

## Feeding response of the polychaete *Sabellaria alveolata* (Sabellariidae) to changes in seston concentration

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### Abstract:

*Sabellaria alveolata* is a tube-building gregarious polychaete that constructs large biogenic reefs. In macrotidal shellfish ecosystems, this species competes for food with cultivated suspension-feeders. The suspension-feeding activity and clearance rate of *S. alveolata* were investigated in response to changes in seston concentration. A flow-through system was designed to study 225 cm<sup>2</sup> reef blocks with more than 500 individuals. The experimental conditions were characterized by increasing concentrations of suspended particulate matter ranging from 6.5 to 153.8 mg L<sup>-1</sup>, while the organic content of the diet (microalgae *Skeletonema costatum*) decreased inversely from 49 to 9%, to mimic the dilution of organic matter by inorganic particles, characteristic of tidal resuspension. We showed that the clearance rate exponentially decreased in relation to an increase in SPM concentration. Clearance rate was estimated at 5.3 10<sup>-3</sup> L h<sup>-1</sup> or 0.93 L h<sup>-1</sup> g<sup>-1</sup> (dry weight) for the lowest seston concentration (SPM = 6.5 mg L<sup>-1</sup>) and reached the asymptote at CR = 1.97 10<sup>-3</sup> L h<sup>-1</sup> or 0.35 L h<sup>-1</sup> g<sup>-1</sup> (dry weight) when SPM exceeded 45 mg L<sup>-1</sup>. Using picture analyses of polychaete movements, we showed that, paradoxically, an increase in SPM concentration did not adversely affect the feeding activity of *S. alveolata* since the number of filtering individuals remained stable from SPM = 6.5 to 55.5 mg L<sup>-1</sup>. These values were applied at the scale of the bay of Mont-Saint-Michel (France) to demonstrate that the filtration pressure of large populations of wild suspension-feeders should not be underestimated when the carrying capacity has to be assessed in the context of increasing bivalve cultures.

**Keywords:** Feeding activity; Reefs; Suspension-feeders; Trophic capacity; Tubicolous polychaete; Bay of Mont-Saint-Michel

### 1. Introduction

*Sabellaria alveolata* is a tube-building suspension-feeding polychaete, widely distributed on European coasts from the Bristol Channel to the Portuguese coast ([Dubois et al., 2002] and [Dubois et al., 2006a]). In fact, it builds the largest biogenic formations on the European coast (Holt et al., 1998). Bioconstructions of *S. alveolata* are colonies typically found as veneers adhering to rocky shores at the mid-level of the intertidal zone. However, the largest structures are found in rare locations where these reefs can cover extensive areas on sandflats in the lower intertidal zone. In the bay of Mont-Saint-Michel, *S. alveolata* reefs create irregularly-shaped, patchy banks that cover approximately 100 ha and are considered the largest reef in Europe (Gruet and Bodeur, 1997 Y. Gruet and Y. Bodeur, Les récifs d'Hermelles. In: J.C. Dauvin, Editor, Les biocénoses marines et littorales françaises des côtes Atlantiques, Manche et Mer du Nord, synthèse, menaces et perspectives, Service du Patrimoine Naturel / IEGB / MNHN Paris Publishers (1997), pp. 168–176. Gruet and Bodeur, 1997). These biogenic reefs are

poorly understood, including their role in the trophic web of the ecosystem they inhabit. In the particular case of the bay of Mont-Saint-Michel, where the cultivation of oysters Crassostrea gigas and Ostrea edulis and mussels Mytilus edulis is the main economic activity (Le Mao et al. 2004), the question of the carrying capacity is of primary importance in a system largely dominated by benthic suspension-feeders (Cloern, 1982). In this bay, the large biogenic reefs (i.e. over 100 ha and up to 60,000 ind m<sup>-2</sup>) might be seen as a significant biological filter. In that context, measurement of the feeding activity of S. alveolata is a necessary step to assess the effects of biogenic reefs at the bay scale, compared with that of other cultivated and wild suspension-feeders.

60 In intertidal areas, filter-feeding organisms are greatly exposed to rapid changes in the availability and nutritional value of suspended particulate matter (hereafter SPM or seston). Because of the local action of wind- or tide-induced currents, the resuspension of sedimentary material, causing short-term variations in inorganic particles, may considerably modify the relative organic concentration of seston available to suspension-feeders. Understanding the effects of seston variations on feeding activity and filtration rates is an important goal in order to evaluate accurately the filtration of suspension-feeders in turbid macrotidal ecosystems. Suspension-feeder responses to changes in seston concentration have revealed a complex set of physiological (Barillé et al., 1997; Navarro and Widdows, 1997), morphological (Barillé et al., 2000; Dutertre et al., 2007) and behavioral adaptations (Iglesias et al., 1996; Newell et al., 70 2001; Riisgård et al., 2003). While bivalves and gastropods have been widely studied (see references above), much less is known about other taxonomic groups such as polychaetes (but see Jordana et al., 2001; Riisgård et al., 2002; Hentschel and Larson, 2005), yet these are the most abundant and diverse group in estuarine and marine environments. Although Dubois et al. (2005) have studied the mechanisms of particle capture and processing in polychaetes

75 Sabellaria alveolata, the effects of seston variations on filtration and feeding activity have not been investigated.

Because of its wide variety of depositional sedimentary environments and its macrotidal-related hydrological features, the bay of Mont-Saint-Michel is characterized by a broad range of suspended particulate matter. Recently, Cayocca et al. (2008) surveyed the sedimentary processes in a shellfish farming environment in the vicinity of the largest S. alveolata reef: while SPM peaks ranged between 200 and 1000 mg L<sup>-1</sup> depending on the flow and ebb conditions, SPM concentrations remained around 50 mg L<sup>-1</sup> over most of the tide period. In the bay of Mont-Saint-Michel, S. alveolata reefs are surrounded by oyster and mussel farming structures (Fig. 1), potentially filtering the same food sources but also locally increasing biodeposition rates and hence SPM concentrations. In this bay, largest mudflats and highest SPM concentration are hence found in the closest proximity to shellfish farming structures (Ehrhold et al., 2003). Using troughs specially designed to allow experimentation on large reef blocks, the objectives of this study were thus (1) to investigate feeding responses (i.e. filtration and feeding activity) of the polychaete S. alveolata in relation to seston concentration and (2) to evaluate the filtration of S. alveolata reefs in the bay of Mont-Saint-Michel in comparison with the filtration of the main cultivated and natural suspension-feeding species.

## 2. Materials and methods

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### 2.1. Sampling and conditioning of Sabellaria alveolata

Portions of reef were taken from the reef located in the eastern part of the bay of Mont-Saint-Michel (i.e. Champeaux reefs 1°29'28.2''O / 48°41'1.15''N; Fig. 1). Samples

100 were extracted with a metal corer of 225 cm<sup>2</sup> surface area (15 X 15 cm) and 15 cm depth, corresponding to the reef layer where Sabellaria alveolata lives (Gruet, 1971). Five reef blocks were collected under similar environmental conditions (sedimentary processes, hydrodynamics, bathymetry). Mud deposits were carefully removed in seawater then samples were put in an aquarium containing natural seawater with an open circuit kept at a constant  
105 temperature (15°C). Individuals were fed algal cultures of Skeletonema costatum, a ubiquitous diatom widely found in European coastal waters and used in bivalve aquaculture (Barillé et al., 2003). During the acclimation period, dead individuals of S. alveolata were removed. Attention was also paid to associated species occurring in micro-crevices, such as small molluscs, other polychaetes or nemertean; these were extracted from reef blocks to  
110 avoid disturbance and to assure that the measured filtration was only due to S. alveolata individuals.

