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Effects of temperature on *in vitro* sediment reworking processes by a gallery biodiffusor, the polychaete *Neanthes virens*

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ABSTRACT: Temperature-induced variations in bioturbation could affect sediment mixing processes in the marine benthic environment. In this study, sediment reworking by *Neanthes virens* (Sars), a widely distributed polychaete in muddy sand communities of northern temperate latitudes, was studied under different temperature conditions representing winter (1°C), spring and fall (6°C), summer (13°C), and tide pool (18°C) temperatures in the lower St. Lawrence Estuary, Québec, Canada. Sediment reworking was quantified using inert fluorescent particles (luminophores) deposited at the sediment surface. Based on the 1-D luminophore distributions obtained after 5 and 30 d, the use of the specific 'gallery-biodiffusor' model allowed us to quantify both biodiffusion (D_b) and biotransport (V_b) due to the organisms. Our results showed temperature effects on sediment transport. The lowest biotransport and biodiffusion coefficients were measured at 1 and 6°C and did not change with time. The highest biodiffusion occurred at 13°C for both sampling periods. At 18°C, biodiffusion was intermediate while biotransport was maximal. Differences between the 13°C biodiffusive transport and the other temperatures increased with time. Low transport values at 1 and 6°C suggest that a quiescent stage exists for this species at these temperatures, with sediment mixing occurring mostly during burrow construction. On the other hand, sediment mixing resulted from both the burrow construction and maintenance phases at higher temperatures (13 and 18°C).

KEY WORDS: Bioturbation · Temperature · *Neanthes virens* · Inert tracers · Functional groups

INTRODUCTION

Temperature is considered one of the major environmental factors affecting the life of marine organisms. Temperature variations influence geographic and bathymetric species distribution patterns (Bhaud et al. 1995, Pörtner 2001). In regions with marked seasonality, temperature is a determinant parameter that controls benthic ecosystem dynamics (Kinne 1970). Temperature affects the reproductive cycle and the duration of the planktonic larval phase (Kinne 1970,

Bhaud et al. 1995). Temperature also determines important physiological processes such as metabolism (Kinne 1970, Yokoyama 1988, Fritzsche & von Oertzen 1995, Blier & Lemieux 2001, Pörtner 2001), growth (Bhaud 1988), and food conversion (Neuhoff 1979). Therefore, general activities such as feeding, digestion, and locomotion, which influence bioturbation processes, are also affected by temperature (Dobbs 1983, Riisgard & Banta 1998). For example, annelid polychaetes of the genus *Nereis*, which are widely distributed in coastal areas of Europe and North Amer-

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ica (Bass & Brafield 1972, Creaser & Clifford 1982, Kristensen 1984, Desrosiers et al. 1994), have shown large changes in pumping activity, ventilation, and oxygen uptake (Kristensen 1983, Rissgård et al. 1992) as well as in feeding and growth rates (Bass & Brafield 1972, Neuhoff 1979, Creaser & Clifford 1982, Kristensen 1984, Desrosiers et al. 1994) after temperature variations. This thermal sensitivity is likely related to specific adaptations and thermal tolerance. For example, *Nereis diversicolor* optimum temperatures are low (5 to 16°C) whereas *Neanthes virens* and *N. succinea* prefer higher temperatures (11 to 20°C and 20 to 35°C respectively) (Kristensen 1983). Therefore, considering the strong effect of temperature on physiological and metabolic processes, we can predict an important impact on the bioturbation activities of benthic organisms with changes in temperature.

