Aquat. Living Resour. 12 (4) (1999) 279–288
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Clearance rate responses of Mediterranean mussels, *Mytilus galloprovincialis*, to variations in the flow, water temperature, food quality and quantity

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Received December 16, 1999; accepted June 10, 1999

Abstract — The impact of Mediterranean mussels (*Mytilus galloprovincialis* Lamarck) on particle removal from the water column under different flow velocities was measured in the laboratory within a recirculating flume. At 20 °C, the filtration rates increased with current velocity up to 20–25 cm·s^{-1}. Filtration rates remained the same at 26 °C. At high phytoplankton concentration (Cryptophyceae: 8 500–11 000 *Cryptomonas* sp. cells·mL^{-1}), filtration rates were low (0.2–0.4 L·h^{-1} per standard individual of 1 g dry weight), whereas higher filtration rates (0.5–2.5 L·h^{-1} per standard individual) were observed with lower concentrations of the algae *Prorocentrum minimum* (Dinophyceae : 1 300–5 800 cells·mL^{-1}). The filtration rates of *M. galloprovincialis* were affected by high phytoplankton loads, and exhibited a maximum related to current velocity. Our results suggest that mussels, feeding over a wide range of seston concentrations and flow velocities, show an adaptive behaviour in an area where environmental conditions are known to vary drastically. © 1999 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

***Mytilus galloprovincialis* / clearance rate / filter feeders / flow velocity / recirculating flume / Mediterranean sea**

Résumé — Variations des taux de filtration des moules méditerranéennes, *Mytilus galloprovincialis*, en fonction de la vitesse du courant, de la température et de la concentration de nourriture. L'impact de la moule méditerranéenne (*Mytilus galloprovincialis* Lamarck) sur les flux de matière particulaire dans la colonne d'eau a été mesuré au laboratoire pour différentes vitesses de courant. Les expériences en laboratoire dans un canal à courant montrent qu'à 20 °C, le taux de filtration augmente avec la vitesse de courant jusqu'à des vitesses de courant de 20 à 25 cm·s^{-1}. Le taux de filtration reste semblable à 26 °C. Lorsque la concentration phytoplanctonique dans la colonne d'eau est élevée (8 500–11 000 cell·mL^{-1} de *Cryptomonas* sp., Cryptophyceae), les taux de filtration sont faibles (0,2–0,4 L·h^{-1} pour un individu standard de 1 g de poids sec). Des taux de filtration plus élevés (0,5–2,5 L·h^{-1} pour un individu standard) sont observés avec des concentrations phytoplanctoniques plus faibles (1 300–5 800 cell·mL^{-1} de *Prorocentrum minimum*, Dinophyceae). Ainsi, les taux de filtration mesurés pour *M. galloprovincialis* varient avec la charge phytoplanctonique et avec la vitesse du courant. Ces résultats suggèrent que les moules méditerranéennes, provenant d'un milieu où les variations de charges sestoniques et de vitesses de courant sont de grande amplitude, ont de grandes capacités d'adaptation. © 1999 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

***Mytilus galloprovincialis* / taux de filtration / organismes filtreurs / vitesse du courant / canal à courant / mer Méditerranée**

1. INTRODUCTION

Filter feeders may have an important impact on benthic–pelagic coupling in coastal ecosystems [9, 12, 20]. Suspension feeders such as mussels graze on phytoplankton [2, 13, 34] and in the Mediterranean sea are cultivated on ropes in the water column. In these areas, phytoplankton uptake often leads to an enhanced sedimentation of particulate organic material thereby creating organic-rich bottom areas while de-

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Table I. Summary of experimental settings and parameters related to mussels (*Mytilus galloprovincialis*) during the experiments. Experimental parameters were averaged from both clearance and control experiments.

	Experiment 1	Experiment 2	Experiment 3	Experiment 4
Date	Aug. 04–05	Aug. 31–Sept. 01	Sept. 25–26	Sept. 26–27
Water temperature (°C)	26	20	20	20
Phytoplankton cells	*Cryptomonas* sp.		*Prorocentrum minimum*	
Duration: control + with mussels (h)	6 + 6	6 + 6	1 + 3	4 + 4
Cell density range (cells·mL^{-1})	15 800–8 500	14 300–8 500	5 700–4 000	3 000–1 300
Number of mussels	20	40	27	
Mussels characteristics:				
Mean length (cm) (± SD)	6.5 ± 0.3	6.7 ± 0.3	5.9 ± 0.3	
Mean wet weight (g)(± SD)	26.31 ± 3.90	25.92 ± 4.40	17.17 ± 3.25	
Mean flesh dry weight (g)(± SD)	1.33 ± 0.41	1.89 ± 0.25	1.06 ± 0.33	
Mean ash free dry weight (g)	1.07	1.72	0.93	
Mean condition index (%)	15.48	19.85	16.26	