## 2.2. Experimental equipment

115 A flow-through system was designed to measure Sabellaria alveolata feeding responses based on an experimental set-up used with suspension-feeding bivalves and polychaetes (Palmer & Williams, 1980; Barillé et al., 1993; Ropert and Gouletquer, 2000). Each block was placed in a 10 L trough with a 2 L flow-through chamber (volume used for filtration measurements) (Fig. 2). There was no connection between the flow-through  
120 chamber and the rest of the trough, keeping the whole reef block under water.

The system, consisting of a set of 6 troughs connected in parallel, received filtered seawater (0.45 µm Millipore R.A. filters) mixed in a 200-liter tank with the experimental diets (Fig. 2). The particulate organic matter (hereafter POM) supplied to the polychaetes was composed of the diatom Skeletonema costatum, kept in the culture collection of the Marine

125 Biology Laboratory of the Science Faculty in Nantes and grown in a culture room  
(temperature: 14°C, light/dark: 14/10 h, light intensity: 100  $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ ). Silt  
(Kaolinite BS1, AGS, Montguyon, France) was added to the algal culture to simulate  
particulate inorganic matter (hereafter PIM) and thus span an increasing range of suspended  
particulate matter (SPM). Five experimental conditions were tested (C1 to C5) based on the  
130 observed range of SPM values in the bay of Mont-Saint-Michel (Cayocca et al., 2008). One  
trough containing a reef block without polychaetes was used as a sedimentation control (i.e.  
the outflow of the control trough was used to represent the inflow in troughs with  
polychaetes). Prerequisites for using flow-through chambers were tested according to the  
recommendations of Riisgård (2001). The flow rate was adjusted with Gilmont<sup>®</sup> flow-meters  
135 to between 2 and 3 L h<sup>-1</sup> - under 1 atm and at 20°C – according to the experimental  
conditions.

### 2.3. Measurements of feeding activity

140 To assess the number of filtering individuals precisely, a remote-controlled high  
resolution CDD camera (3  $10^6$  pixels) was fixed on a frame above the troughs, so that pictures  
of any trough could be taken without disturbing the polychaetes during the course of the  
experiment. One picture of the reef surface was taken every 6 minutes for one hour in one  
randomly selected trough. Because of light penetration in the water above the reef blocks,  
145 only the experimental conditions with  $\text{SPM} \leq 50 \text{ mg L}^{-1}$  (i.e. C1 to C3) enabled a reliable  
interpretation of the pictures. Digital pictures were processed according to a two-step  
standardized protocol, using image processing software Adobe<sup>®</sup> Photoshop-CS3<sup>®</sup> (Fig. 3): (1)  
a picture of each reef surface was reshaped to the size of the reef block (i.e. 15 cm x 15 cm)  
and used as a reference to map all the tube apertures (empty circles) and to obtain an empty

150 grid (Figs. 3a to 3d); (2) the map of the tube apertures was superimposed on each picture  
taken during the course of the experiment and empty circles containing a filtering polychaete  
were color-coded in black before all empty circles were removed (Figs. 3e and 3f). It was  
easy to determine whether or not a tube aperture contained a filtering polychaete because of  
the whitish color of the prostomium bearing tentacular filaments (see pictures in Dubois et al.,  
155 2005). To quantify the number of individuals that switched from a feeding mode to a non-  
feeding mode between two pictures, two successive color-coded maps of filtering polychaetes  
were superimposed by deleting all common filled circles (Fig. 4).

#### 2.4. Measurements of filtration

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Reef blocks were placed in experimental conditions 1 hour before any measurement. Particle  
size distributions were determined using a Multisizer particle counter fitted with a 100  $\mu\text{m}$   
aperture. Particle counts were carried out with coefficients of coincidence  $< 5\%$ . All particle  
sizes were expressed as Equivalent Spherical Diameter (ESD). Clearance rate was calculated  
165 with particles above a threshold of 6  $\mu\text{m}$  ESD, shown in previous studies (Dubois et al., 2003)  
to be cleared with 100% efficiency. Considering the mean flow in individual troughs, the  
clearance rate ( $\text{L}\cdot\text{h}^{-1}$ ) was calculated as:

$$\text{CR} = [(\text{inflow} - \text{outflow}) / \text{inflow}] * \text{flow rate}$$

After experiments, all individuals were killed in 4.5% formalized seawater. Tubes  
170 were disintegrated in seawater. All Sabellaria alveolata individuals were collected counted  
and their weight was estimated after drying for 48 h at 60°C.

#### 2.5. Seston concentration

175 The amount of SPM, PIM and POM in the diet was obtained by the loss-on-ignition  
method. Water samples were filtered on pre-weighed GF/F filters dried at 60°C for 24 h for  
SPM determination. POM was estimated as the filter weight loss after subsequent ignition of  
samples (450°C for 4 h). PIM was deduced from the difference between these two  
measurements. POM concentrations were corrected for the loss of Kaolinite structural water  
180 (Barillé-Boyer et al., 2003). Experimental conditions are shown in Table 1.

## 2.6. Statistical analysis

One-way ANOVA was used to test for differences in clearance rate and filtering  
185 activity between experimental conditions. Data were accordingly checked for normality and  
homogeneity of variance. A significance level of  $p < 0.05$  was used in all tests. When  
significant, pairwise post-hoc comparisons were performed using the Tukey HSD test.  
Variations in CR were fitted against SPM using an exponential decay curve  $CR = CR_0 + a \times$   
 $\exp^{(-\lambda \text{ SPM})}$ , where  $CR_0$  is the asymptotic CR value,  $a$  is the intercept, and  $\lambda$  is the slope.  
190 Parameter estimation was achieved with Sigmastat 2.0 by using the downhill simplex method.  
All curve fittings between CR observations and the asymptotic model were tested by analyses  
of variance ( $p < 0.05$ ).

## **3. Results**

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### 3.1. Filtering activity

After destruction of the reef blocks, the collection of all individuals revealed that the  
estimated number of worms using image analysis (i.e. with tube apertures) was very close to

200 the actual number of worms (Table 2). The mean difference between the counted tube apertures and the actual number of polychaetes found in each reef block (3.12%, SE = 1.60) indicated that the image analysis provided a good estimate of the number of potentially filtering polychaetes. After destruction and drying, the mean dry weight for a reef block was 3.18 g (SE = 0.11) for a mean number of 576 individuals (SE = 13).