The perturbation of the sedimentary environment through the activities of benthic invertebrates is known as bioturbation (Rhoads & Young 1970, Lee & Swartz 1980, Aller 1982) and affects many biotic and abiotic sediment parameters. When inhabited by populations of small organisms (<1 mm), surficial sediments become porous and unstable (Meadows & Meadows 1991, Rowden et al. 1998). Such sediments are more fluid and friable, meaning they are more easily suspended and displaced by water currents (Grant et al. 1982). Also, burrow ventilation enhances oxygen penetration to deeper sediments (Aller 1982). This water circulation (bioirrigation) brings oxygenated water to the burrow and evacuates waste products to the water column. The presence of oxygen in deeper sediments favours the degradation of buried organic matter (OM), which then contributes to oxygen consumption and the regeneration of anoxic conditions (Kristensen et al. 1995). Intermittent bioirrigation and rapid movements of particles and solutes between different redox environments (redox oscillation) create a complex and dynamic mosaic of oxic/anoxic interfaces in sediment (Kristensen 2000) and favour OM degradation (Aller 1994) and the chemical speciation of numerous compounds (i.e. Fe^{2+} , Fe^{3+}) (Hulth et al. 1999).

Since bioturbation greatly modulates the physical and chemical characteristics of benthic ecosystems, many bioturbators have been identified as 'ecosystem engineers' (Lawton 1994).

To better understand the impact of bioturbation on ecosystems, the study of a dominant species is mandatory. In northern temperate latitudes, muddy sand communities are dominated by a ubiquitous polychaete, *Neanthes virens* (Sars) (Desrosiers & Brêthes 1984, Commito & Ambrose 1985). *N. virens* is a tubicolous organism that lives in a semi-permanent, U-shaped burrow (Bass & Brafield 1972, Desrosiers et al. 1994). Maintenance of this burrow generates intense

perturbations of the sediment column. Near the surface, sediment particles and particulate OM (POM) are moved by a biodiffusion-type transport (François et al. 2002). Biodiffusion occurs mainly in surficial sediments and is similar to molecular diffusion processes that randomly mix particles (Guinasso & Schink 1975, Boudreau 1986a, François et al. 1997). In deeper sediments, particles are moved from the surface directly to the bottom of the burrow. This bioadvective transport (=non-local transport, sensu Boudreau 1986b, or bio-transport sensu Gerino et al. 1998) results in a net transport process instead of a diffusion process (Aller & Yingst 1978, François et al. 1997). Feeding activities such as foraging and burrow maintenance by nereids are important sources of biogenic perturbations (Charrois 1990, Gerino 1990, François et al. 1997, 2002). Because of this, seasonal temperature variations in the northern hemisphere should modulate the activity of polychaetes, which in turn might partly dictate modifications of the physico-chemical status of sediments through variations in bioturbation processes.

The aim of the present study was to examine the *in vitro* temperature influence on the sediment reworking kinetics induced by *Neanthes virens*. We designed and carried out experiments at different temperatures to determine the bioturbation effects on the vertical distribution of an inert tracer. In bioturbation studies, there are 2 main types of models: biodiffusive or bioadvective (e.g. Aller & Yingst 1978, Boudreau 1986a, François et al. 1997). Sediment reworking resulting from the activities of tubicolous species can result in biodiffusive or bioadvective particle transport, either in succession or simultaneously in space and time (François et al. 2002). Therefore, quantitative bioturbation parameters were determined using the gallery biodiffusor model recently developed by François et al. (2002) for *Nereis diversicolor*.

MATERIALS AND METHODS

Experimental setting. The experiment was performed at the aquaculture research lab of the Institut des sciences de la mer de Rimouski (ISMER) in Pointe-au-Père, Québec, Canada. We filled 48 cores (PVC tubes 30 cm in length and 10 cm in diameter) with fresh, screened sediment (1 mm mesh to remove macrofauna) that was then covered with 10 cm of seawater. The microcosms were randomly distributed in water tanks set at 1, 6, 13, and 18°C to represent winter, spring/fall, summer, and summer tide pool temperatures in the lower St. Lawrence Estuary, respectively (Desrosiers et al. 1994). Overlying seawater was renewed once every 2 d. Aeration did not induce resuspension. Twelve microcosms were used for each

