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Activities by *Hediste diversicolor* under different light regimes: Experimental quantification of particle reworking using time-resolved imaging

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ABSTRACT

Particle reworking by the ragworm *Hediste diversicolor* was assessed by quantifying the transport of fluorescent particles (luminophores) added to the surface sediment during a 10 day experiment. Plexiglass cores and thin glass aquaria with fauna and controls were exposed to either 12 hour light/dark cycles or constant darkness. Luminophore distributions were evaluated by side-view imaging of the aquaria together with destructive sectioning and quantification of tracer distributions in both types of microcosms at the end of experiments. Tracer distributions were evaluated by the gallery-diffusor model, from which the biodiffusion (D_b) and the non-local transport (r) coefficients were determined. In addition, the maximum penetration depth (MPD) of luminophores, the 2-D redistribution coefficient, and the transport rate were used as a suite of proxies to quantify particle reworking by fauna.

All measured reworking proxies demonstrated a general decrease in transport of luminophores in darkness compared to light/dark cycles. The difference was significant for proxies determined from sectioning. Imaging of particle transport demonstrated that rates were ~30% higher during light/dark cycles, with ~constant amount of particles transported on a daily basis. The effect of light was consistent in the two microcosm types. However, there was a significant difference in D_b, while r and MPD were not significantly different between the cores and aquaria. Overall, these results suggest a light-triggered surface feeding by *H. diversicolor*. Our study highlights the importance of experimental settings for quantification of particle transport by fauna, and that light conditions and types of experimental microcosms need to be carefully considered during investigations of bioturbation in illuminated environments.

1. Introduction

Benthic macrofauna significantly influences early diagenesis and the fate of organic material deposited on the sediment surface. Faunal activities not only alter the physical geometry and biogeochemical structure of the sediment, but also affect the transport of particles, solutes and gases across the sediment–water interface and across redox boundaries within the sediment (Aller, 1994; Rhoads, 1974). This is done mainly by redistributing material during e.g. feeding, burrowing, ventilation, tube construction, and fecal pellet formation (Aller, 1982; Kristensen et al., 2012). It is therefore essential to quantify particle and solute mixing induced from bioturbating fauna and to include faunal reworking activities in qualitative and quantitative models describing biogeochemistry and element cycling in surface sediments. Reworking parameters for particle transport by fauna are normally extracted from experimental quantification of the vertical distribution of tracers and subsequent reaction-transport modeling (Aller, 1982; Berner, 1980; Boudreau, 1997). The most frequently applied model for particle transport relies on the biodiffusive approach in which the conservation of mass and Fick's first law of diffusion are combined into the biodiffusion coefficient, D_b (Boudreau, 1986; Goldberg and Koide, 1962; Guinasso and Schink, 1975). The underlying theoretical assumptions in the biodiffusion model have recently been reevaluated and partly revised (Meysman et al., 2010). Despite that model constraints are often violated (Lecroart et al., 2010; Wheatcroft et al., 1990), tracer distributions obtained from the biodiffusion model are frequently in close accordance with those obtained from direct measurements (Meysman et al., 2003). Models for particle reworking have occasionally been modified to also include biological transport of particles in a non-diffusive manner. Such modifications are referred to as the non-local transport or anomalous reworking (Fisher et al., 1980; Meysman et al., 2010; Smith et al., 1986). Francois et al. (1997, 2002) have developed a suite of

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models that couple to the reworking modes of individual species. Of these, above all the gallery-diffusor model (François et al., 2002) has successfully been applied to evaluate reworking activities by *Hediste diversicolor* (Duport et al., 2006; Mermillod-Blondin et al., 2004). The rapid transport of particles from the sediment surface to deeper sediment layers is estimated by the non-local transport coefficient, r, while the diffusive-like transport in surface sediments is estimated by the biodiffusion coefficient, D_b.

A vast majority of previous experiments designed to assess particle reworking activities by *H. diversicolor* have integrated particle reworking over the experimental period (often 10 to 30 days). In these studies, the vertical distributions of tracers were mainly quantified by manual efforts following sectioning of sediment cores in discrete sediment layers with inherent destructive sampling protocols (Duport et al., 2006; François et al., 2002; Hedman et al., 2011). Therefore, the temporal evolution of reworking parameters (or proxies) is normally excluded and not quantified. Gilbert et al. (2003) developed a technique for 2-dimensional experimental quantification of particle displacement by fauna using side-view imaging of fluorescent particles (luminophores). With the non-destructive side-view imaging of luminophores emerging as a complementary technique to estimate particle reworking, there is also a potential for high-resolution (temporal and spatial) studies of bioturbation activities by benthic macrofauna (Maire et al., 2008; Schiffers et al., 2011). A number of bioturbation experiments have since been conducted using concepts originating from the fluorescence imaging approach (Maire et al., 2006; Piot et al., 2008; Schiffers et al., 2011), including imaging of faunal activities in situ (Solan et al., 2004). However, the thin aquaria used for imaging experiments may bias quantification of reworking proxies. Potential artifacts associated with experimental settings include e.g. alterations in reworking behavior due to wall effects and the physical geometry of the microcosm. To our knowledge, there is no previous study that quantifies and compares reworking proxies in cores and aquaria.