205 Overall, between 40 and 50% of polychaetes were filtering during the course of the experiment, whatever the experimental conditions (C1 to C3) (Fig. 5a). A significantly lower percentage for the mean of filtering polychaetes (43.2%; Tukey,  $p \leq 0.009$ ) was noticed for C1 (SPM = 6.5 mg L<sup>-1</sup>) compared to C2 (46.3%; SPM = 12.3 mg L<sup>-1</sup>) and C3 (47.4%; SPM = 55.5 mg L<sup>-1</sup>) (Fig. 5a). Between two pictures of filtering activity (Fig. 5b), from 5 to 10% of  
210 individuals (ca. 40 to 50 individuals) switched from a feeding to a non-feeding mode, or vice versa. This number did not differ significantly in relation to the experimental conditions (ANOVA,  $p = 0.057$ ) (Table 3), even though it was slightly higher for the condition C3 at the beginning of the experiment.

### 215 3.2. Filtration in relation to SPM concentration

Size spectra obtained using the particle counter typically showed 3 peaks (Fig. 6) at the outflow of the troughs: peak C corresponded to the microalgae Skeletonema costatum, spanning between 7 and 16 µm ESD, peak B to Kaolinite calibrated particles (3-4 µm ESD)  
220 while peak A was unexpected. Microscopy analysis revealed that it corresponded to spermatozoa (2-3 µm ESD). As a result, clearance rates (CR) were calculated using the 6-16 µm ESD size range, ensuring that all particles were cleared with 100% efficiency.

Clearance rates significantly decreased (ANOVA,  $p \leq 6.17 \cdot 10^{-4}$ ) with increasing seston concentrations (Fig. 7). The highest CR of 1.28 L h<sup>-1</sup> per reef block was estimated for



225 C1 (without Kaolinite) and subsequently decreased for C2 (PIM = 9.5 mg L<sup>-1</sup>) to 0.88 L h<sup>-1</sup>  
 per reef block. Clearance rates remained below 0.7 L h<sup>-1</sup> per reef block for C3 to C5, without  
 significant changes. The CR of reef blocks standardized with the percentages of filtering  
 individuals (assuming this percentage did not change from C3 to C5) varied from 2.96 L.h<sup>-1</sup>  
 (C1) to 0.90 L.h<sup>-1</sup> (C4). Individual CR was also calculated using the number of filtering  
 230 polychaetes and a functional relationship was established between CR and SPM using an  
 exponential decay curve (Fig. 8). The model showed a sharp decrease in individual CR in the  
 SPM range 0-20 mg L<sup>-1</sup>, followed by an asymptotic value around 2 10<sup>-3</sup> L h<sup>-1</sup> ind<sup>-1</sup>. The  
 influence of SPM concentration on CR was hence expressed by the following equation:

$$\text{CR} = 1.97 \cdot 10^{-3} + 8.61 \cdot 10^{-3} e^{-0.146 \times \text{SPM}} \quad (\text{R}^2 = 0.951; p < 0.05)$$

235 Considering an individual dry weight of 5.6 mg (see Table 2), the individual CR was  
 estimated at 5.3 10<sup>-3</sup> L h<sup>-1</sup> or 0.93 L h<sup>-1</sup> g<sup>-1</sup> (dry weight) for the initial condition (no Kaolinite,  
 SPM = 6.5 mg L<sup>-1</sup>) and reached the asymptote at CR = 1.97 10<sup>-3</sup> L h<sup>-1</sup> or 0.35 L h<sup>-1</sup> g<sup>-1</sup> (dry  
 weight) when SPM exceeded 45 mg L<sup>-1</sup>.

#### 240 4. Discussion

The effect of seston concentration on suspension-feeder activity and/or clearance rates  
 has been widely discussed in the literature (see, for example, Shumway et al., 1985; Bayne et  
 al., 1989; Navarro and Widdows, 1997; Barillé et al., 2006) but investigations have focused  
 245 mainly on mollusc species in general and bivalves in particular. In that context, the Pacific  
 oyster Crassostrea gigas and the blue mussel Mytilus edulis have been intensively studied  
 (e.g. Barillé et al., 1997 and references therein). This research has revealed a complex set of  
 physiological and morphological adaptations to high SPM concentrations: clearances rates  
 have been shown to decrease in response to increasing particle concentration and several

250 measurements have demonstrated complex mechanisms of particle processing and sorting to  
maintain feeding rates under high SPM concentrations and to limit clogging of the gills  
(Barillé et al., 2000). Similar behavioral adaptations have been shown in other mollusc  
species such as sea scallop Placopecten magellanicus (Cranford and Gordon, 1992), the  
cockle Cerastoderma edule (Navarro and Widdows, 1997), the slipper limpet Crepidula  
255 fornicata (Barillé et al., 2006), and the clam Mercenaria mercenaria (Bricelj and Malouf,  
1984). However, the effects of seston concentration have been rarely investigated in other  
taxonomic groups, notably polychaetes. Spionids (Polychaeta: Spionidae), facultative  
suspension- or deposit-feeders, are the most studied polychaete group (e.g. Bock and Miller,  
1996; Hentschel and Larson, 2005) but other polychaete families remain far less examined.

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#### 4.1. Particle loads and feeding activity of Sabellaria alveolata

Very few changes were noticed in Sabellaria alveolata behavior in relation to SPM  
concentration. While increasing seston loads is commonly known to hamper suspension-  
265 feeder filtration activity, we found a significant increase in the number of active polychaetes  
between SPM = 6.5 and 12.3 mg L<sup>-1</sup> and no change between SPM = 12.3 and 55.5 mg L<sup>-1</sup>.  
We initially hypothesized a decrease in the number of filtering polychaetes or a higher  
turnover rate in polychaetes switching between filtering and non-filtering modes, as evidence  
of SPM disturbances. On the contrary, less than 10% of individuals were switching between  
270 two snapshots, whatever the experimental conditions. These limited changes are probably  
due to natural inter-individual interactions forcing polychaetes to withdraw into their tubes,  
and do not reflect any physical constraints linked to increasing SPM. A small but significant  
increase in the percentage of filtering worms was even noticed when Kaolinite was added to  
the diet (SPM = 12.3 mg L<sup>-1</sup>). Flow speed is known to stimulate suspension-feeding activity

275 and to induce a switch between deposit-feeding and suspension-feeding modes in spionids  
(Taghon et al., 1980; Eckman and Duggins, 1993). Higher water velocities increase  
resuspended material and hence seston concentrations. We have shown here that SPM loads  
may also have a positive effect in inducing S. alveolata individuals to filter since an increase  
in filtering individuals was evidenced for SPM value  $< 50 \text{ mg L}^{-1}$ . For technical reason, it  
280 was not possible to determine effects of higher SPM loads and further hypotheses would have  
been too speculative.

Previous experiments using video-endoscopy (Dubois et al., 2005; Dubois et al.,  
2006b) revealed that S. alveolata exhibits several mechanisms related to pre-ingestive particle  
processing: (1) bi-directional particle transport on the tentacles, acting as a preliminary  
285 sorting mechanism before collection in food grooves, (2) pseudofeces production allowing  
individuals to reject excess particles before ingestion and (3) contribution of two peribuccal  
palps to clean up filamentary tentacles when overloaded. All these mechanisms probably  
contribute to maintain feeding activity under high seston concentration.