pleting the water column of particles [18, 21]. The potential depletion of particulate matter in the water column can be estimated from the clearance rates of mussels [4, 23, 36] but the data have mainly been obtained with *Mytilus edulis*, in laboratory experiments or in situ in intertidal coastal zones of oceans. In the Mediterranean sea, the main species cultivated is *Mytilus galloprovincialis*, on which few data on metabolic rates are available [8, 29, 30]. There are also data on biodeposits and the energy budget of *M. galloprovincialis* in shellfish farms [18, 19], which indicate the importance of currents for food availability to mussels. We examined the influence of current velocity on clearance rates of *M. galloprovincialis*. This environmental factor is known to influence food flux to the filter feeders, clearance rates and growth ([17, 26, 39], see [40] for a recent state-of-the-art review). This topic is controversial as contradictory results are reported in the literature. For instance, Wildish and Miyares [41] observed that clearance rates of *M. edulis* decreased as flow velocity reached 15–20 cm·s^{-1}, while Jorgensen [25] suggested that water processing rate is not affected by the ambient hydrodynamic conditions up to a critical flow velocity.

Thus, our aim in this study is two-fold: 1) to provide the quantitative data on clearance rate of *M. galloprovincialis* in order to allow an estimation of depletion events; and 2) to examine the relationship between clearance rates and environmental conditions.

2. MATERIALS AND METHODS

2.1. The mussels

The laboratory experiments were carried out in August and September 1995. Adult mussels of *M. galloprovincialis* were collected in the Gulf of Fos on cultivation ropes of a shellfish farm unit, at a depth of about 3 m, 3 days before the beginning of the experiment. Each unit was a 15 × 50 m structure supporting 1 000–1 500 ropes. At the collection site, the main current entered the units on the smallest side. All structures were located along the 5 m isobath [3]. The mean shell length of sampled mussels was about 6 cm (*table I*). After cleaning the shells from all epibionts, the mussels were placed in laboratory tanks with an open flow of natural seawater pumped from near the laboratory, for at least 2 days before the beginning of the experiments. Water temperature in the tanks was similar to that found in the sampling area (20 and 26 °C, depending on the period of the experiment) (*table I*). Sea water oxygen content was measured with an Orbisphere oxymeter (model 2609) and kept saturated by air bubbling. Mussels were fed twice a day with laboratory cultivated algae *Cryptomonas* sp. (experiments 1 and 2) or *Prorocentrum minimum* (experiments 3 and 4). Phytoplankton concentration was calculated to be in the range of the corresponding experiment. Mussels were placed on a 0.4 × 0.4 m PVC sheet to which, after some hours, they attached themselves. This PVC sheet was used to transfer the mussels into the flume for the experiments (see below). After each experiment, the mussels were measured to the nearest millimetre and weighed. Shell and flesh dry weights were obtained after drying in an oven (60 °C, 36 h). Ash-free dry weight of flesh (AF) was calculated from the weight loss at 500 °C until constant weight. A condition index was calculated as:

$$\text{condition index} = (\text{flesh dry weight}/\text{shell weight}) \times 100 \quad (1)$$

for the stock of mussels used for each experiment.

2.2. The phytoplankton cells

Two phytoplankton species were used as food for mussels, *Cryptomonas* sp. (Cryptophyceae) and *P. minimum* Strain Pm S1 (Dinophyceae). These species are representative of spring bloom phytoplankton communities in the mussel farming area [16]. Cryptomonads were also used because they are known to be well ingested by bivalves [35]. Both were isolated from the French Mediterranean coast and are main-