temperature, 6 inhabited (with polychaetes) and 6 without macrofauna as experimental controls. The polychaete density used is representative of the area where they were collected (i.e. 500 ind. m⁻², Desrosiers et al. 1994). Following a 1 mo stabilization period, field-collected *Neanthes virens* (0.93 ± 0.41 g each, mean ± SD) were added to the cores and left to acclimate for 2 wk (Miron et al. 1991) prior to luminophore addition. The worms were adequately fed with *Enteromorpha* sp. algae during the experiment and thus did not suffer from starvation. To quantify the sediment reworking, a frozen sediment 'cake' (1 cm thick, 10 cm diameter) containing 1 g of luminophores mixed with fresh, screened sediments (Gerino 1990, Gilbert et al. 1995) was deposited on the top of each core. The luminophores were composed of natural sediment particles ranging in size from 212 to 250 µm and dyed with a fluorescent paint (Mahaut & Graf 1987). We assumed that the tracer was inert and thus could be used as a conservative marker. Experiments were performed over 30 d under a 12:12 light:dark regime. In order to study the effect of temperature on both the 2 phases of *N. virens* burrow construction (i.e. building and maintenance; Miron et al. 1991), sampling occurred on Days 5 and 30.

Sediment reworking. On each sampling day, the microcosms were frozen to terminate bioturbation activities and to facilitate the sampling processes (Gerino 1990). The frozen cores were then carefully hand sliced to obtain a set of 0.5 cm thick (0 to 2 cm deep), 1 cm thick (2 to 10 cm deep), and 2 cm thick (10 to 18 cm deep) sediment layers for each core. Each sediment sample was freeze-dried for 48 h and homogenized. Three subsamples of 0.25 g were sieved on a 250 µm sieve and the luminophores were counted directly under UV light (Gerino 1990, Gilbert et al. 1995). To transform the counts of luminophores to weight for each sample, we determined a conversion factor (1.3 × 10⁻⁵ g luminophore⁻¹) for the luminophore mixture used in this experiment.

The biodiffusion (D_b) and biotransport (V_b) coefficients were calculated from the vertical distributions of luminophores modeled by the classical biodiffusion (Gerino et al. 1994) and gallery-biodiffusor models. The latter was specifically developed on *Nereis diversicolor* by François et al. (2002). This mechanistic model is time- and space-dependent and uses ordinary differential equations. It utilizes 3 kinds of parameters: (1) biological parameters such as the size of the zone affected by bioturbation, the rate of biodiffusion, and the rate of biotransport; (2) physical parameters such as the output to the water-column coefficient and the rate of physical mixing due to local water currents; and (3) biogeochemical parameters such as the tracer decay rate. A series of theoretical curves are first calculated. Using

the least-square fitting method, the curve with the best fit of the observed distribution is kept and the biodiffusion and biotransport coefficients are extracted. This model is appropriate for organisms that dig galleries (François et al. 2002) as it has been observed for *Neanthes virens* in nature and in microcosms.

Statistical analysis. Two bioturbation models were used: the biodiffusor and the gallery-biodiffusor models (François et al. 2002). To determine the best model, we used a Kolmogorov-Smirnov goodness of fit test to compare the observed and calculated distributions (Gerino et al. 1994). Differences between the quantity of buried luminophores, the modeled biodiffusion and biotransport coefficients were studied separately using a 2-way ANOVA with time and temperature treated as fixed factors (Type I model ANOVA, Zar 1984). Bartlett's test ($\alpha = 0.05$) was employed to test *a priori* the homogeneity of variance. Heteroscedastic data were log- or arcsinus-transformed to obtain homogeneity of variances.

RESULTS

Burying profiles

The luminophore burying profiles showed an exponential decrease in the number of luminophores from the surface to the bottom of each core (Fig. 1). In the control cores, nearly all the luminophores remained at the surface, while 4.6% of the original amount was mixed into the sediments down to 2 cm.