An automated video system has previously been developed to quantify the feeding  
290 activity of a small batch (12 to 15 individuals) of non-gregarious serpulid polychaetes Ditrupa  
arietina (Duchêne et al., 2000; Jordana et al., 2000). Such an automated system is not suitable  
for studying reef blocks with hundreds of individuals. Besides, using a large number of  
individuals enables a better estimate of inter-individual and intra-population activity (Dubois  
et al., 2003). Experiments on D. arietina revealed a strong inter-individual variability in the  
295 filtering activity: worms filtered neither continuously nor according to a particular rhythm,  
and no relationship was found between POM and filtration activity (Jordana et al., 2000). S.  
alveolata appears to have a steadier filtering activity: otherwise, a larger percentage of worms  
would have switched between filtering and non-filtering modes. Probably because of the  
above-mentioned mechanisms – which have not been shown in serpulid polychaetes – S.

300 alveolata is adapted to turbid systems and can maintain its filtering activity under high seston loads. This is particularly important for an intertidal species, since the highest SPM concentrations are encountered at the beginning of the flow and at the end of the ebb tides (Cayocca et al., 2008).

#### 305 4.2. Particle loads and clearance rate of Sabellaria alveolata

Reports on the effects of seston on polychaete clearance rates remain very scarce in the literature. Riisgård et al. (2002) showed that an increase in algal concentration corresponded to a decrease in clearance rate for both Ditrupa arietina and Euchone papillosa (Polychaeta: Sabellidae): a 5-fold increase in POM led to a minimum 50% decrease in clearance rate in these species, presumably because of limits in the gut capacity. Hentschel and Larson (2005) measured that the growth rate of interface-feeding spionid polychaetes (facultative suspension/deposit feeders) was differently affected by flow speed and the accordingly modified concentration of suspended food particles. In this study, we have shown that the clearance rates (CRs) of Sabellaria alveolata are adversely affected by an increase in SPM. The decrease appeared to be sharp for  $SPM < 45 \text{ mg L}^{-1}$  while CR reached a plateau for higher SPM values. Such a relationship, modeled by a decreasing exponential function, is typical of animals living in intertidal areas (Barillé et al., 1997; Navarro and Widdows, 1997). Considering the feeding activity results – i.e. no adverse effect of SPM on the number of filtering individuals – the relationship between CR and SPM indicates that a larger number of individuals are filter-feeding but that individual clearance rates are lower. In suspension-feeding invertebrates, SPM has two types of effect: (1) it induces regulation mechanisms to cope with SPM loads (pre-ingestive sorting and production of pseudofeces) and (2) it provokes a cessation of filtration due to physical constraints on the sorting organs

325 (e.g. clogging of gills). In this study, as filtration activity was not altered at high SPM concentrations (ca. 100 mg L<sup>-1</sup>), we hypothesize that the decrease in clearance rates was due to the gut capacity.

A preliminary estimate of Sabellaria alveolata CR was 0.75 mL h<sup>-1</sup> ind<sup>-1</sup> (Dubois et al., 2003), which is 7 to 2.5 times less than the CRs estimated in this study, for a condition  
 330 without Kaolinite and a condition with SPM > 45 mg L<sup>-1</sup> respectively. Such a difference is not only due to the assumption in Dubois et al. (2003) that all the worms were filtering (ca. 2 times error factor). We suggest here that the difference with the Dubois et al. (2003) experiment is also due to the physiological state of the polychaetes, and more precisely the reproductive state, since the former experiment was carried out in winter (when individuals  
 335 were under minimal physiological requirements and activity), while samples for this study were extracted in spring. As an example, Bruschetti et al. (2008) recently showed that the seasonal grazing effect of the reef-forming polychaete Ficopomatus enigmaticus (Serpulidae) on phytoplankton was ca. 3 times lower in winter (19%) than in summer (56%). The clearance rate values obtained here can be compared with CRs for other polychaetes, even if  
 340 the experimental conditions and CR calculations often remain different. At the plateau, S. alveolata CR was estimated at 0.35 L h<sup>-1</sup> g<sup>-1</sup> dry weight (or 0.065 L h<sup>-1</sup> g<sup>-1</sup> fresh weight). These values are about one order of magnitude lower than CRs calculated using colloidal graphite suspension by Dales (1957) for sabellids (Sabella pavonina and Myxicola infundibulum, 0.39 and 0.10 L h<sup>-1</sup> gfw<sup>-1</sup>, respectively) and serpulids (Pomatoceros triqueter  
 345 1.40 L h<sup>-1</sup> gfw<sup>-1</sup>, Hydroides norvegica 0.90 L h<sup>-1</sup> gfw<sup>-1</sup>, Spirorbis borealis 0.95 L h<sup>-1</sup> gfw<sup>-1</sup> and Salmacina dysteri 2.09 L h<sup>-1</sup> gfw<sup>-1</sup>). The S. alveolata CR was however close to the CR determined by Wells (1970) for the sabellariid Sabellaria kaiparaensis (0.018 L h<sup>-1</sup> ind<sup>-1</sup>) using the same colloidal graphite suspension as Dales (1957). Sabellariids thus seem to have lower CRs than other suspension-feeding groups represented by sabellids and serpulids, to such an

350 extent that sabellariid membership of the suspension-feeding group may be debated (see discussion in Dubois et al., 2006b and Riisgård and Nielsen, 2006). The question of whether or not S. alveolata is an exclusive suspension-feeder or if it exhibits changes in its feeding mode (interface-feeder) like spionids (Taghon et al., 1980; Dauer et al., 1981) has still to be addressed.

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#### 4.3. Application: estimating the overall filtration pressure of Sabellaria alveolata reefs in the bay of Mont-Saint-Michel

Our approach allowed the extrapolation of reef block CR to overall population  
 360 filtration pressure. Using reef blocks instead of single tubes provided a realistic simulation of inter-individual behavior and of the number of individuals actually filtering. In addition, the seston loads used in this experiment reproduced the field turbidity measured in the area surrounding the reefs in the bay of Mont-Saint-Michel. Over an 8-day period, Cayocca et al. (2008) recently showed that the turbidity peaked transiently early during the flow (reaching  
 365 up to 1000 mg.L<sup>-1</sup>) but was around 50 mg L<sup>-1</sup> at 30 cm above the sediment over most of the tide period. The CR calculated for a 225 cm<sup>2</sup> reef block with 50 mg.L<sup>-1</sup> SPM could be used to estimate the water volume cleared by all of the S. alveolata reefs in the bay of Mont-Saint-Michel. Hence, considering that 1 m<sup>2</sup> of S. alveolata reef cleared 46 L.h<sup>-1</sup> (1.03 L.h<sup>-1</sup> for a reef block) and also considering that reefs are submerged 13 hours a day for a mean tide (P.  
 370 Cugier, unpublished data), we estimated the volume cleared each day at 598 L m<sup>-2</sup>. In the bay of Mont-Saint-Michel, S. alveolata reefs spread over 252 ha (i.e. 252 10<sup>4</sup> m<sup>2</sup>) when considering 3D shape and evolutionary stages of the reef (Dubois, 2003): thus the filtration pressure is estimated at 1.31 10<sup>6</sup> m<sup>3</sup> day<sup>-1</sup>. This represents the lowest estimate of filtration pressure since the lowest CR value was used in this calculation. A similar calculation using