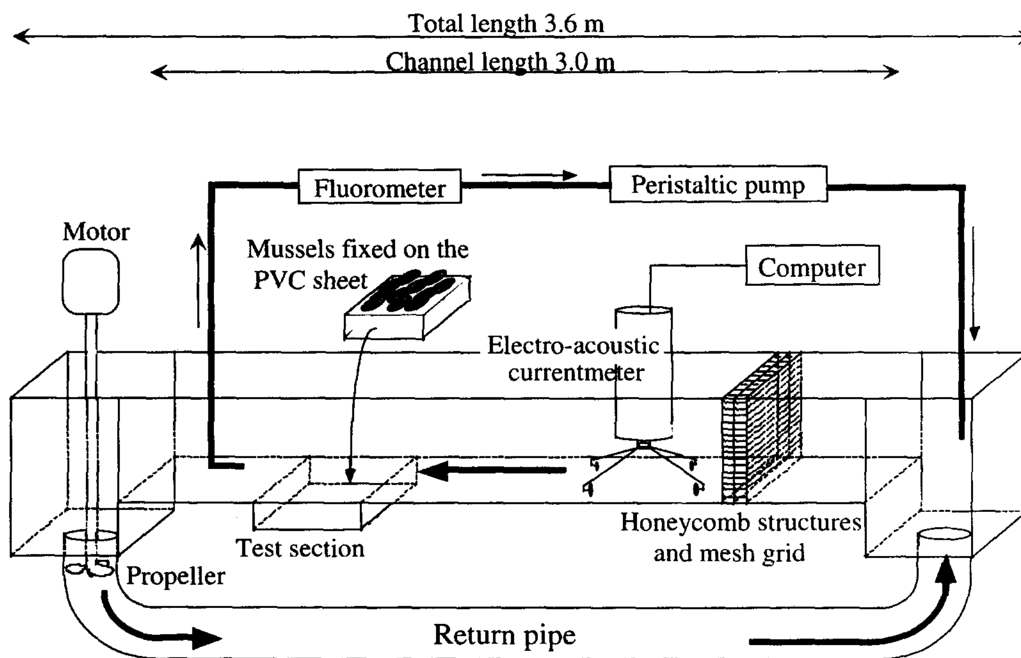

Figure 1. The recirculating flume: the PVC sheet is positioned on the test section in the channel during experiments with mussels. For fluorescence measurements, water was sampled 5 cm above the bottom, downstream of the test section by means of a peristaltic pump positioned after a fluorometer on a parallel tubing. Thick arrows indicate flow direction in the flume, thin arrows indicate flow direction in the parallel tubing.

tained in culture in the laboratory (B. Berland Collection, centre d'océanologie de Marseille).

Cell size was determined by means of a Coulter Counter, and ranged from 7 to 10 µm for *Cryptomonas* sp. and from 12 to 13 µm for *P. minimum*. Microalgae were grown in semi-continuous cultures using Antia et al. [1] medium in natural daylight and at 23–24 °C. For the experiments, cultures were harvested in late log-phase of growth, when they reached a density of about 230 000 cells·mL^{-1} for *Cryptomonas* and 90 000 cells·mL^{-1} for *Prorocentrum*. Cell densities in cultures were determined using a Neubauer haemocytometer. Cells in each sample (at least 400 algal cells) were counted four times, giving an accuracy of 10% [27]. For both strains, relationships between in vivo fluorescence and cells number were calibrated using a Turner Design 112 fluorometer.

2.3. The recirculating flume (*figure 1*)

The clearance rates were determined in a 3.6 m long PVC recirculating flume as described in Denis et al. [14] and adapted from Cole et al. [10]. The width and height of the main channel were 0.4 m. Recirculation of the water over the test section (0.4 × 0.4 m) located 2.1 m downstream of the main channel entry was ensured by a return pipe. A variable speed electric motor coupled to a propeller allowed us to obtain free-stream velocities ranging from 5 to 40 cm·s^{-1} in the channel. Two honeycomb structures of 4 cm in length and a 1 mm mesh grid were placed at the entrance of the main channel, so that the flow in the channel, and particularly over the test section, was steady. According to Nowell and Jumars [31], the water depth in the main channel should be fixed to 10 cm so that the sidewall effects may be neglected. Additional boundary layer measurements were conducted prior to the experiments with an electro-acoustic currentmeter (Meeres-Electronik Gmbh). Flow structure was determined upstream of the test section which was covered with a smooth PVC sheet, and the development of the boundary layer was recorded for each flow velocity (*figure 2*).

2.4. The experimental device

The flume was filled with 280 L of natural oligotrophic seawater (salinity: 38) pumped from near the laboratory and filtered through 1 µm mesh, considering that smaller particles are removed with a low efficiency [40]. Algae cultures were added (see below) and the flume was then filled up to 300 L with filtered seawater. During the experiment, the water was sampled from 5 cm above the bottom, downstream of the test section, by means of a peristaltic pump positioned after a fluorometer on a parallel tubing (*figure 1*). In vivo fluorescence was monitored continuously by means of the calibrated fluorometer. The background in vivo fluorescence of the filtered sea water in the flume was negligible. In vivo fluorescence (F, arbitrary units, range: 0.2–48) values obtained were related to cell density in the flume (D, cells·mL^{-1}) using the following equations:

$$D = 624.6\, F + 195.1 \quad (2)$$
($n = 7$; $r^2 = 0.999$; $P < 0.001$) for *Cryptomonas*

$$D = 625.0\, F + 170.2 \quad (3)$$
($n = 6$; $r^2 = 0.999$; $P < 0.001$) for *Prorocentrum*

