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

Daniel Ouellette1, Gaston Desrosiers1,*, Jean-Pierre Gagne1, Franck Gilbert2, Jean-Christophe Poggiale2, Pierre U. Blier3, Georges Stora2

1Institut des sciences de la mer de Rimouski (ISMER), Université du Québec à Rimouski, 310 allée des Ursulines, Rimouski, Québec G5L 3A1, Canada
2Laboratoire d’Océanographie et de Biogéochimie, Université de la Méditerranée, COM, Campus de Luminy, case 901, Marseille 13288, Cedex 9, France
3Département de biologie, chimie, sciences de la santé, Université du Québec à Rimouski, 300 allée des Ursulines, Rimouski, Québec G5L 3A1, Canada

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, Risgard & Banta 1998). For example, annelid polychaetes of the genus Nereis, which are widely distributed in coastal areas of Europe and North Amer-
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 & Bréthes 1984, Commiso & 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, Desroisières 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 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) temperature profiles. The 1 and 6°C profiles on Days 5 and 30 showed an 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
The time factor (i.e. differences between the values for Days 5 and 30) also had an effect (ANOVA; $F_{1, 22} = 15.17; p < 0.01; \text{Table 1}$) mainly due to the increase of the difference between the $13^\circ C$ values and the others with time. A time $\times$ temperature interaction was noted (ANOVA; $F_{3,16} = 6.217; p < 0.05; \text{Table 1}$).

**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 ($V_b; \text{cm} \text{d}^{-1}$) 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; $F_{3, 20} = 9.23; p < 0.01; \text{Table 1}$). The highest value was at $13^\circ C$.
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 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.

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F-ratio</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>0.013</td>
<td>1</td>
<td>0.013</td>
<td>15.174</td>
<td>0.0030</td>
</tr>
<tr>
<td>Temp.</td>
<td>0.060</td>
<td>3</td>
<td>0.020</td>
<td>23.572</td>
<td>0.0001</td>
</tr>
<tr>
<td>Time × Temp.</td>
<td>0.016</td>
<td>3</td>
<td>0.005</td>
<td>6.214</td>
<td>0.0118</td>
</tr>
<tr>
<td>Error</td>
<td>0.008</td>
<td>11</td>
<td>0.001</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Log $D_b$**

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F-ratio</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>0.609</td>
<td>1</td>
<td>0.609</td>
<td>5.662</td>
<td>0.0365</td>
</tr>
<tr>
<td>Temp.</td>
<td>2.979</td>
<td>3</td>
<td>0.993</td>
<td>9.228</td>
<td>0.0024</td>
</tr>
<tr>
<td>Time × Temp.</td>
<td>0.086</td>
<td>3</td>
<td>0.029</td>
<td>0.266</td>
<td>0.8482</td>
</tr>
<tr>
<td>Error</td>
<td>1.184</td>
<td>11</td>
<td>0.108</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Log $V_b$**

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F-ratio</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>0.444</td>
<td>1</td>
<td>0.444</td>
<td>5.081</td>
<td>0.0456</td>
</tr>
<tr>
<td>Temp.</td>
<td>1.987</td>
<td>3</td>
<td>0.662</td>
<td>7.582</td>
<td>0.0050</td>
</tr>
<tr>
<td>Time × Temp.</td>
<td>0.102</td>
<td>3</td>
<td>0.034</td>
<td>0.391</td>
<td>0.7621</td>
</tr>
<tr>
<td>Error</td>
<td>0.961</td>
<td>11</td>
<td>0.087</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**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.

<table>
<thead>
<tr>
<th></th>
<th>Max. negative difference</th>
<th>Max. positive difference</th>
<th>D</th>
<th>p level</th>
</tr>
</thead>
<tbody>
<tr>
<td>GAL_DIF</td>
<td>−0.423</td>
<td>0.286</td>
<td>0.429</td>
<td>p &gt; 0.10</td>
</tr>
<tr>
<td>BIODIFF</td>
<td>−0.1429</td>
<td>0.714</td>
<td>0.714</td>
<td>p &lt; 0.10</td>
</tr>
</tbody>
</table>
turbation source of our study. In the inhabited micro-
cosms, 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 in-
creased with time. The maximum depth reached by
the tracers also varied with time and temperature. The
luminophores were generally found deeper in micro-
cosms 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 sedi-
ments. 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-
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 lumino-
phores (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 sur-
ficial 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 in-
crease of both the biodiffusive and bioadvective trans-
port measured on Day 30 is consistent with the behav-
ioral 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 biortransport 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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