375 CR for SPM =  $6.5 \text{ mg L}^{-1}$  (i.e.  $2.96 \text{ L h}^{-1}$ ) provides a volume cleared by S. alveolata reefs of  
4.31  $10^6 \text{ m}^3 \text{ day}^{-1}$ . These values are compared to volumes of cleared water for cultivated  
oysters (native oyster Ostrea edulis and Pacific oyster Crassostrea gigas), blue mussel  
(Mytilus edulis), and invasive slipper limpet (Crepidula fornicata) in Table 4. While the  
volume cleared per square meter of S. alveolata reef is far lower than the  $100 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$   
380 calculated for dense mussel beds (Jørgensen, 1990), we note that, at the bay scale, the  
filtration pressure of the reefs is the same order of magnitude as the filtration pressure of the  
cultivated oyster and mussel populations, as well as the filtration pressure of the remarkably  
large Lanice conchilega beds (Godet et al., 2008) covering 190 ha in the bay. This shellfish  
ecosystem is also largely dominated by the invasive species C. fornicata whose filtration  
385 pressure greatly exceeds other benthic compartments and unbalances the trophic web of the  
bay (Leloup et al., 2008). This rough estimate shows that further modeling of the carrying  
capacities of systems hosting large reefs of S. alveolata should include the filtration pressure  
of this polychaete. Many estuarine and marine shellfish environments are colonized by large  
populations of natural gregarious suspension-feeding polychaetes such as Lanice conchilega  
390 (Denis et al., 2007; Godet et al., 2008), Sabella spallanzanii (Licciano et al., 2007) or  
Ficopomatus enigmaticus (Bruschetti et al., 2008). The influence of large polychaete  
populations in shallow coastal waters is often underestimated and this study shows that  
further investigations are needed to determine their ecological role in the coastal food web.

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550 **Figure captions**

**Fig. 1.** Location of Sabellaria alveolata reefs within the bay of Mont-Saint-Michel (black circles). Note the spread of the cultivated oyster and mussel beds.

555 **Fig. 2.** Experimental set-up with details of the troughs containing Sabellaria alveolata reef blocks. Diagram of troughs modified from Dubois et al. (2003).

**Fig. 3.** Standardization using image processing software Adobe® Photoshop-CS3® to determine the number of filtering individuals. (a) initial picture of reef surface; (b) picture of reef surface reshaped to the size of the reef block (i.e. 15 cm x 15 cm); (c) map of all tube apertures; (d) reference map of tube apertures (empty circles) superimposed on each picture of the set; (e) determination of filtering and non-filtering individuals; (f) final pattern of filtering individuals.

565 **Fig. 4.** Standardization using image processing software Adobe® Photoshop-CS3® to determine the difference in the number of filtering individuals between 2 successive pictures. (a) map of filtering individuals, represented by gray dots, for one picture; (b) map of filtering individuals for the following picture; (c) superimposition of the two successive pictures; individuals that did not switch between filtering and non-filtering modes appear as black dots; 570 (d) removal of non-switching individuals and counting of individuals that switched between the two modes.

**Fig. 5.** (a) Percentage of filtering polychaetes according to SPM concentration for the first 3 experimental conditions (C1 = 6.5 mg L<sup>-1</sup>, C2 = 12.3 mg L<sup>-1</sup>, C3 = 55.5 mg L<sup>-1</sup>); (b) 575 Percentage of polychaetes switching from a feeding to a non-feeding mode (and vice versa) between two successive pictures for the first 3 experimental conditions.

**Fig. 6.** Example of particle size spectra at the outflow of the troughs showing Skeletonema costatum peak (C) between 7 and 16 µm ESD, and two overlapping peaks, corresponding to 580 an emission of spermatozoa (A) between 2 and 4 µm ESD and to the Kaolinite peak (B) between 4 and 5 µm ESD. To facilitate representation, the volume of particles (in mm<sup>3</sup>.mL<sup>-1</sup>) was used as a unit.

**Fig. 7.** Mean clearance rates (n = 5; SE bars are shown) of Sabellaria alveolata calculated 585 according to five experimental conditions, with increasing suspended particulate matter. Black bars represent non-standardized clearance rates of reef blocks and gray bars represent standardized clearance rates of reef blocks adjusted to the number of actual filtering individuals. Letters indicate significant post-hoc comparison results.

590 **Fig. 8.** Variations in mean individual clearance rates (n = 5; SE bars are shown) of Sabellaria alveolata fitted against SPM using an exponential decay curve.



**Table 1**

Characteristics of experimental diets (C1 to C5) supplied to Sabellaria alveolata.

|    | SPM<br>mean (SE) | POM<br>mean (SE) | PIM<br>mean (SE) |
|----|------------------|------------------|------------------|
| C1 | 6.5 (0.4)        | 3.2 (0.2)        | 3.3 (0.2)        |
| C2 | 12.3 (1,5)       | 2.9 (0.4)        | 9.5 (1.1)        |
| C3 | 55.5 (1.0)       | 2.6 (0.2)        | 52.9 (0.9)       |
| C4 | 102.7 (1.0)      | 10.6 (0.7)       | 92.1 (0.4)       |
| C5 | 153.8 (2.1)      | 13.2 (3.9)       | 140.6 (1.9)      |

595

SPM: suspended particulate matter ( $\text{mg L}^{-1}$ ); POM: particulate organic matter ( $\text{mg L}^{-1}$ ); PIM: particulate inorganic matter ( $\text{mg L}^{-1}$ ). Data presented are means of three replicates per experimental condition (SE: standard error). POM was constituted by the diatom Skeletonema costatum and inorganic material by Kaolinite particles. C1 represents a condition without Kaolinite, the inorganic matter having originated from the microalgae frustules.