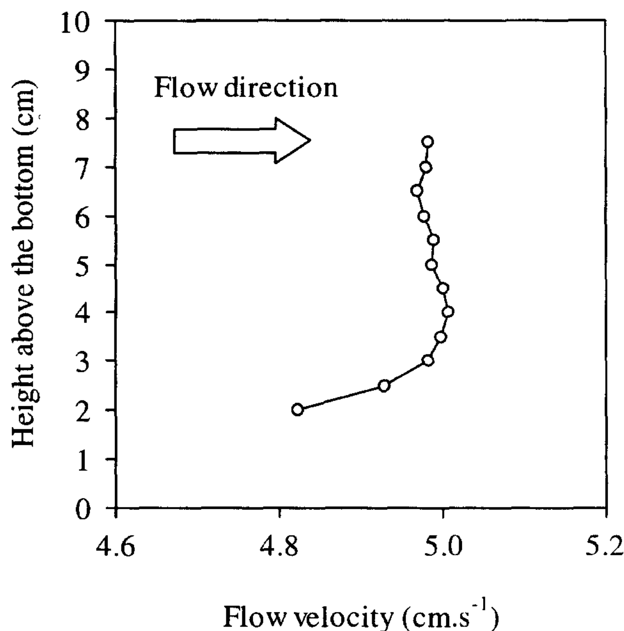

Figure 2. Typical boundary layer development measured just upstream of the test section (covered with a PVC sheet, without mussels) of the recirculating flume (free-stream velocity: 5 cm·s^{-1}, temperature: 20 °C). Values close to the bottom and above 8 cm could not be obtained because of the size of the currentmeter sensors.

An average fluorescence value was recorded every minute. After the fluorescence measurement, the water was returned to the flume upstream of the regulating structures. The flow in the peristaltic pump was adjusted so that the response delay of the fluorometer could be neglected. The free-stream velocity was also monitored continuously using the electro-acoustic currentmeter (Meeres-Electronik Gmbh) and an average value was recorded every 30 s. The currentmeter was placed at a depth of 3 cm in the main channel just downstream of the flow stabilizing structures so that it did not cause any turbulence or eddy development over the test section.

2.4.1. Experiments 1 and 2

In order to estimate the phytoplankton clearance rate by *M. galloprovincialis*, two experiments were conducted in August with *Cryptomonas* sp. at different water temperatures (see *table I*). Each experiment lasted 2 days; first day: control experiment without mussels; second day: experiment with mussels.

On the first day, according to the density of *Cryptomonas* sp. in the culture media (about 230 000 cells·mL^{-1}), the volume to pour into the flume was calculated to obtain a concentration of about 16 000 cells·mL^{-1} at the beginning of each experiment (or 25.8 µg Chl *a*·L^{-1}), in the range of earlier studies [10, 15, 41]. This concentration was higher than the one recorded during spring blooms in the sampling area [19]. After filling the flume, a control experiment was conducted without mussels, to estimate the amount of algal cells settling onto the bottom, adsorbed to the sidewalls or resulting from production in the flume. The control experiment lasted 6 h. Fluorescence was monitored continuously and flow velocity was stepwise increased by 5 cm·s^{-1} every hour, from 5 to 30 cm·s^{-1}. For each flow velocity, an additional 150 mL of water was sampled after 45 min for cell counting. Cell counts were carried out using a 0.5 mm deep Nageotte cell, as described above. At the end of this procedure, the motor was turned off overnight.

The following day, before the mussels were placed on the test section, flow velocity was increased to 30 cm·s^{-1} for a few minutes to mix the 300 L of water, in order to avoid the eventual stratification of water or of phytoplankton cells. Then the flow velocity was decreased to 5 cm·s^{-1} and the experiment began when flow velocity and fluorescence were stable. Fluorescence was monitored continuously. The PVC sheet with the mussels was then positioned on the test section of the flume. Flow velocity was increased stepwise from 5 to 30 cm·s^{-1}, following the same experimental protocol as in the control experiment.

In experiment 2, the number of animals was twice that in experiment 1. Then, food availability for each individual was apparently not the same. But, in both experiments, cell density was quite high and Wildish and Kristmanson [40] demonstrated that above the low flow velocity of 1.44 cm·s^{-1} at all densities of blue mussels, no seston depletion occurred on the test section.

2.4.2. Experiments 3 and 4

To assess the impact of the algal cells given as food for the mussels, two other experiments were performed in September, with *P. minimum*. The initial cell density (3 000–6 000 cells·mL^{-1}) was much lower than with *Cryptomonas*. Chlorophyll *a* content was less than 10 µg·L^{-1}. During experiment 3, only one flow velocity (5 cm·s^{-1}) was applied. The experiment without mussels was performed on the same day. The experiments with mussels were carried out three times with the same flow velocity. The 4th experiment was carried out following the same procedure as in experiments 1 and 2. However, only four flow velocities were tested and the control experiments was performed on the same day.

All experiments were performed in the laboratory in artificial light.

2.5. The clearance rate calculations

Clearance rates were estimated for each flow velocity from the difference in slope of fluorescence decrease versus time between the experiments with and without mussels at the same water flows (see [11] for a review). In vivo fluorescence records were correlated to cell density (from microscopic numerations), to allow the calculation of an accurate value of cell density decrease during the experiments. The specific loss rate in the control experiment without mussels, *a'*

(h^{-1}), was calculated from the slope of a linear regression of ln (estimated cell density) against time:

$$a' = d(\ln(\text{cell density}))/dt \quad (4)$$

The same calculation with mussels on the test section gave the specific loss rate with mussels, a (h^{-1}):

$$a = d(\ln(\text{cell density}))/dt \quad (5)$$

A specific linear regression was obtained for each flow velocity over 1 h of experiment. Consequently, the average clearance rate of individual mussels, Y ($L \cdot h^{-1}$ per mussel) is given by:

$$Y = V/n \cdot (a' - a) \quad (6)$$

where Y is the average clearance rate per individual ($L \cdot h^{-1}$), V is the volume of water in the flume (L) and n is the number of mussels on the test section.