On Day 5, differences were observed among the temperature profiles. There were more luminophores between 2 and 4 cm at 13 and 18°C (0.082 and 0.086 mg luminophores cm⁻³, respectively) compared to the amounts found at 1 and 6°C (0.034 and 0.055 mg luminophores cm⁻³, respectively). In all cases, luminophores were buried to a maximum depth of 9 cm. On Day 30, differences among profiles for each temperature were more pronounced and revealed 2 groupings: the lower (1 and 6°C) and higher (13 and 18°C) temperatures. The 1 and 6°C profiles had a steeper exponential decrease of the luminophore concentrations with depth compared to the 13 and 18°C profiles. Therefore, there were more luminophores buried in the sediments at 13 and 18°C than at 1 and 6°C. Luminophores were found deeper in the sediments (13 cm) on Day 30 for all temperatures. When comparing all profiles for Day 5 and Day 30, we observed a greater quantity of luminophores buried on Day 30. Furthermore, the 1 and 6°C profiles on Days 5 and 30 were very similar.

On Days 5 and 30, quantity of buried luminophores differed significantly among the temperatures

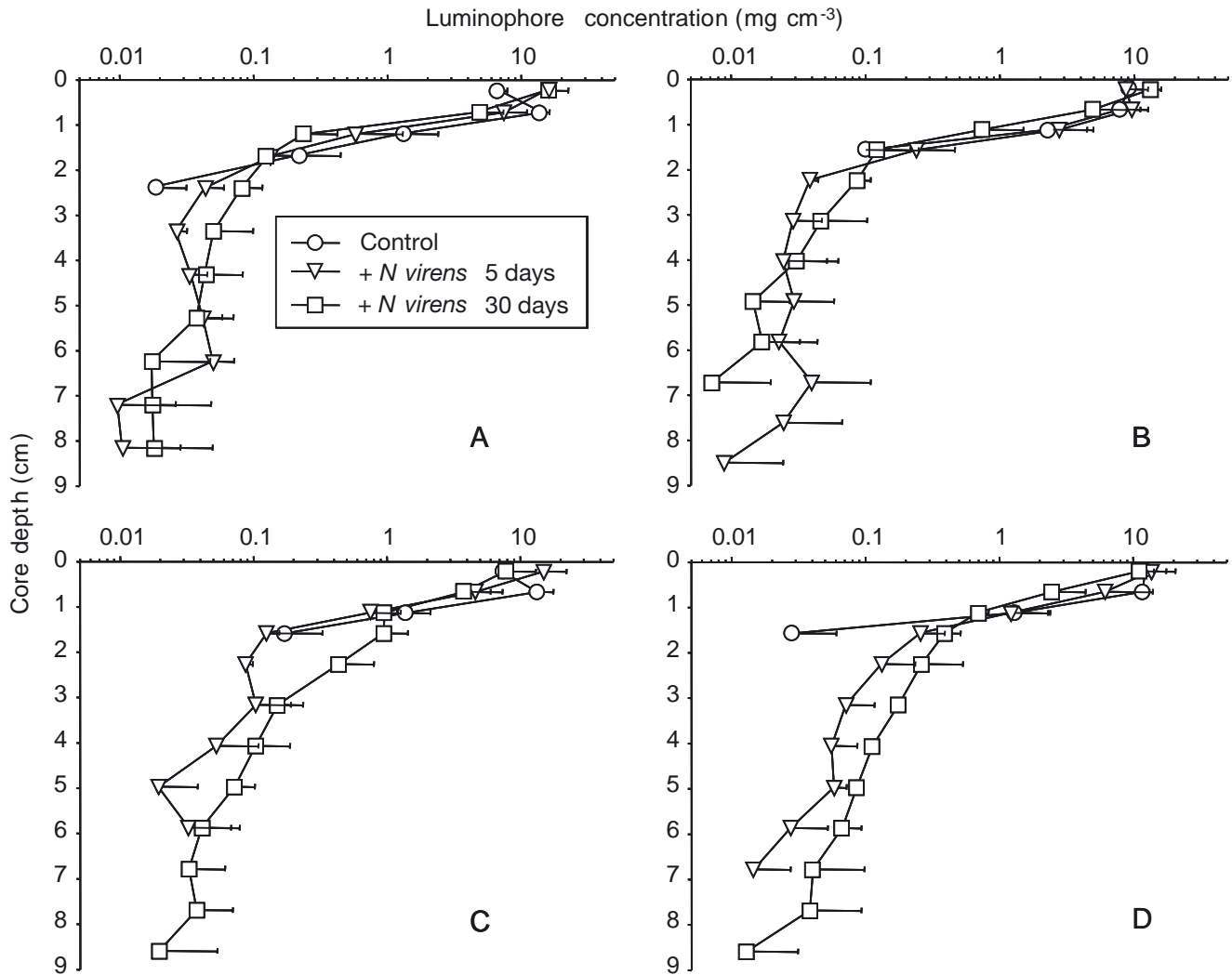


Fig. 1. Vertical distribution of luminophores in the control (Day 5) and inhabited (Days 5 and 30) sediments for each temperature: (A) 1°C; (B) 6°C; (C) 13°C; (D) 18°C. Values are mean \pm SD for triplicates. Since the control profiles did not change between Days 5 and 30, only control Day 5 profiles are presented

(ANOVA; $F_{3,20} = 23.57$; $p = 0.001$; Table 1) with the highest quantities of buried luminophores found at 13°C. The time factor (i.e. differences between the values for Days 5 and 30) also had an effect (ANOVA; $F_{1,22} = 15.17$; $p < 0.01$; Table 1) mainly due to the increase of the difference between the 13°C values and the others with time. A time \times temperature interaction was noted (ANOVA; $F_{3,16} = 6.217$; $p < 0.05$; Table 1).