600

**Table 2**

605 Number of polychaetes in each reef block (15 cm x 15 cm) estimated and counted after destruction of all tubes. Total weight obtained after 48 h at 60°C.

| Reef block n°                          | 1    | 2    | 3    | 4    | 5    |
|--|------|------|------|------|------|
| Counted number of individuals (n° ind) | 607  | 559  | 601  | 549  | 567  |
| Estimated tube aperture (n° ind)       | 593  | 552  | 581  | 510  | 558  |
| Error estimated / counted (%)          | 2.31 | 1.25 | 3.33 | 7.10 | 1.59 |
| Total dry weight (g)                   | 3.62 | 3.19 | 2.98 | 3.15 | 2.99 |

610

**Table 3**

Percentages (mean  $\pm$  SE; n = 10) of filtering individuals and individuals switching from a feeding to a non-feeding mode, in relation to experimental conditions. Because of light penetration, counting was only carried out for experimental conditions up to SPM = 55.5 mg

615 L<sup>-1</sup>.

|   | Suspended Particulate Matter |                              |                              |
|---|------------------------------|------------------------------|------------------------------|
|   | C1 = 6.5 mg L <sup>-1</sup>  | C2 = 12.3 mg L <sup>-1</sup> | C3 = 55.5 mg L <sup>-1</sup> |
| Filtering individuals (mean %)                    | 43.2 $\pm$ 0.81              | 46.3 $\pm$ 0.93              | 47.4 $\pm$ 1.0               |
| Variations between 2 successive pictures (mean %) | 6.12 $\pm$ 0.38              | 6.79 $\pm$ 0.35              | 7.67 $\pm$ 0.49              |

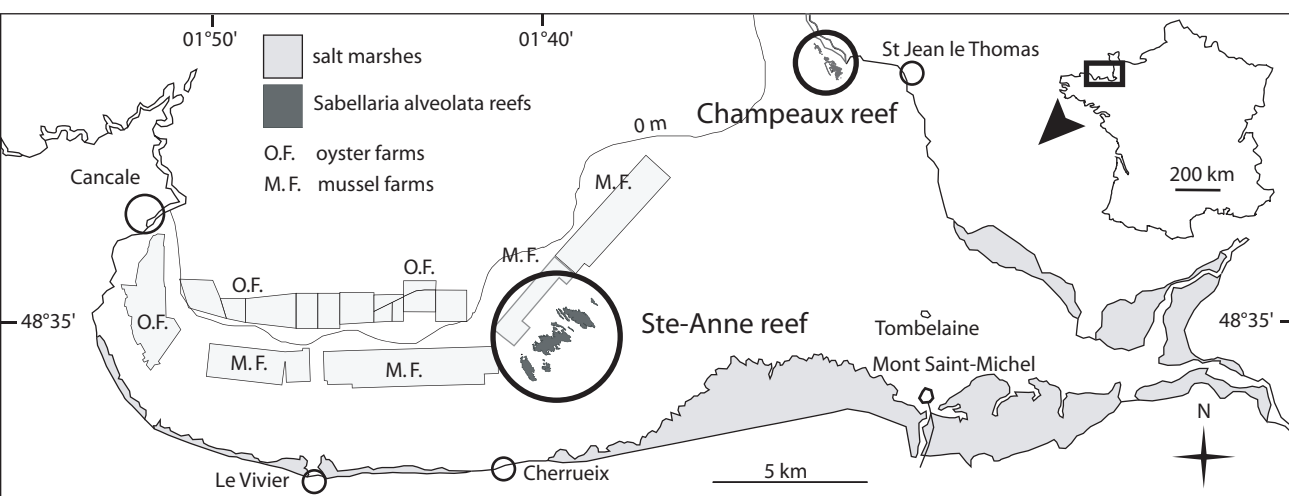
**Table 4**

Estimates of the filtration pressure of the main intertidal suspension-feeding cultivated and natural species in the bay of Mont-Saint-Michel.

|   | Biomass <sup>(1)</sup> |                    | CR<br>(L h <sup>-1</sup><br>gdw <sup>-1</sup> ) | Food source   | T<br>(°C) | Immersion<br>(h day <sup>-1</sup> ) | Filtration<br>pressure<br>(10 <sup>6</sup> m <sup>3</sup><br>day <sup>-1</sup> ) |
|---|------------------------|--------------------|---|---|-----------|-------------------------------------|--|
|   | (t fresh<br>weight)    | (t dry<br>weight)  |   |   |           |                                     |  |
| Pacific oyster<br><u>Crassostrea gigas</u>    | 2025                   | 30.7               | 4.2 <sup>(3)</sup>                              | Natural   | 17        | 13                                  | 1.67   |
| European flat oyster<br><u>Ostrea edulis</u>  | 615                    | 9.5                | 0.6 <sup>(4)</sup>                              | <u>Skeletonema<br/>costatum</u>   | 15        | 24                                  | 0.14   |
| Blue mussel<br><u>Mytilus edulis</u>          | 6900                   | 271.4              | 1.5 <sup>(5)</sup>                              | Natural   | 16        | 13                                  | 5.28   |
| Slipper limpet<br><u>Crepidula fornicata</u>  | 136650                 | 6828.5             | 0.76 <sup>(6)</sup>                             | <u>Nitzschia<br/>aurariae</u> and<br><u>Entomoneis<br/>pseudoduplex</u> | 15        | 24                                  | 124.57   |
| Sandmason worm<br><u>Janice conchilega</u>    | 1181 <sup>(2)</sup>    | 169 <sup>(2)</sup> | 0.4 <sup>(7)</sup>                              | <u>Chaetoceros<br/>calcitrans</u>                                       | 18        | 13                                  | 0.88   |
| Honeycomb worm<br><u>Sabellaria alveolata</u> | 1570                   | 287                | 0.35 <sup>(8)</sup>                             | <u>Skeletonema<br/>costatum</u>   | 15        | 13                                  | 1.31   |

<sup>(1)</sup>Unless otherwise stated, biomass data originates from the French National Program of Coastal Environment (extracted from Leloup et al., 2008); <sup>(2)</sup> Godet et al., 2008; <sup>(3)</sup> Ropert and Gouletquer, 2000; <sup>(4)</sup> Haure et al., 1998; <sup>(5)</sup> Prins et al., 1994; <sup>(6)</sup> Barillé et al., 2006; <sup>(7)</sup> Denis et al, 2007 (data for large individuals); <sup>(8)</sup> this study. Immersion period for C. gigas, M. edulis and L. conchilega was the same as for S. alveolata reefs ± 1 hour; other species were immersed for 24 hours a day.

Figure 1



**Figure 2** determination of particle size distribution

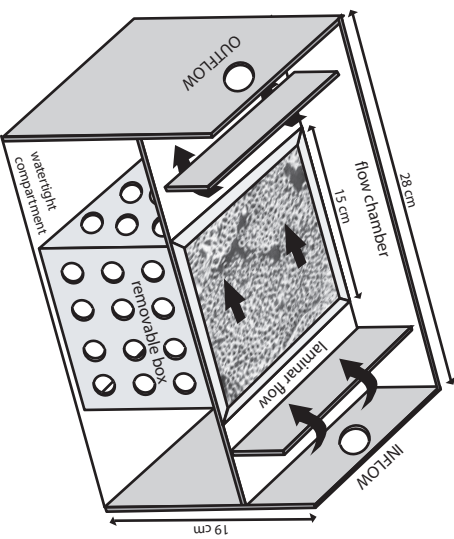
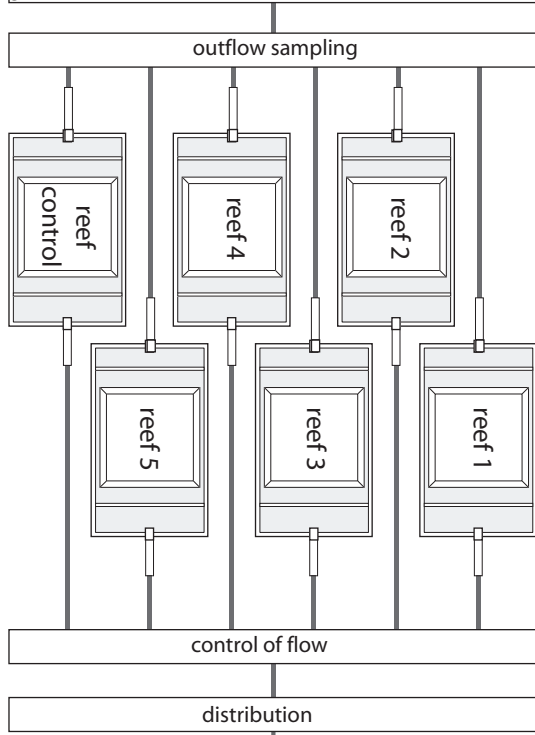


