Kinetics of tidal resuspension of microbiota: testing the effects of sediment cohesiveness and bioturbation using flume experiments

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ABSTRACT: Resuspension of the top few sediment layers of tidal mud flats is known to enhance plank-tonic biomass of microbiota (benthic diatoms and bacteria). This process is mainly controlled by tidal shear stress and cohesiveness of mud, and is also influenced by bioturbation activities. Laboratory experiments in a race track flume were performed to test the interactive effects of these factors on both the critical entrainment and resuspension kinetics of microbiota from silt-clay sediments from the Marennes-Oléron Bay, France. The marine snail *Hydrobia ulvae* was used to mimic surface biotur-bation activities. As expected, the kinetics of microbial resuspension versus shear stress were largely controlled by the cohesiveness of silt-clay sediments. However, our results indicate that the effect of surface tracking by *H. ulvae* on microbial resuspension was clearly dependent on the interaction between sediment cohesiveness and shear velocity. Evidence was also found that microphytobenthos and bacteria are not simultaneously resuspended from silt-clay bioturbated sediments. This supports the theory that diatoms within the easily eroded mucus matrix behave actively and bacteria adhering to fine silt particles eroded at higher critical shear velocities behave passively.

KEY WORDS: Microphytobenthos · Bacteria · Resuspension · Bioturbation *Hydrobia ulvae* · Shear velocity · Sediment cohesiveness Flume experiment

INTRODUCTION

Resuspension of benthic microalgae and bacteria enhances planktonic microbial biomass (Varela & Penas 1985, Shaffer & Sullivan 1988, Wainright 1990, de Jonge & van Beusekom 1992, 1995). For instance, the contribution of resuspended microphytobenthos to total phytoplankton can make up about 60% of the total phytoplankton in the Dollard estuary (de Jonge & van Beusekom 1992); Baillie & Welsh (1980) even cal-culated, in the Branford Harbor estuary, that if only 10 to 15% of the mudflat sediments were resuspended by tidal currents to a depth of 1 mm it could account for the chlorophyll levels inside the estuary. It thus appears that microbial resuspension must be of great importance to the nutrition of zooplankton and filter-feeders (Roman & Tenore 1978, de Jonge & van Beuse-kom 1992), and, more broadly, to the calculation of energy budgets in intertidal mudflats. However, al-though the importance of microbial resuspension has been demonstrated at the ecosystem level, very little is known about the mechanisms which control it.

Very few studies have so far specifically addressed the issue of microbial resuspension (Wainright 1990, Denis et al. 1996), and they have restricted themselves to the determination of the critical shear velocity which leads to resuspension of microphytobenthos or bacteria from intact sediments. Such an approach, although very valuable for inter-site comparison purposes, is however inappropriate for a thorough analysis of the biological and physical processes involved in microbial

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resuspension. The full complexity of the benthic micro-environment — including flow characteristics (Nowel & Jumars 1984), sediment properties (Mehta 1988) and biological activity (Rhoads & Boyer 1982) — has to be taken into account using an experimental approach which allows for interactions between the different factors to be dealt with. Jumars et al. (1981) have already stressed with the aid of a simple model the importance of flow-sediment-organism interaction on particulate resuspension.

This article aims to explain the effects of shear velocity, sediment cohesiveness, bioturbation and their potential interactions on the resuspension kinetics of microphytobenthos and bacteria under simulated tidal conditions. Flume experiments were designed to simulate a tidal flow (ebb or flood tide) on different unconsolidated sedimentary environments (representative of the mudflat conditions): different levels of sediment cohesiveness were tested with or without an enrichment of macrofauna. The range of sediment cohesiveness that was tested is representative of the readily resuspendable surficial mud in the Bay of Marennes-Oléron (France). The marine snail *Hydrobia ulvae* (Pennant) was used to mimic bioturbation activity in the experiments, not only because it is one of the most abundant macrofauna species in European estuaries and sheltered muddy shores (Reise 1985), but also because its various bioturbation behaviors are well described (see e.g. Barnes 1981). Besides the effect of each factor on microbial resuspension, one particular issue that we addressed in these experiments is how a change of the sediment properties affects bioturbation and what the consequences are for microbial resuspension.

MATERIAL AND METHODS

The experimental flume. Experiments were performed using the laboratory flume 'HYCOBENTHOS' (HYdrodynamisme et COmportement du BENTHOS) at 'Laboratoire maritime de Dinard', France. The flume has a race track shape and has a total length of 13 m, a cross section of 0.5 m and a depth of 0.3 m. The flume is composed of an experimental section, where the sediment is introduced and then eroded, and, on the opposite side, a driving section which generates the fluid movement. The latter section is made of 14 disks (80 cm diameter, 5 mm thickness) rotating around a horizontal axis so that seawater is moved by friction; the speed of the generated current is a function of the angular speed of the disks (see Champalbert & Marchand 1994, de Montaudouin & Bachelet 1996 for more details). The working section located along the 3.5 m long straight line opposite the wheel is 0.4 m² (1 m

length, 0.4 m wide): the width is smaller than the flume's cross section to prevent wall effects. These characteristics of the flume allow the simulation of benthic environments according to Nowell & Jumars' (1987) theoretical and experimental considerations. The flume was filled with seawater which had been pumped from the neighbouring bay a few hours before the experiments and which had been filtered through 1 μm filters to remove phytoplankton. The water height within the flume was 20 cm. A series of preliminary experiments had previously been performed in order to determine the optimal operating conditions of the flume.