To compare our results with those obtained with other species of bivalves, the clearance rates were also calculated per gram of dry weight, by replacing n in the above formula by the total dry weight of the n mussels (DW, g) in the flume.

$$Y = V/DW \cdot (a' - a) \quad (7)$$

To account for physiological differences, results were standardized to those for an equivalent mussel of 1 g dry soft tissue weight as follows:

$$Y_s = Y (1/W_e)^b \quad (8)$$

where Y_s is the standardized clearance rate ($L \cdot h^{-1}$ per standard individual of 1 g), W_e is the mean dry weight (g) of the mussels, Y is the average clearance rate per individual ($L \cdot h^{-1}$) and b is the weight exponent (0.540).

The weight exponent, b, was calculated for oxygen consumption of *M. galloprovincialis* in situ (Alliot, unpublished data), assuming that it is close to b in clearance rate/weight relationships. According to the literature, the weight exponent for oxygen consumption and clearance rate are different. However, since we had no data on *M. galloprovincialis*, we used the coefficient calculated for oxygen consumption, which is quite similar to the weight exponent found for the clearance rate of *M. edulis* (0.5) [37].

3. RESULTS

Experimental conditions and mussel characteristics are summarized in *table I*. During the observation period, the condition index was the lowest at the beginning of August and the highest in late August, when mussels were about to spawn as was confirmed by dissection after experiment 2.

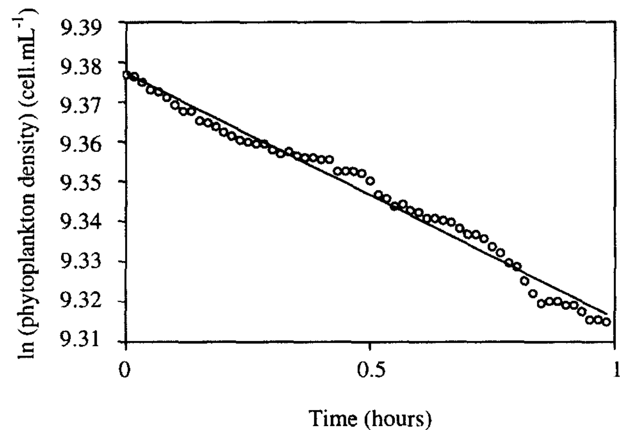

Figure 3. Decrease in *Cryptomonas* sp. density during experiment 2 (flow velocity = 10 $cm \cdot s^{-1}$). Each data point represents cell density for 1 min interval. Line is the regression slope of logarithm (estimated cell density of *Cryptomonas* sp.) versus time: $Y = 0.062X + 9.377$ (r^2 = 0.98).

3.1. In vivo fluorescence

During experiment 1, an important decrease in the in vivo fluorescence (≈ 3 000 $cells \cdot mL^{-1}$) occurred during the night, between the end of the control experiment and the beginning of the experiment with mussels on the following day, probably due to a high mortality and/or settlement of phytoplankton cells overnight.

Records of in vivo fluorescence showed slight variations over very short periods (*figure 3*), but these variations did not show any evident trend. Clearance rates were then calculated from all the data for each flow velocity. For the changes in fluorescence versus time, correlation coefficients (r^2) obtained with mussels were always higher than 0.85, whereas those calculated in the control experiments (without mussels) showed great variations with flow velocities. The standard deviation calculated for each slope was always low.

3.2. Clearance rates

Cell density decrease occurred in all experiments and was higher with mussels (*figure 4a,b*). Clearance rates of phytoplankton cells varied from 0.2 to 2.5 $L \cdot h^{-1}$ per mussel. The lowest values were recorded with *Cryptomonas* sp. in experiments 1 and 2. Clearance rates varied with flow velocity (*table II*).

– With *Cryptomonas*, the highest rate was recorded for the lowest velocity (5 $cm \cdot s^{-1}$) and remained similar for all other velocities in experiment 1. In experiment 2, clearance rates increased with flow velocity until 25 $cm \cdot s^{-1}$, and decreased at higher velocity.