Figure 3

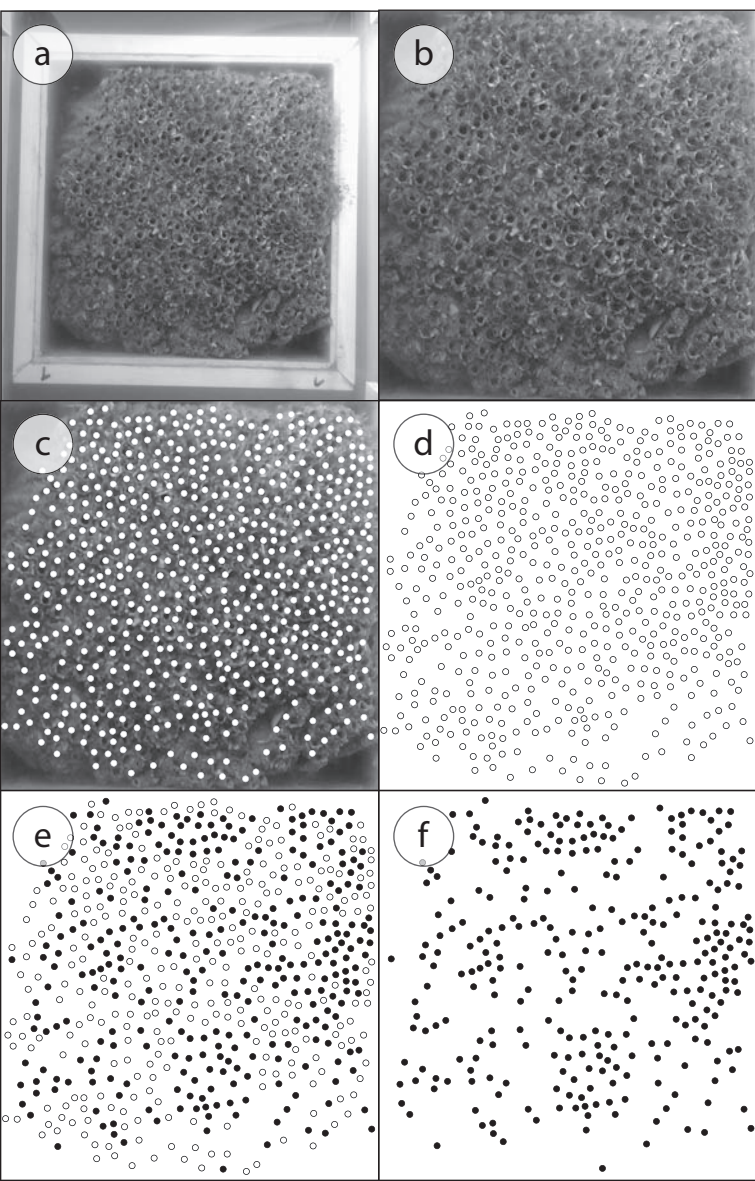


Figure 4

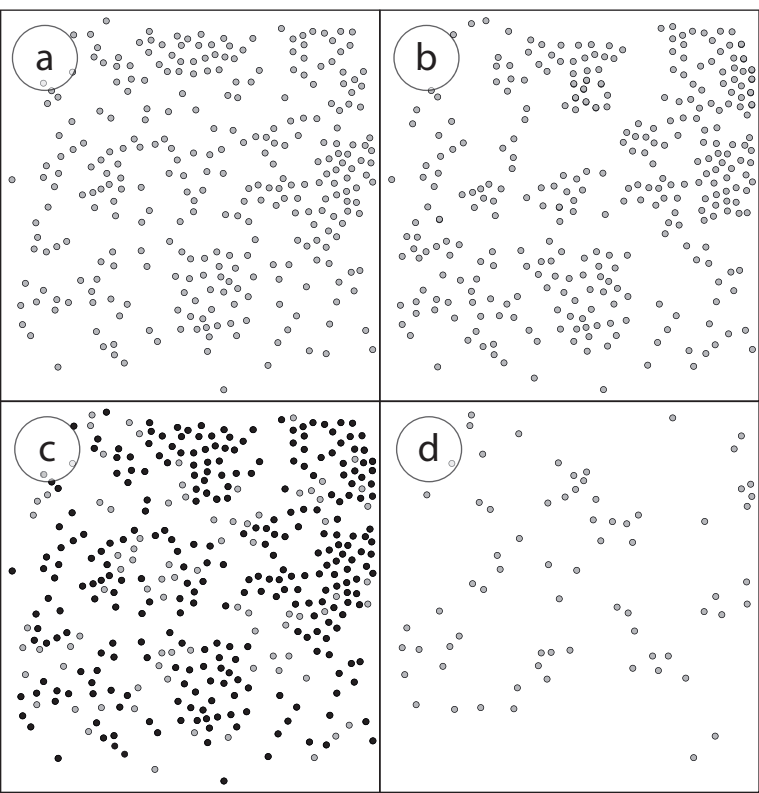




Figure 5

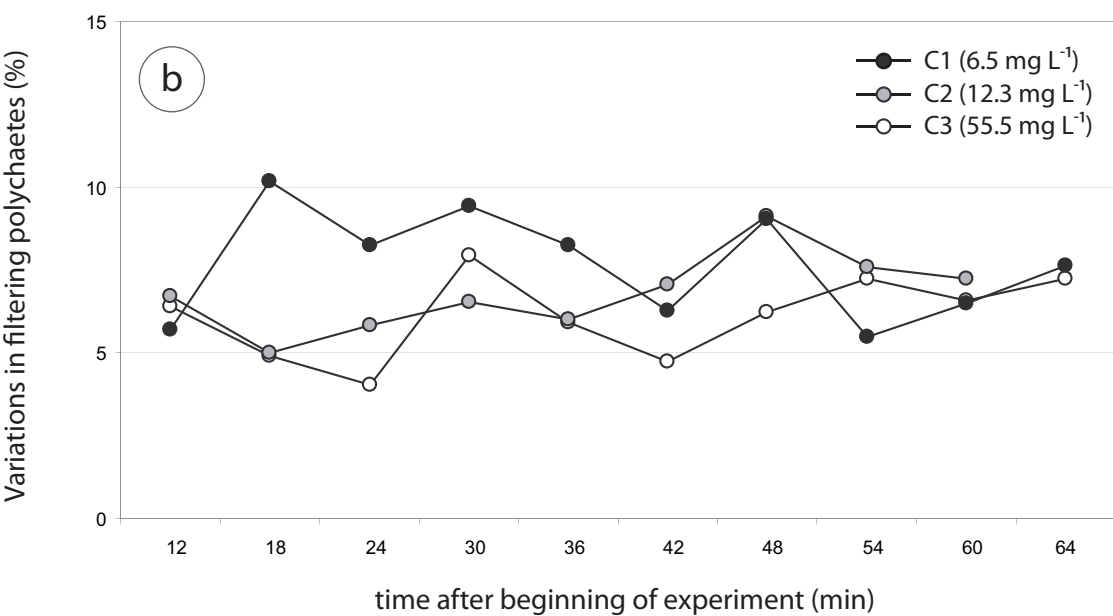