Characteristics of the generated flow. Typically, tidal current velocities at 15 cm above the intertidal flat in Marennes-Oléron Bay are in the range 5 to 50 cm s⁻¹ (Raillard et al. 1994). Velocity profiles in the race track flume were obtained with an ultrasonic current meter (Minilab model SD-12, Sensor Data, Bergen, Norway) and determined for a range of free stream velocities similar to those found in the field: 5.5 ± 0.2 to 48.9 ± 2.1 cm s⁻¹ (mean ± SD) at 15 cm above the bottom. Shear velocities (u_*, cm s⁻¹) were calculated from the logarithmic section of the corresponding velocity profiles according to Nowell et al. (1981) and ranged from 0.32 ± 0.01 to 2.62 ± 0.05 cm s⁻¹ (mean ± SD).

Physical characteristics of the sediment. The sediment used for the experiments came from Brouage mudflat in the eastern part of Marennes-Oléron Bay (see Sauriau et al. 1989 for a detailed sedimentary map). Only the top cm of the sediment was used. This was a silty sediment with 98% of particles <50 μm and a mean size averaging 4 to 6 μm as determined by laser diffraction method (Bassoulet unpubl.). Rheological properties of pure cohesive sediments (i.e. cohesiveness) depend mainly on their concentration (Migniot 1968), and an empirical relationship can be established between the concentration of the sediment (Ts, g l⁻¹) and the yield value (τ_y, N m⁻²). Parameters of the power law ($\tau_y = 4.7 \times 10^{-7} Ts^{2.89}$, n = 92, R² = 0.86) were determined with a Brookfield LTVD viscometer for a rotor speed of 0.3 rev min⁻¹.

In order to evaluate the variations in silty sediment entrainment due to biological activity under different rheological conditions, experiments were carried out using 3 different sediment concentrations (181 ± 6, 212 ± 2 and 252 ± 1 g l⁻¹) (mean ± SD) corresponding to the 3 following yield values: 1.60, 2.40 and 4.10 N m⁻². This range is representative of pure mud found in the field. The highest cohesiveness corresponds to the sediment that was sampled. The lower levels of cohesiveness were obtained by diluting the sediment with seawater from the sampling site.

Faunal enrichment. The gastropod *Hydrobia ulvae* is a surface deposit-feeder of which adult densities

average more than 3000 ind. m^{-2} at an upper mudflat level of 3 to 5 m above the extreme low spring-tide level in Marennes-Oléron Bay. For the experiment with faunal enrichment, we added 10^4 ind. m^{-2} of which the size range was 4 to 6 mm. This density is close to the highest levels of *H. ulvae* adults recorded in the bay (Sauriau 1987). Individuals of *H. ulvae* were gently spread at the surface of the sediment in the working section and were left to crawl and bury themselves during filling of the flume (2 h period).

Experimental design and ANOVA analysis. The experiments were organized according to a partially-hierarchical design with 3 fixed factors: sediment cohesiveness (3 levels); density of *Hydrobia ulvae* (with and without faunal enrichment); and shear velocity. The first 2 factors, *H. ulvae* density and sediment cohesiveness, were fully crossed and organized as a 2-way design with replications. Two replications of this complete 3 × 2 factorial experiment were conducted in a random sequence of 12 flume experiments. Within each flume experiment, the current velocity was increased step by step (12 shear velocity levels ranging from 0.32 to 2.62 cm s^{-1}). The shear velocity factor was therefore nested within the flume experiment factor.

This partially-hierarchical design (see Brownlee 1965 for a detailed definition) can be compared to a split-plot design (Potvin 1993) which involved 2 between-flume-experiment crossed-factors and a within-flume-experiment factor The unit of comparison for *H. ulvae* density and sediment cohesiveness factors was 1 flume experiment, while different shear velocities were applied within each flume experiment. Each flume experiment is random assuming that the main factors *H. ulvae* density and sediment cohesiveness have to be tested over the flume experiment variability (Table 1). The response variables were log-transformed in order to fit ANOVA assumptions (Sokal & Rohlf 1981). The ANOVA analysis was performed using the MINITAB package, release 10.