– With *Prorocentrum*, at 20 °C, clearance rates increased with flow velocity up to 20 $cm \cdot s^{-1}$. The lowest clearance rates were recorded for a flow veloc-

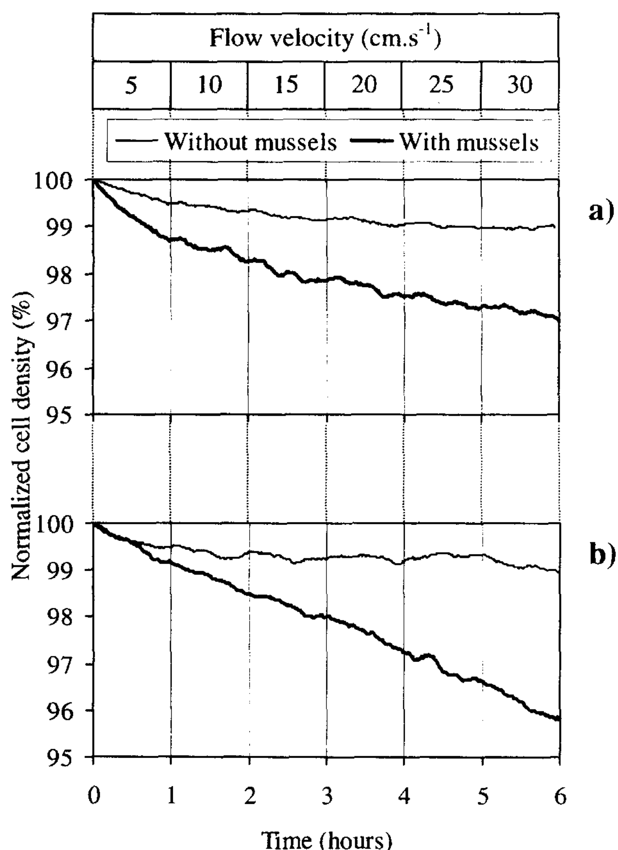

Figure 4. Variation with time of cell density normalized to initial density of *Cryptomonas* sp. during the clearance experiment (with *Mytilus galloprovincialis*) and the control experiment (without mussels). Flow velocity was increased by 5 $cm \cdot s^{-1}$ every hour for each experiment. a) Experiment 1, 20 mussels, water temperature 26 °C ; b) experiment 2, 40 mussels, water temperature 20 °C.

ity of 5 $cm \cdot s^{-1}$ and varied between 0.47 and 1.22 $L \cdot h^{-1}$ per mussel.

Results were expressed per standard animal, as a quantity of cells ingested per mussel, and always varied following the same pattern (*table II*).

4. DISCUSSION

In our experiments, the estimates of clearance rates were in the lower part of the range usually measured for *M. edulis* (0.5–5.5 $L \cdot h^{-1}$ per standard individual) [4, 23, 37]. Prins et al. [33], in a semi-natural mussel bed, found mean values for clearance rates ranging from 1 to 2 $L \cdot h^{-1} \cdot g^{-1}$of dry weight. As pointed out by Jorgensen [25], these values would correspond to the pumping rate of the mussels only if all mussels along the tunnel had the exhalant apertures facing the open water. In our experiments, mussel density was very low, thus limiting the eventual refiltration process and preventing a phytoplankton depletion over the test section. Mussels were submitted to qualitatively different flow types, which could affect the water processing rate with low-turbulent mixing or venturi effect [32]. The decrease in in vivo fluorescence in the water may have been slightly underestimated, however, owing to the possible production of pseudofaeces, especially in experiments 1 and 2 when cell density was high. Faeces and, if any, pseudofaeces could not be collected because they settled in the return pipe of the recirculating flume.

Several factors may also have contributed to lowering the clearance rate of mussels.

Our results were obtained with fed mussels in 1 h duration experiments, assuming a continuous filtration activity. We had no evidence that each mussel had a continuous filtration activity as results were obtained with a pool of animals for each experiment. Winter [43] suggested that the blue mussel might adjust the feeding rates by switching on and off the ciliary pump for some periods.

Temperature was quite high during experiment 1 (26 °C) and may have influenced the clearance rates. Massé and Parache [28] found that upper temperature tolerance for *M. galloprovincialis* was 29.5 °C. Walne [38] found a gradual increase in clearance rate with temperature, but the highest temperature tested was 20 °C. Results for other species (*Crassostrea gigas*) also show that clearance rates increase up to an optimum temperature above which rates decrease rapidly [5].

Clearance rates are also influenced by the physiological status of filter-feeders and clearance rates may decrease in larger animals such as the ones in our experiments [4]. Clearance rates also decrease in *C. gigas* at the end of gamete maturation [5]. This might explain why clearance rates in experiment 2, when expressed per gram of dry weight, were lower than in experiment 1, while algal species and cell density were similar.

Cell density might be another factor that has an impact on clearance rate. A high concentration of suspended matter, even phytoplankton cells, was shown to limit clearance rates [4] and hence growth rates [7]. As pointed out earlier [22, 24], clearance rate declines with increasing availability of diets that are pure algae, as is the case in our experiments. Our results are consistent with the data of Fisher et al. [15] on *M. galloprovincialis* who found clearance rates of the diatom *Thalassiosira pseudonana* (27 400 $cell \cdot mL^{-1}$) in the range: 0.2–2 $L \cdot h^{-1}$ per mussel.