Bioturbation kinetics

Fig. 2 and Table 2 present the comparison of observed and modeled data. The results show that the

observed distribution and the gallery-biodiffusor distribution over the first 7 cm did not differ significantly (Kolmogorov-Smirnov goodness-of-fit $D_{0.05, 7} = 0.429$; $p > 0.1$). The difference between the observed distribution and the biodiffusor was significant ($D_{0.05, 7} = 0.714$; $p < 0.1$). These results show that the gallery-biodiffusor model fit the *Neanthes virens* activities.

Table 3 and Fig. 3 present the coefficients of biodiffusion (D_b ; $\text{cm}^2 \text{d}^{-1}$) and biotransport (V_b ; cm d^{-1}) calculated for the different reworked sediments on Days 5 and 30 for the 4 experimental temperatures.

On Days 5 and 30, biodiffusion values differed significantly among the temperatures (ANOVA; $F_{3,20} = 9.23$; $p < 0.01$; Table 1). The highest value was at 13°C

Table 1. Detailed results of the ANOVA test performed on the quantity of buried luminophores, and the D_b and V_b parameters obtained with the gallery-biodiffusor model

Arcsin quantity of buried luminophores					
Source	SS	df	MS	F-ratio	p-value
Time	0.013	1	0.013	15.174	0.0030
Temp.	0.060	3	0.020	23.572	0.0001
Time × Temp.	0.016	3	0.005	6.214	0.0118
Error	0.008	11	0.001		
Log D_b					
Source	SS	df	MS	F-ratio	p-value
Time	0.609	1	0.609	5.662	0.0365
Temp.	2.979	3	0.993	9.228	0.0024
Time × Temp.	0.086	3	0.029	0.266	0.8482
Error	1.184	11	0.108		
Log V_b					
Source	SS	df	MS	F-ratio	p-value
Time	0.444	1	0.444	5.081	0.0456
Temp.	1.987	3	0.662	7.582	0.0050
Time × Temp.	0.102	3	0.034	0.391	0.7621
Error	0.961	11	0.087		