Sampling. For each flume experiment and at each velocity step, the current velocity was maintained for a 20 min period in order to reach a steady state of suspended sediment concentration. This value was determined during the first set of resuspension experiments and is consistent with the time-step used by other laboratory erosion studies (Davis 1993, Denis et al. 1996). Just before increasing the velocity, water was sampled for measuring chl *a* concentration (used as an index of microalgal biomass) and counting bacteria. Three 100 ml water samples were drawn downstream from the experimental section (at the surface, at mid-depth, and just above the bottom) for chl *a* measurements using the fluorometric method (Lorenzen 1966). Only 1 sample (mid-depth) was used for bacteria counting. Total bacterial abundances were determined in sub-

samples filtered through black 0.2 µm Nuclepore filters after staining with 5 µg ml^{-1} acridine orange (Hobbie et al. 1977, Meyer-Reil 1977). To dislodge bacteria, we diluted the fixed mud samples with tetrasodium pyrophosphate (Na$_2$P$_2$O$_7$, 0.01 M final concentration) and sonicated them with a Sonimasse 520 equiped with a miniprobe at 40 % of maximum power for 30 s (Velji & Albright 1986, 1993) At least 200 cells were enumerated in 10 to 20 fields per sample at 1250× magnification using an epifluorescence microscope.

RESULTS AND DISCUSSION

Kinetics of microbial resuspension

The cumulative response curves of microphytobenthos and bacteria resuspension are presented in Figs. 1 & 2; the curves account for the initiation and the dynamics of microbial resuspension (up to the mass resuspension of sediment; afterwards the process is limited by the availability of sediment in the working area of the flume) when the sediment-water interface is experimentally subjected to a simulated tidal erosion. A logarithmic scale on the *y*-axis is used to detect the early stages of resuspension by emphasizing changes in the lower range of chl *a* concentration or bacterial density scales.

Partially-hierarchical 3-way ANOVAs, performed on log-transformed chl *a* and bacterial concentrations, clearly show that the 2 main effects (bioturbation and sediment cohesiveness) are statistically significant on both microalgal and bacterial resuspension (Table 1). The interaction between bioturbation and sediment cohesiveness is not significant, but the interaction between bioturbation, sediment cohesiveness and shear velocity is significant ($p = 0.019$ and $p = 0.012$ for microalgae and bacteria, respectively; Table 1). This indicates that the effects of bioturbation, sediment cohesiveness and of their interactions have to be analysed in the context of the resuspension kinetics because they change during the course of the simulated tidal erosion.

The significant effect of sediment cohesiveness on both microalgal ($p < 0.001$) and bacterial ($p < 0.001$) resuspension (Table 1) is evident from Figs. 1 & 2: the steepness of the curves as well as the duration of the resuspension process decreases as sediment cohesiveness increases. The general pattern is clearly a mass resuspension occurring at the critical shear velocity (u_{*c}) in the case of the least cohesive sediment ($\tau_y = 1.6$ N m^{-2}), a more gradual resuspension process for the intermediate cohesiveness ($\tau_y = 2.4$ N m^{-2}), and a strong resistance to erosion for the most cohesive sediment ($\tau_y = 4.1$ N m^{-2}) which limits microbial resuspen-