In our experiments, it is difficult to determine whether the type of algae could explain the different clearance rate as cell density and cell volumes (*Prorocentrum* ≈ 1 000 μm^3, *Cryptomonas* ≈ 350 μm^3) were different. Phytoplankton load might be the main factor that explains the higher clearance rates on *Prorocentrum*. If all our data are pooled, particulate matter in filtered water being negligible, there is a significant relationship between clearance rate and mean cell density (*figure 5*). Hawkins et al. [23] recorded a similar relationship between clearance rate

Table II. Clearance of phytoplankton (*Cryptomonas* sp. – experiments 1 and 2; and *Prorocentrum minimum* – experiments 3 and 4) by Mediterranean mussels (*Mytilus galloprovincialis*) under different flow velocities. The slopes (respectively *a'* and *a* ± standard deviation, see text) of the regression of logarithm (estimated cell density) against time are indicated for control (without mussels) and clearance (with mussels) experiments. The average clearance rates were calculated per mussel, per gram of dry weight, and per standard individual of 1 g dry flesh weight. The amount of cells ingested per individual were calculated from the decrease in total cell number over a 1 h period and the number of mussels in the flume.

	Flow velocity	Linear regression of d(ln(cell density))/dt				Calculated clearance rate			Initial cell density	Cells ingested per mussel
		Without mussels		With mussels		Per mussel	Per g of dry weight	Per standard individual		
	($cm \cdot s^{-1}$)	slope a' (h^{-1})	r^2	slope a (h^{-1})	r^2	($L \cdot h^{-1}$)	($L \cdot h^{-1}$)	($L \cdot h^{-1}$)	($cells \cdot mL^{-1}$)	(10^3 $cells \cdot h^{-1}$)
Exp. 1	5	–0.050 ± 0.001	0.99	–0.120 ± 0.002	0.99	1.05	0.79	1.01	11 426	11 022
	10	–0.020 ± 0.001	0.90	–0.040 ± 0.002	0.85	0.30	0.23	0.29	10 137	2 951
	15	–0.023 ± 0.001	0.93	–0.048 ± 0.002	0.87	0.38	0.28	0.36	9 716	3 516
	20	–0.020 ± 0.001	0.86	–0.043 ± 0.002	0.90	0.35	0.26	0.33	9 358	3 128
	25	–0.009 ± 0.001	0.66	–0.029 ± 0.002	0.87	0.29	0.23	0.29	9 063	2 668
	30	–0.003 ± 0.001	0.15	–0.025 ± 0.001	0.86	0.33	0.25	0.32	8 887	2 892
Exp. 2	5	–0.050 ± 0.002	0.92	–0.082 ± 0.001	0.99	0.24	0.12	0.20	12 796	2 875
	10	–0.027 ± 0.002	0.78	–0.062 ± 0.001	0.98	0.26	0.13	0.21	11 813	2 966
	15	–0.019 ± 0.002	0.58	–0.060 ± 0.002	0.95	0.31	0.16	0.26	11 092	3 279
	20	–0.014 ± 0.002	0.50	–0.073 ± 0.001	0.99	0.45	0.23	0.37	10 603	4 493
	25	–0.008 ± 0.001	0.39	–0.072 ± 0.002	0.88	0.48	0.25	0.40	9 864	4 550
	30	–0.029 ± 0.002	0.83	–0.083 ± 0.001	0.99	0.40	0.21	0.34	9 301	3 562
Exp. 3	5	–0.138 ± 0.007	0.94	–0.180 ± 0.003	0.98	0.47	0.44	0.49	4 091	1 629
	5	–0.138 ± 0.007	0.94	–0.210 ± 0.003	0.99	0.80	0.75	0.83	5 764	3 876
	5	–0.138 ± 0.007	0.94	–0.210 ± 0.002	0.99	0.80	0.75	0.83	5 318	3 576
Exp. 4	5	–0.168 ± 0.013	0.46	–0.278 ± 0.002	0.92	1.22	1.15	1.27	3 000	2 935
	10	–0.108 ± 0.002	0.54	–0.237 ± 0.008	0.99	1.43	1.35	1.49	2 000	2 414
	20	–0.039 ± 0.016	0.01	–0.257 ± 0.005	0.98	2.42	2.28	2.52	1 700	3 558
	25	–0.004 ± 0.005	0.01	–0.209 ± 0.005	0.98	2.28	2.14	2.37	1 355	2 779

of *M. edulis* and organic particulate matter within seston. We must point out that in other experiments with *M. edulis* authors used still higher concentrations than we did without obtaining such low clearance rates. Jorgensen [25] reported that the concentration of algal cells required for maximum growth was about 4 400 $cells \cdot mL^{-1}$. When the algal concentration was higher (about 12 000 $cells \cdot mL^{-1}$), the growth potential of *M. edulis* was fully exploited but clearance rates were reduced.