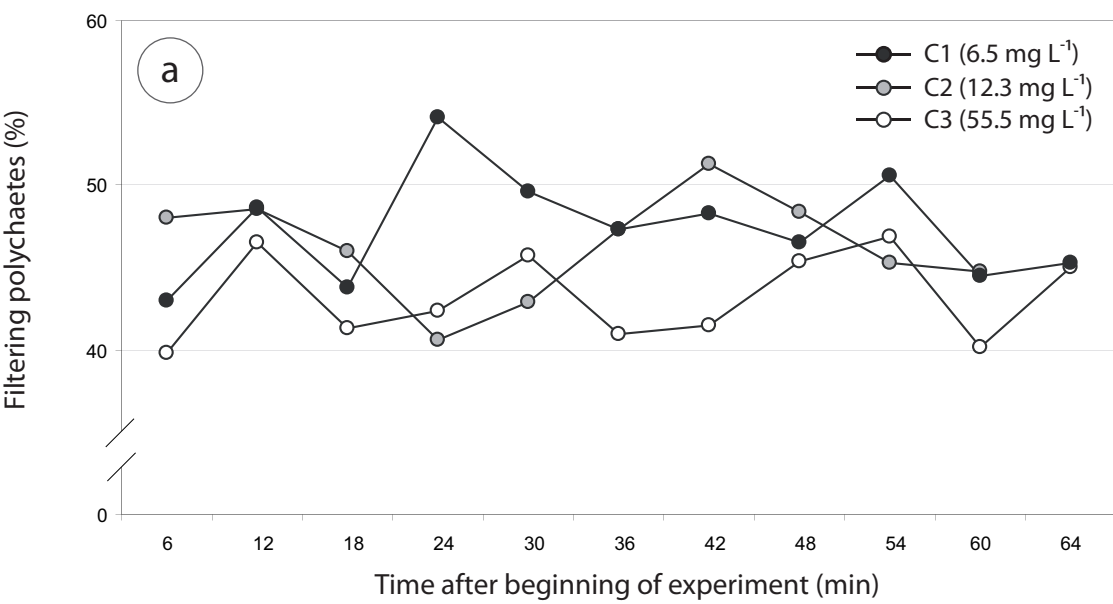


Figure 6

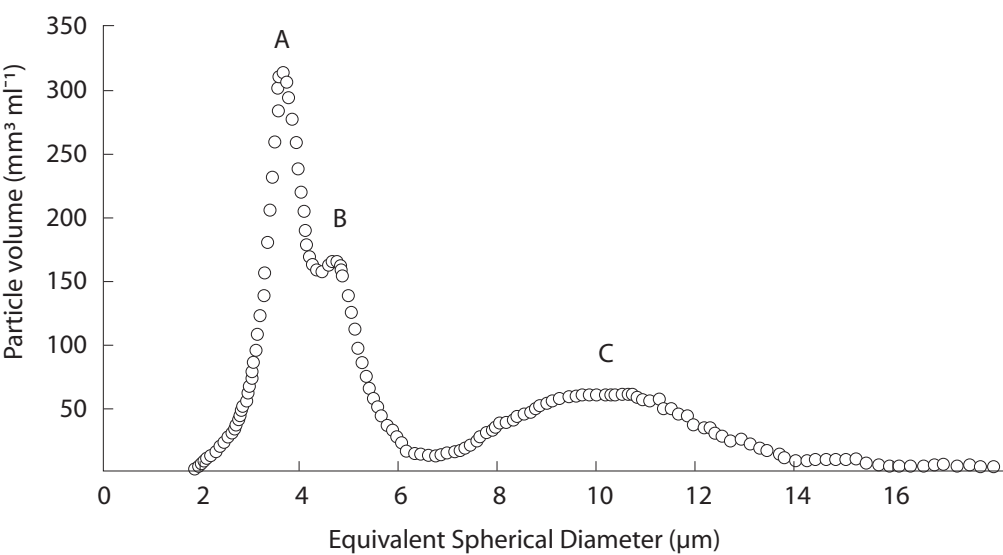


Figure 7

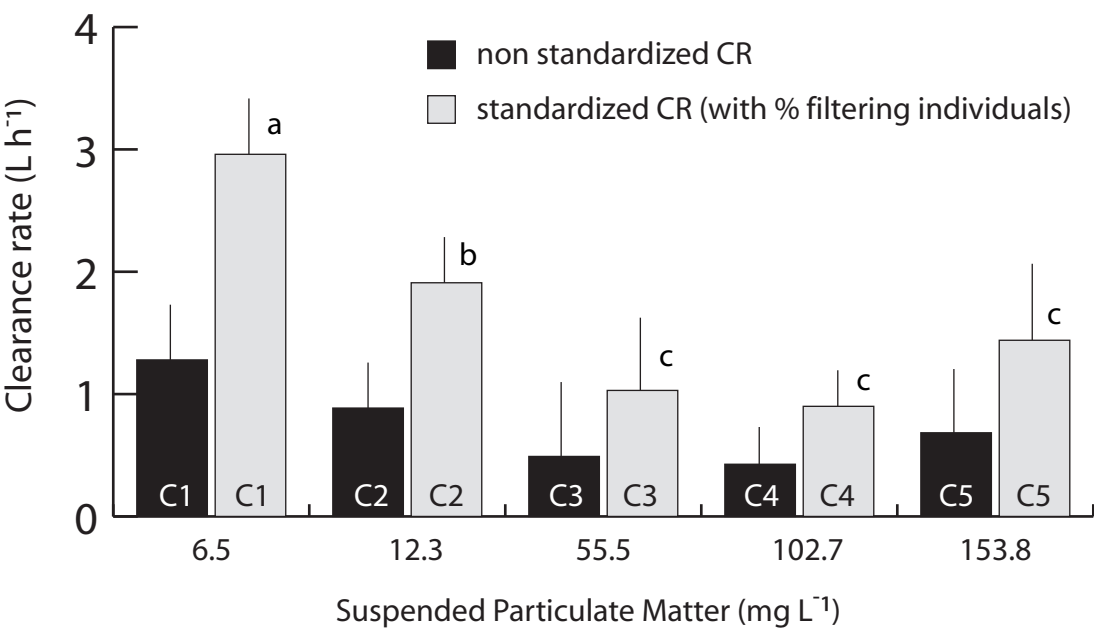


Figure 8