$\tau_y = 1\ 60\ N\ m^{-2}$

$\tau_y = 2.40\ N\ m^{-2}$

$\tau_y = 4\ 10\ N\ m^{-2}$
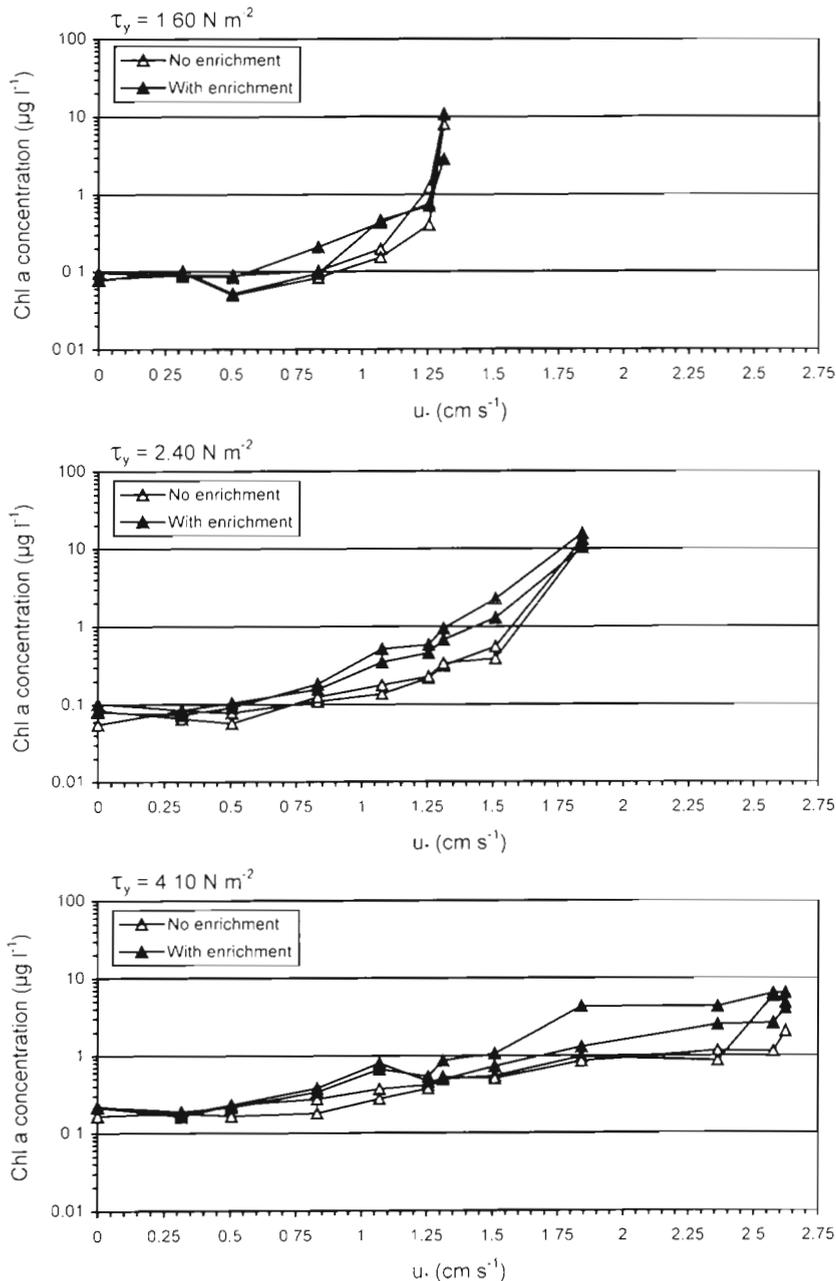
Fig. 1. Cumulative response curve of microphytobenthos resuspension. The cumulative chl a concentration is plotted against the shear velocity (u_*) for 3 different cohesiveness values (τ_y). ($\triangle$) Duplicated experiments without macrofaunal enrichment; ($\blacktriangle$) duplicated experiments with addition of *Hydrobia ulvae*. Because the kinetics of resuspension differed as a function of sediment cohesiveness, the maximum chl a resuspension (of the order of 10 µg l^{-1}) was not achieved at the same shear velocity

The significant bioturbation effect due to *Hydrobia ulvae* (p = 0.009 and p = 0.004 for microalgae and bacteria, respectively; Table 1) is also pointed out in Figs. 1 & 2: the intensity of the effect, however, changes as a function of both the sediment cohesiveness and the shear velocity (due to the significant interaction between bioturbation, sediment cohesiveness and shear velocity). Therefore, in order to point out and to analyse this additional biological effect (it is also a cumulative effect), we express it as a percentage of the physical effect (see legend of Fig. 3 for details of the calculation) and plot it in Fig. 3 as a function of the shear velocity for the 3 different sediment cohesiveness values. It is then clear that the enhancement effect due to bioturbation is restricted to a narrow range of shear velocities in the case of the least cohesive sediment: up to 155% at 1.08 cm s^{-1}, then no effect from 1.26 cm s^{-1} onwards, for microalgae (Fig. 3A), and almost negligible effect for bacteria from the lowest shear velocity onwards (less than 10%; Fig. 3B). The bioturbation effect greatly increases resuspension for the intermediate cohesiveness (up to ca 300% for microalgae and ca 100% for bacteria) and is active for a larger range of intermediate shear velocities up to 1.51 cm s^{-1} for both microalgae and bacteria. Then, at 1.84 cm s^{-1} the biological effect drops dramatically (down to ca 10%). Finally, at the highest sediment cohesiveness, the biological effect seems to be active over the full range of shear velocities which were tested, and reached enhancement levels of resuspension of about 240% and 120% for microalgae and bacteria, respectively.

It turns out that the biological effect occurs at the start of resuspension, and it appears to be all the more

sion. Thus, the enhancement of microbial biomass in the water column by tidal currents is strongly controlled by the sediment cohesiveness: the more cohesive the sediment, the higher the shear velocity (or tidal current above the sea bed) has to be to resuspend an equal quantity of cells.

effective, in terms of shear velocity range (hence intensity since it is a cumulative effect), when the sediment cohesiveness is higher (within the experimental conditions): in other words, the enhancement of microbial resuspension by *Hydrobia ulvae* is clearly mediated by the interaction between the sediment cohesiveness

and the shear velocity (p < 0.001 for both microalgae and bacteria; Table 1). If we further extrapolate this interaction to actual field conditions during high tide on an intertidal mud-flat, the enhancement of microbial resuspension by *H. ulvae* should be effective only within a temporal window (defined by the range of shear velocity within which *H. ulvae* is effective), the duration of this window being directly dependent on the sediment cohesiveness (Fig. 3). As a result, it is evident that the observation of this interaction opens new perspectives for ecophysiological studies concerning filter-feeder nutrition.