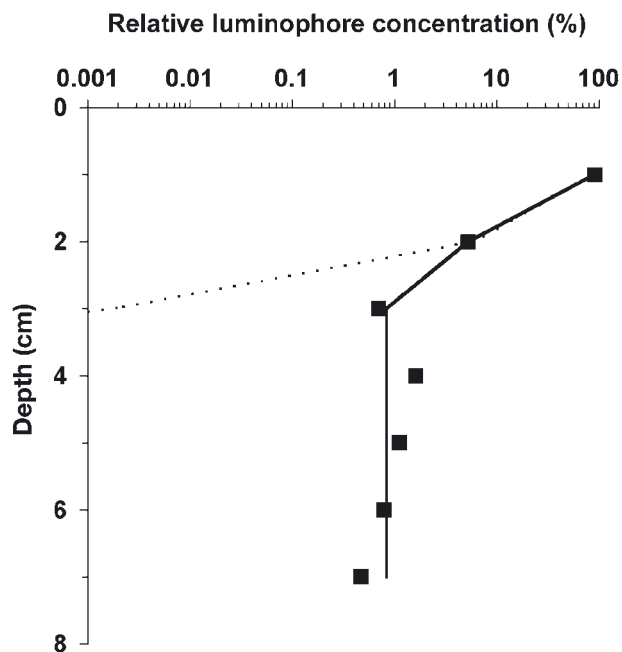


Fig. 2. Comparison of modeled luminophore distribution (biodiffusor model: dotted line; gallery-biodiffusor model: solid line) and observed luminophore distribution (■). Modeled and observed data are from microcosms at 13°C inhabited by *Neanthes virens* and sampled at Day 30

for both periods. In addition, the difference between the 13°C values and the others was larger on Day 30. The time factor (i.e. differences between the values for Days 5 and 30) had a small effect (ANOVA; $F_{1,22} = 5.66$; $p < 0.1$; Table 1). No time × temperature interaction was noted (ANOVA; $F_{3,16} = 0.27$; $p = 0.85$; Table 1).

With the biotransport values, temperature also had a significant effect (ANOVA; $F_{3,20} = 7.58$; $p < 0.01$; Table 1). There were differences between the low temperatures (i.e. 1 and 6°C) and 13°C, and between the low temperatures and 18°C. On Day 30, these differences were greater. Differences between Days 5 and 30 were slightly significant (ANOVA; $F_{1,22} = 5.08$; $p < 0.1$; Table 1). No time × temperature interaction was noted (ANOVA; $F_{3,16} = 0.391$; $p = 0.76$; Table 1).

DISCUSSION

The experimental setting allowed us to clearly discriminate the effect of temperature from other parameters such as food availability, light, and benthic community structure. Therefore, the observed variations of the bioturbation intensities are only associated with temperature variations.

In the control sediment, no more than 4.6% of luminophores were found beneath 1 cm (thickness of the deposition cake) and down to 2 cm. This may be explained by density differences between luminophores and sediments, inducing a little particle displacement toward deeper sediments. Also, meiofauna may have been responsible for this tracer migration. These small (<1 mm) organisms build microstructures that destabilize surficial sediments (Nehring et al. 1990, Giere 1993, Tita et al. 2000, Michaud et al. 2003), allowing surficial particles to penetrate deeper into the sediments (Gerino et al. 1998). However, particle displacement by meiofauna would have caused an increased penetration of the tracers with time, which was not the case in the controls between Days 5 and 30. Therefore, we conclude that meiofauna is not an important bio-

Table 2. Detailed results of the Kolmogorov-Smirnov goodness-of-fit (D) test used to compare calculated (GAL_DIF: gallery-biodiffusor model; BIODIFF: biodiffusor model) and observed distributions

	Max. negative difference	Max. positive difference	D	p level
GAL_DIFF	-0.423	0.286	0.429	$p > 0.10$
BIODIFF	-0.1429	0.714	0.714	$p < 0.10$

