter-feeding—recently supplemented by a critical

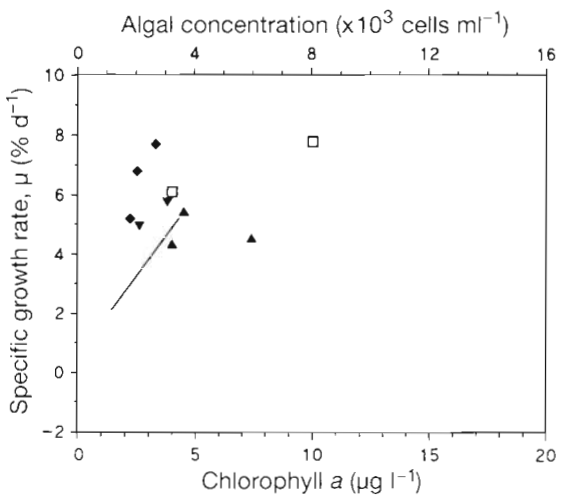

Fig. 6. *Mytilus edulis*. Specific growth rate in field experiments as a function of food concentration expressed as chl *a* l^{-1} (lower axis) and algal equivalents (*Rhodomonas* sp.) concentration (upper axis). Present work: (◆) I; (▲) II; (▼) III. (□) Maximum growth rates found for mussels in the Limfjord by Riisgård & Poulsen (1981); line: regression line (n = 35, r^2 = 0.55) for growth data obtained for net-bag-transplanted mussels in Kerteminde Fjord/Kertinge Nor by Riisgård et al. (1994)

note (Jørgensen 1996)—which gives a comprehensive review of the most recent literature. Jørgensen (1996) advocates that food uptake in filter-feeding bivalves is 'a highly automatized process which is characterized by the full exploitation of the capacity of the filter-pump in processing the ambient water when conditions are optimal'. This view appears to be supported by the present work. Thus, a likely interpretation of the present findings (also in agreement with the presented growth model) is that the filtration capacity, even in the presence of considerable amounts of silt, always seems to be utilized at algal concentrations like those generally found in nature, where the phytoplankton concentrations in most cases are too low to ensure exploitation of the growth potential. Thus, in the period 1976 to 1989 the median chlorophyll *a* concentration between March and December varied between 1.7 and 7.7 µg chl *a* l^{-1} in the open coastal areas around Funen (Fyns Amts 1990). Further, a median value of 5.1 µg chl *a* l^{-1} (corresponding to 4×10^3 *Rhodomonas* cells ml^{-1}) has been found for 27 Danish fjords and coastal waters, a figure based on approximately 1350 measurements on water samples collected between March and October during the period 1985 to 1991 (Sand-Jensen et al. 1994). Thus, it is clear that the phytoplankton biomass in Danish waters does generally not exceed the level above which the maximum filtration rate of *Mytilus edulis* may be influenced (reduced). For these reasons it is likely that the *M. edulis* filter-pump is adapted to operate continuously at prevailing natural algal concentrations which may be especially low in the near-bottom water over mussel beds (Wildish & Kristmanson 1984, Fréchette & Bourget 1985a, b, Fréchette et al. 1989, Loo & Rosenberg 1989, Jørgensen 1990). Also, from an energetic point of view, only an insignificant saving may be gained by reducing the filtration rate (Riisgård & Larsen 1995). The above argument may reduce the importance of the observation of low filtration rates in Table 3 to a rather uninteresting laboratory phenomenon seen only in experiments with unnaturally high algal concentrations. This point of view has been advanced previously by Riisgård (1991), who showed that the pattern in reduction of filtration rate at different high algal concentrations was very similar, with no regulation of filtration rate with respect to ambient algal concentration.

The present work has shown that admixture of silt in the range of 2.9 to 6.5 mg silt l^{-1} caused production of pseudofaeces irrespective of the algal concentration (Table 3). It is well known that mussels feeding on a suspension of algae mixed with silt may sort algae from silt for preferential ingestion of the algal cells (Kiørboe et al. 1980, Kiørboe & Møhlenberg 1981, Jørgensen 1990, 1996). Depending on the effectiveness of particle sorting, algal cells of nutritive value may, however, be enrolled in pseudofaeces and rejected. Such a cut off of food otherwise ingested should therefore reduce the specific growth rate at algal concentrations below 4500 *Rhodomonas* cells ml^{-1} in the present work. To judge from Fig. 2 this was not the case, possibly because the food loss via pseudofaeces was insignificant.

Due to the low initial condition index of the mussels used in the present work the shell growth rate (ΔL, mm mo^{-1}) was relatively slow, up to 4 to 5 mm mo^{-1} (Table 1), compared to maximum values of about 9 to 10 mm mo^{-1} recorded in nature (Jørgensen 1990; Table 8 therein). This underlines the fact that shell growth rate may in general be a poor parameter for assessing biomass production in bivalves (cf. Hilbish 1986)

Acknowledgements. We thank Prof. C. Barker Jørgensen and Dr Douglas Hunter for valuable comments on the manuscript. We also thank the 3 reviewers for constructive critism.

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This article was submitted to the editor

Manuscript first received: February 29, 1996
Revised version accepted: June 11, 1996