Determination of the critical shear velocity

A more classical approach in erosion studies is to determine the critical shear velocity of resuspended particles. There are however no easy and precise means of determining it in such mesocosms. It is usually achieved by visual observation for sediment resuspension, but the method may be subjective (Nowell et al. 1981) and is inappropriate for microbiota. So, we based its determination on a graphical examination (from Figs. 1 & 2). We then compared the results obtained by this approach with the visual observations which had been recorded during the flume experiments (i.e. critical shear velocity inducing initiation of mucus and silt motion). Results reported in Fig. 4A are in good agreement with the values of u_{*c} published in the literature for microphytobenthos (for instance 0.75 to 1 cm s^{-1}; Denis et al. 1996), but are slightly higher than those recorded for bacteria (0.95 to 1.35 cm s^{-1}; Wainright 1990). However, in the latter case the sediment was sandy, making it difficult to compare the values of u_{*c}.

Two-way ANOVAs show that the sediment cohesiveness significantly increases u_{*c} for bacteria (p < 0.001) and significantly affects microphytobenthos (but no general trend of increase;
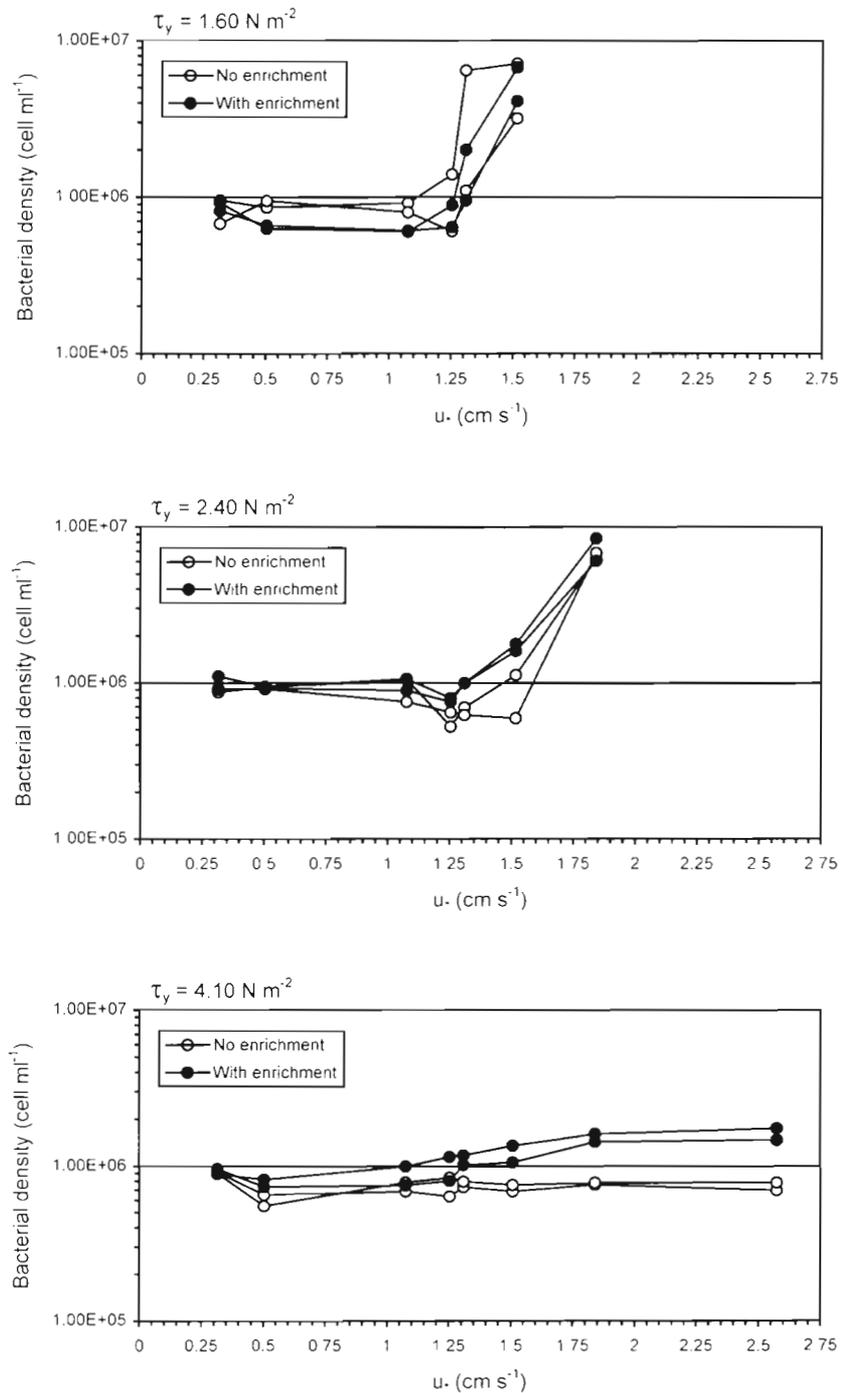
Fig. 2. Cumulative response curve of bacterial resuspension. The cumulative bacterial density is plotted against the shear velocity (u_*) for 3 different cohesiveness values (τ_y). (O) Duplicated experiments without macrofaunal enrichment; (●) duplicated experiments with addition of *Hydrobia ulvae*. Because the kinetics of resuspension differed as a function of sediment cohesiveness, the maximum bacterial cell resuspension (of the order of 1×10^7 cells l^{-1}) was not achieved at the same shear velocity. In contrast to microphytobenthos, bacteria were not counted at every shear velocity tested; however, this does not affect our results for the kinetics of resuspension or the determination of the critical shear velocity (the latter is determined with the same precision as for microphytobenthos)