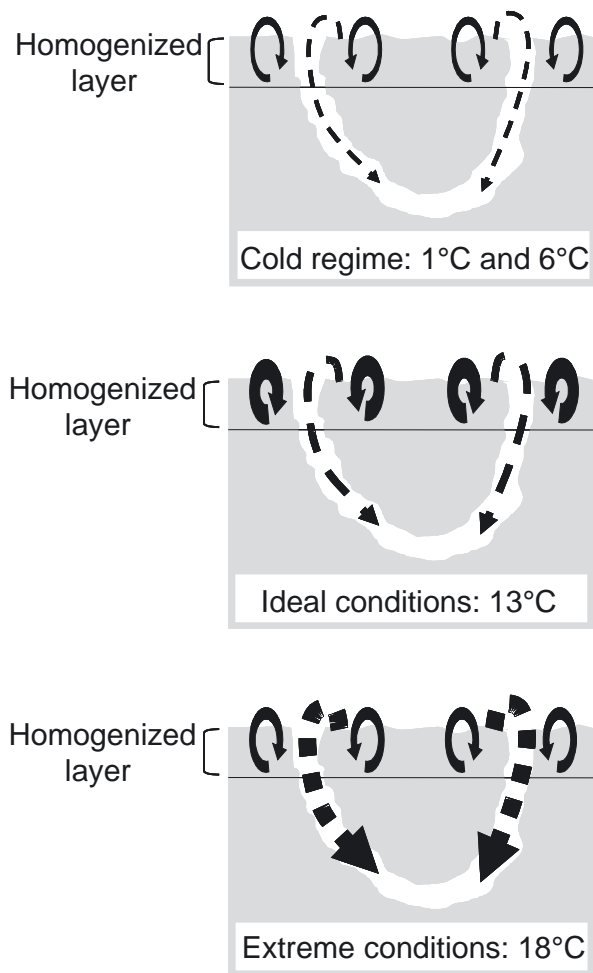


Fig. 3. Relative intensities of sediment mixing modes resulting from bioturbation activities of *Neanthes virens* after 30 d. Solid arrows: biodiffusive transport (D_b); dotted arrows: bioadvective transport (V_b). Variations in the line thickness indicate the relative intensity of the transport

turbation source of our study. In the inhabited microcosms, tracer distributions were grouped into 2 temperature regimes: 1 to 6°C (cold) and 13 to 18°C (warm). The differences between the 2 regimes increased with time. The maximum depth reached by the tracers also varied with time and temperature. The luminophores were generally found deeper in microcosms sampled on Day 30. The tracers were also found deeper at warm temperatures (13 and 18°C).

As described by Miron et al. (1991), the construction of a new burrow by *Neanthes virens* is divided into 2 phases. The first phase, the building and prospecting phase, is characterized by the creation of numerous galleries due to displacements of *N. virens* in sediments. It occurs in the first 5 to 7 d following arrival in a new environment. When *N. virens* moves into the sediments, particles are pushed away from the poly-

Table 3. Biodiffusion (D_b) and bioadvection (V_b) coefficients calculated with the gallery-biodiffusor model in sediment cores inhabited by *Nereis virens*. Values are mean \pm SD; n = 3. Mean cold: average value for 1 and 6°C data; mean warm: average value for 13 and 18°C data

Temp. (°C)	D_b ($10^{-3} \text{ cm}^2 \text{ d}^{-1}$)	V_b ($10^{-3} \text{ cm}^2 \text{ d}^{-1}$)
5 d		
1	1.97 \pm 0.52	1.52 \pm 0.74
6	3.60 \pm 2.54	2.37 \pm 1.55
13	14.6 \pm 4.77	5.65 \pm 2.28
18	8.64 \pm 2.07	5.56 \pm 2.08
Mean cold	2.79	1.95
Mean warm	11.6	5.60
30 d		
1	3.6 \pm 2.54	2.37 \pm 1.55
6	9.25 \pm 6.50	3.06 \pm 1.23
13	51.6 \pm 8.11	13.9 \pm 0.03
18	20.8 \pm 1.47	20.6 \pm 2.11
Mean cold	6.42	2.71
Mean warm	36.2	17.3