During our study, the maximum value (1.4 $L \cdot h^{-1}$ per mussel) obtained in experiment 1 for the flow velocity of 5 $cm \cdot s^{-1}$, is likely due to some artefact in the experimental protocol. The in vivo fluorescence decreased overnight and, as temperature was high (26 °C), a number of algal cells may have died and been deposited after the control experiment. As the water was mixed before the experiment with mussels on the following day, by increasing flow velocity up to 30 $cm \cdot s^{-1}$ those cells may have been resuspended. They might have settled again when flow velocity was lowered and the decrease in in vivo fluorescence was then greater than expected from filtering activity alone.

Grenz et al. [19] studied the benthic–pelagic coupling in a mussel farming structure at the same site for 18 months. They measured biodeposits, growth and gamete production, in order to establish the budget of the flux of particulate matter through a farming unit using a clearance rate of 5 $L^{-1} \cdot h^{-1} \cdot g^{-1}$ dry weight (based on literature for *M. edulis*). They concluded that food deficiency should be expected for the other farming units downstream. The unbalanced budget established by these authors was explained by an overestimation of the clearance rates used. It is reco-

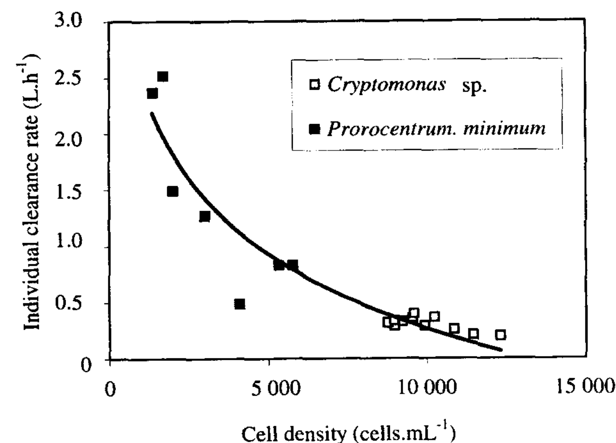

Figure 5. Relationships between cell density (*Cryptomonas* sp. and *Prorocentrum minimum*) and the averaged clearance rates of *Mytilus galloprovincialis* Lamark (data from all experiments pooled). The logarithmic relation between clearance rate and cell density is: $Y = 0.962 \ln X - 9.13$ ($r^2 = 0.89$).

gnized that different responses are observed in bivalves feeding upon natural supensions of lower organic content [22], but our clearance rates of 1–2 $L \cdot h^{-1} \cdot g^{-1}$, obtained in the laboratory, would be more in agreement with the particulate matter budget [19].

As pointed out by Calahan et al. [7], experimenting with bay scallops, the effects of food concentration might be much more pronounced than the effects of flow velocity.

Clearance rates were nevertheless influenced by flow velocity and increased with velocity up to 20–25 $cm \cdot s^{-1}$. Butman et al. [6] suggested that clearance of mussels could increase with flow velocity while Wildish and Miyares [41] show decreasing clearance velocities with increasing flow speeds over the range 6–23 $cm \cdot s^{-1}$ when individuals are studied. According to Jorgensen [25], water processing would not be affected by the ambient hydrodynamic conditions up to critical flow velocities. However, our results are consistent with data of Wildish et al. [42] on the combined effects of food concentration and flow velocity in the giant scallop. The rates at which the microalgae are cleared increase with flow velocity up to a maximum which might be influenced by seston load.

5. CONCLUSION

Clearance rates as measured in our experiments showed that the number of cells cleared per hour by mussels (1 600–4 $500 \cdot 10^3 cells \cdot h^{-1}$ per individual) varies in a smaller range than variations in initial cell densities in the water (1 500–12 000 $cells \cdot mL^{-1}$). The effects of food concentration were much more pronounced than the effects of flow velocity alone. The low clearance rates obtained for mussels fed on *Cryptomonas* sp. coincided with the highest cell concentration in the flume, with chlorophyll *a* concentrations higher than in natural conditions, even during spring blooms. Nevertheless, at 20 °C the mussels showed a maximum clearance rate for a free-stream velocity of 25 $cm \cdot s^{-1}$ even when they were about to spawn. Clearance rates showed a general trend to increase up to this velocity, but this could not be demonstrated statistically. At 26 °C, the clearance rates remained the same for all flow velocities tested. These first results suggest that *M. galloprovincialis* is well adapted to low cell density and over a wide range of current velocities. Further studies on clearance rates of *M. galloprovincialis* must take seston fluxes into account with different seston loads for each flow velocity.

Acknowledgements

The authors would like to thank three anonymous reviewers for their valuable suggestions to improve the manuscript. The authors are most grateful to E. Bourget (GIROQ- Laval University) for useful comments, J.-M. Deslous-Paoli (Ifremer Sète) for providing analytical support, B. Berland for providing the algal cultures, and M.-F. Fontaine, M. Grosjean for technical assistance.

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