Table 1. Partially-hierarchical 3-way ANOVA on log-transformed chl *a* and bacterial concentrations. The flume experiment factor is random assuming that the main factors Bioturbation and Cohesiveness have to be tested over the flume experiment variability

Source of variation	df	SS	MS	F	p
Chl *a* (log µg l^{-1})					
Bioturbation	1	1.093	1.093	14.60	0.009
Cohesiveness	2	10.194	5.097	68.04	<0.001
Bioturbation × Cohesiveness	2	0.049	0.025	0.33	0.729
Flume run (bioturbation cohesiveness)	6	0.449	0.074	4.89	<0.001
Shear velocity	11	95.744	8.704	568.51	<0.001
Bioturbation × Shear velocity	11	0.288	0.026	1.71	0.089
Cohesiveness × Shear velocity	22	13.817	0.628	41.02	<0.001
Bioturbation × Cohesiveness × Shear velocity	22	0.661	0.030	1.96	0.019
Error	66	1.010	0.015		
Total	143	123.309			
Bacteria (log cell ml^{-1})					
Bioturbation	1	0.400	0.400	21.07	0.004
Cohesiveness	2	2.114	1.057	55.64	<0.001
Bioturbation × Cohesiveness	2	0.025	0.012	0.67	0.545
Flume run (bioturbation cohesiveness)	6	0.113	0.019	3.36	0.008
Shear velocity	8	16.121	2.015	355.94	<0.001
Bioturbation × Shear velocity	8	0.289	0.036	6.39	<0.001
Cohesiveness × Shear velocity	16	3.576	0.223	39.48	<0.001
Bioturbation × Cohesiveness × Shear velocity	16	0.212	0.013	2.35	0.012
Error	48	0.271	0.005		
Total	107	23.125			
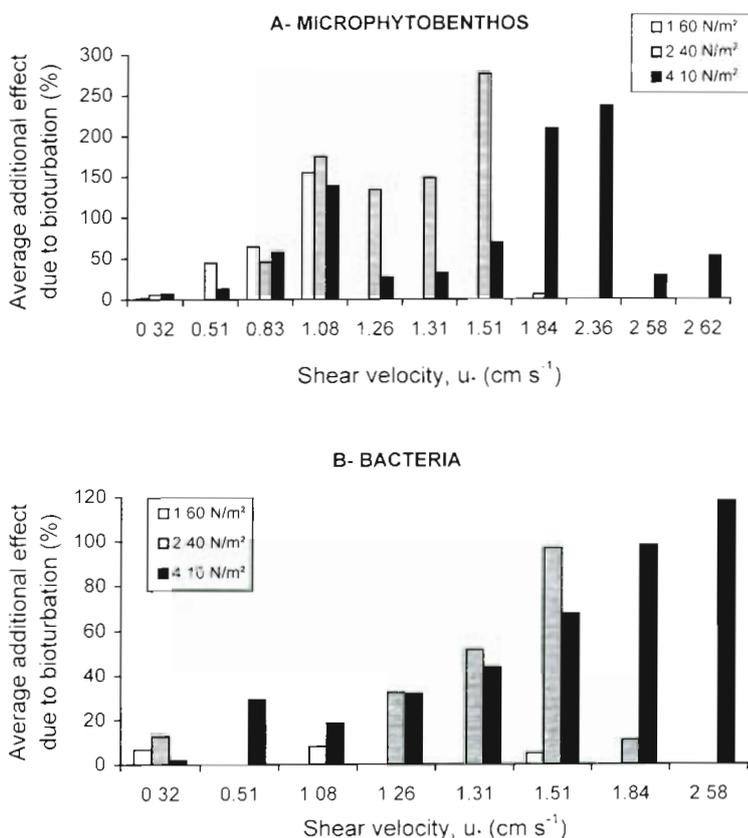
p = 0.002), and that bioturbation significantly decreases u_{*c} for both bacteria (p = 0.002) and microphytobenthos (p = 0.05). However, u_{*c} for bacteria is ultimately controlled by the interaction between sediment cohesiveness and bioturbation (p = 0.002; Fig. 4A): the decreasing effect of bioturbation on u_{*c} is all the more important when the sediment cohesiveness is higher. This interaction term is, however, not significant for microphytobenthos (p = 0.269), thus suggesting that the decreasing effect of bioturbation on u_{*c} is not dependent on the sediment cohesiveness.