chaete's body. Particle movement is thus very small. Also, when moving in sediments, *N. virens* leaves a thin layer of mucus covering the walls of the newly formed galleries. One of the effects of this mucus is to hold sediment grains together to form a stable wall (Houel 1998). The consequences of these processes are low biodiffusive and bioadvective sediment transport rates. In our experiment, the polychaetes received a relatively large amount of sediments and luminophores (the cakes) that forced them to partially rebuild their burrows near the surface. Therefore, sediment reworking during this phase created relatively low biodiffusive and bioadvective transport rates on Day 5. According to Miron et al. (1991), *N. virens* maintains its burrow during the second phase by moving surface particles mixed with mucus to the burrow linings (maintenance phase). Particles are also moved to the burrow when *N. virens* search for food at the sediment surface. Food searching is more important during this phase than in the previous phase. By these actions, the worm increases the biodiffusive distribution in the superficial layers. Maintenance and food search also induce a rapid and direct transfer of surface particles towards the bottom of the burrow when *N. virens* moves back to its burrow (Charrois 1990). Particle movement in this manner represents bioadvective transport. The increase of both the biodiffusive and bioadvective transport measured on Day 30 is consistent with the behavioural changes by *N. virens* during the experiment.

Our results showed that both transports were affected by temperature according to the duration of the sampling periods. On Day 5, temperature seemed to have little impact on *Neanthes virens* activities,

with equivalent biodiffusive and bioadvective transports for each temperature, while both processes were highly affected by temperature after 30 d. This strongly suggests an acclimation process allowing the annelids to reduce their metabolism and activities at low temperatures while increasing them at higher temperatures. Therefore *Neanthes virens*, as a mesothermal invertebrate, does not compensate at low temperatures but rather decreases its activity and likely inhibits its metabolic demands to minimize its energy requirement. Conversely, active periods (high temperature) should correspond to a high availability of nutritional resources. This high thermal sensitivity of physiological processes (activity) precludes a high temperature dependence of bioturbation processes and biophysical status of sediments. Since the burrow is a vital structure (Miron et al. 1991), *N. virens* must rebuild it after a sediment deposition (Desrosiers et al. 1994), a process that may be slower in a cold regime. Our results showed that biotransport and biodiffusive transport were low in the colder temperatures (1 and 6°C) on both Days 5 and 30. A quiescent period induced by low temperatures, as observed in the field by Desrosiers et al. (1994), could explain the low variations observed for the bioturbation coefficients with time. At the higher temperatures (13 and 18°C) after 5 d, the biotransport and biodiffusion coefficients were close to the coldest temperature. On the other hand, after 30 d they were significantly higher. These temperatures correspond to summer conditions in the water column and tide pools in the lower St. Lawrence Estuary (Miron & Desrosiers 1990). At 18°C, the results showed a decrease in the biodiffusion coefficient and an increase in the biotransport coefficient compared to 13°C. Bioadvective transport by polychaetes is mainly due to water currents induced by dorso-ventral oscillations of the organism (bioirrigation) that destabilize surface particles and carry them to the bottom of the burrow (François et al. 2002). Kristensen (1983) also obtained an increase in bioirrigation activities by *N. virens* at a warm (20°C) temperature that was probably due to an increased demand in oxygen for metabolic activities. The low biodiffusion coefficient could be related to a reduction of food searching activities (Deschênes 2001), of particle storage in the upper part of the burrow (Olivier et al. 1996), and/or to a longer bioirrigation period by the worm (Miron et al. 1992).

Our results showed that sediment reworking processes by *Neanthes virens* are affected by temperature. Two temperature regimes were observed: cold and warm. Sediment reworking in the cold regime was rather low for both the biodiffusive and bioadvective transports, compared to the polychaete activities under the warm regimes.

Bioturbation has great implications in OM degradation processes. If the seasonal variability of the bioturbation intensity induces a fluctuation of these OM degradation processes, it could affect the entire organization of the intertidal ecosystem since OM regulates the life cycle of many benthic organisms (Kemp & Boynton 1981). Consequently, the existing OM degradation estimates that are calculated on an annual basis would need seasonal corrections. Also, bioturbation models are based on steady-state or idealized conditions. They do not include temperature in the calculation of marker distribution profiles. The accuracy of bioturbation predictions would be greater with temperature-influenced models, allowing bioturbation kinetics to be evaluated on a seasonal basis instead of on an annual basis. Finally, the results also show that the thermal preferendum for *Neanthes virens* is narrow. In the context of global warming, the adaptability of *N. virens* populations in regions affected by large temperature variations needs further investigation.

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