The increase of u_{*c} for bacteria due to sediment cohesiveness is consistent with what can be predicted from the relationship between u_{*c} and the sediment co-

Fig. 3. Enhanced microbial resuspension due to bioturbation by *Hydrobia ulvae* for the 3 levels of sediment cohesiveness (average yield value, τ_y, N m^{-2}). Calculation is based on cumulative response curves of Figs. 1 & 2. Additional cumulative effect due to bioturbation (%) = [(X with enrichment − X no enrichment)/X no enrichment] × 100. (A): X = chl *a* concentration, (B): X = bacterial density

hesiveness of unconsolidated sediments (Migniot 1968): there is a proportional increase of u_{*c} as a function of sediment cohesiveness. In addition, the effect of bioturbation is also consistent with the results of Nowell et al. (1981), who showed that tracking by animals increases the boundary roughness and decreases the erosion threshold. In the specific case of *Hydrobia ulvae*, the presence of shells at the sediment-water interface also increases the rugosity, and furthermore this gastropod secretes mucus at the surface of the sediment. The visual observations made during the experiments indicate that this mucus was eroded and suspended together with agglomerated sediment before the free sediment surface was eroded itself It is then worth noting that, in many cases, the resuspension of these mucus-sediment agglomerates occurred at the u_{*c} values as those for microbiota resuspension in the experiments with faunal enrichment (Fig. 4B). As a result, secretion of the mucus by *H. ulvae* with a further agglomeration of the sediment surface (together with microbes inhabiting it) might explain why the critical shear velocity is decreased in the presence of *H. ulvae*. However, this is the first report of an interaction between sediment cohesiveness and bioturbation on bacterial resuspension.

Finally, paired comparisons based on a *t*-test (Sokal & Rohlf 1981) indicate that pooled values of u_{*c} are different between bacteria and microalgae (2-tailed test, p < 0.001). In addition, microalgae exhibited lower u_{*c} than bacteria in every case (Fig. 4A; 1-tailed test, p < 0.001), thus suggesting a highly significant differential resuspension of microbial communities. During tidal resuspension when the current velocity increases, microalgae appear to be resuspended first, followed by bacteria. This difference between the critical erosion velocity of microalgae and bacteria is further significantly affected by the interaction between sediment cohesiveness and bioturbation (2-way ANOVA, p < 0.001): the difference (hence the
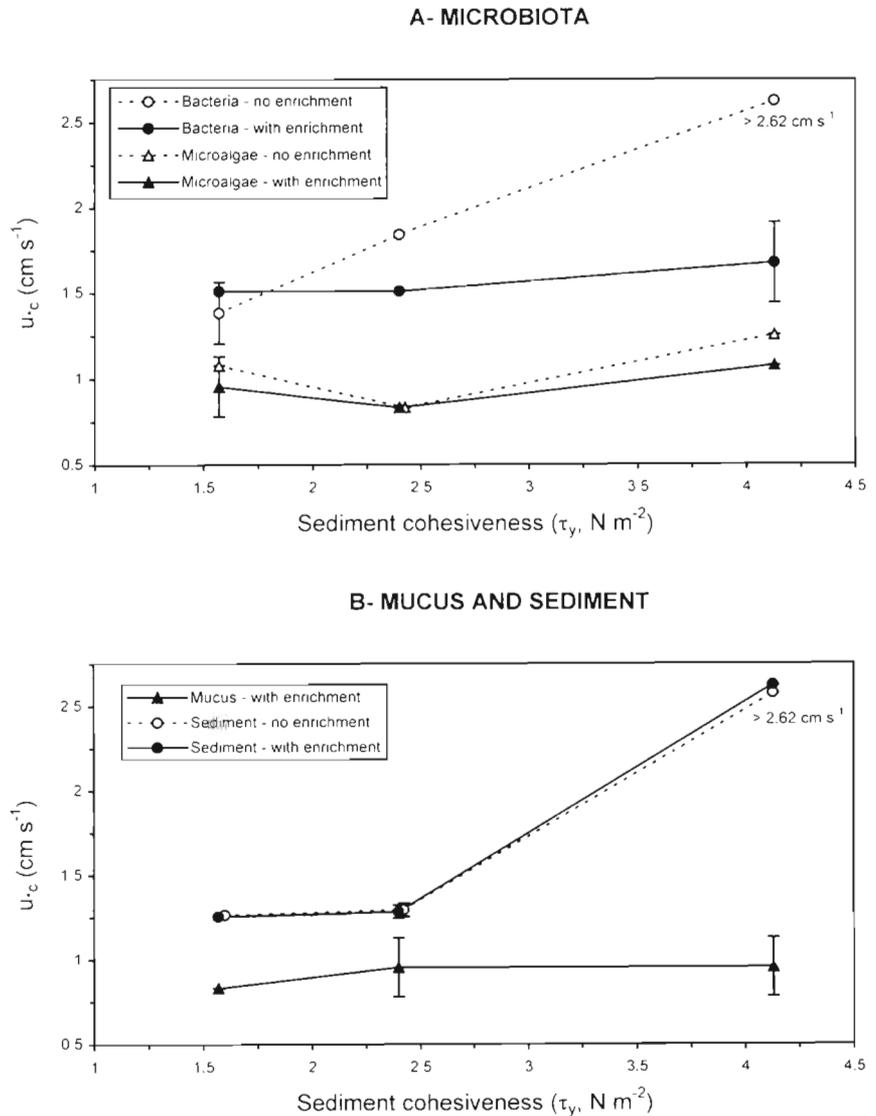
Fig. 4. Critical shear velocity (u_{*c}) as a function of sediment cohesiveness (τ_y) and bioturbation effect (with and without addition of *Hydrobia ulvae*). (A) u_{*c} for microalgae and bacteria, determined from Figs. 1 & 2. (B) u_{*c} for mucus and sediment, determined by visual observation of the sediment surface during the experiments; there is only 1 dataset of u_{*c} for the mucus since it does not exist when there is no addition of macrofauna on the sediment (the 'no enrichment' treatment)

time lag) between u_{*c} for bacteria and microalgae is all the more increased by bioturbation when the sediment cohesiveness is higher (note also that the sediment cohesiveness increases this difference, p = 0.003). Besides, if we compare the effect of *Hydrobia ulvae* on the overall kinetics of microalgal and bacterial resuspensions, it appears that the enhancement of resuspension was relatively more important for microalgae (Fig. 3, maximum enhancement of about 300% vs 120% for bacteria). This is the first report of such a difference between resuspension thresholds of microalgae and bacteria.

Hypotheses on the early resuspension of microphytobenthos

This observed difference in resuspension might firstly be explained by a behavioral difference: intertidal benthic microalgae are generally composed of motile diatoms (this was the case with the experimental sediment, Cariou-Le Gall & Blanchard 1995), while bacteria are mainly attached to sediment particles. In field conditions, the motility of microalgae is controlled by an endogenous rhythm (Aleem 1950, Callame & Debyser 1954, Palmer & Round 1967, Round 1979, Paterson 1989, Paterson et al. 1990) so that they migrate upwards to the top of the sediment surface during low tide. In the conditions which prevailed in our flume experiments (mixed sediment not subjected to tidal influences for several days), microalgae were very likely no longer controlled by the endogenous rhythm, but they could nevertheless have migrated upwards to the surface mud to seek light for photosynthesis. In doing so, they would have accumulated at the sediment surface (while bacteria would not have), where they would be more likely to be resuspended or to be trapped in the mucus secreted by *Hydrobia ulvae*, and then eroded. This hypothesis is supported by our visual observation of sediment and mucus motion during the experiments (Fig. 4B): mucus is always resuspended at lower shear velocites than sediment. Moreover, in terms of critical shear velocities (Fig. 4A, B), the resuspension pattern of mucus is very similar to that of microalgae while the resuspension threshold pattern of bacteria is very similar to that of the sediment. Finally, the hypothesis of the diatom-enriched mucus is further supported by observations of a previous study showing that freshly produced trails of another gastropod (*Monodonta turbinata*) are almost free of bacteria (Herndl & Peduzzi 1989).

An alternative hypothesis is that the trophic behavior of *Hydrobia ulvae* might have influenced microbial resuspension because of feeding preference on bacteria. Duration of experiments was indeed consistent with the time span needed by *H. ulvae* to fill its gut (i.e. 30 to 40 min according to Fenchel et al. 1975). However, there is increasing evidence that microalgae, instead of bacteria, represent the primary food source of this species (Jensen & Siegismund 1980, Morrisey 1988 and references cited therein).

Several conclusions may be drawn from this study: (1) The kinetics of microbial resuspension clearly shows that the critical shear velocity is not a sufficient indicator of erosion processes in that it does not depend on resuspension rates above the critical threshold. This opinion is in agreement with that of Grant & Daborn (1994) who insist on the decoupling of erosion rate and threshold. (2) The cohesiveness of the sediment has a large impact on the kinetics of microbial resuspension and on the critical erosion threshold; therefore, studies dealing with resuspension must report the value of the sediment cohesiveness. (3) The enhancement effect of *Hydrobia ulvae* on microbial resuspension is controlled by the interaction between the sediment cohesiveness and the shear velocity. (4) There is a differential resuspension among the different microbial communities.

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