The common ragworm *H. diversicolor* (Polychaeta, Nereididae), normally classified as a gallery-diffusor in terms of mode of particle reworking (François et al., 2002), is a frequently used model species for experimental studies of bioturbation by benthic macrofauna. The polychaete is commonly found in marine and brackish waters of the littoral zone across the Atlantic coasts of North America and Europe (Scaps, 2002). *H. diversicolor* has during several studies been demonstrated as a major bioturbator with significant influence on the biogeochemical structure, function, and dynamics of surface sediments. For example, bioturbating activities by *H. diversicolor* may have considerable, but often not easily predicted, effects on organic matter cycling and nutrient fluxes in shallow-water sediments (Kristensen et al., 1992; Nizzoli et al., 2007; Papaspyrou et al., 2010). In addition, activities by *H. diversicolor* may have significant effects on phytoplankton production (Vedel et al., 1994), as well as on the initiation, growth and sustenance of macroalgal mats and seagrass beds in shallow-water embayments (Hughes et al., 2000; Nordström et al., 2006).

There are several environmental factors that affect the behavior of *H. diversicolor* and thereby also the magnitude and extent of bioturbation. Availability of food supply (Nogaro et al., 2008; Papaspyrou et al., 2010), tidal cycles (Esselink and Zwarts, 1989) and availability of light (Lambert et al., 1992; Tang and Kristensen, 2007; Wenzhöfer and Glud, 2004) provide examples that have been included in studies focused on the behavior of *H. diversicolor*. Investigations that specifically describe how the availability of light affects bioturbation and sediment reworking by *H. diversicolor* have up to now concentrated on the short-term (24–36 h) behavior during feeding (Lambert et al., 1992), the oxygen uptake (Wenzhöfer and Glud, 2004) and the benthic metabolism (Tang and Kristensen, 2007).

The overall aim of the study was to quantify particle displacement by *H. diversicolor* using the non-destructive fluorescence imaging approach and the destructive manual sectioning technique. Imaging was primarily used for high resolution quantification of reworking proxies in both time and space. Specific objectives were to investigate how experimental proxies for particle reworking were affected by 1) the exposure of *H. diversicolor* to constant darkness as compared to 12 h light/dark cycles, and 2) sediment–water incubations in thin glass aquaria as compared to incubations in Plexiglass cores.

2. Materials and methods

2.1. Experimental design and general overview

In this tracer-pulse experiment, the effects of i) light/dark cycles compared with constant darkness (statistical factor "Light") and ii) Plexiglass cores compared with glass aquaria (statistical factor "Microcosm") on particle reworking activities by *H. diversicolor* were investigated in a factorial design. Individuals of *H. diversicolor* were added to microcosms (Plexiglass cores (C) or thin glass aquaria (A)) and were either exposed to 12 h light/dark cycles (Li/Da), or to constant darkness (Dark) ($n = 6$). There were also corresponding control treatments without fauna added ($n = 6$).

Particle displacement was evaluated from vertical profiles obtained by sectioning of sediment and modeling (François et al., 2002) ($n = 6$) and from time-resolved imaging of the fluorescent particles in thin aquaria (Gilbert et al., 2003) (I; $n = 3$). In addition to D_b, r and maximum penetration depth of luminophores (MPD) (Maire et al., 2006), the fluorescence imaging approach provided bioturbation proxies associated with 2-D redistribution, and transport rates.

2.2. Sampling and set-up

Surface sediment (0–5 cm) and *H. diversicolor* were sampled by hand from a shallow bay on the Swedish west coast (Rågårdsvik, N 58°12′32″; E 11°26′47″) in May 2007 (Table 1). The sampling area is microtidal with an average tidal amplitude of ~20 cm and a salinity between 20 and 25 (Pihl and Rosenberg, 1982). The sampling area has been described as silty and semi-enclosed with high organic matter content and high porosity in the surface sediment. The benthic macrofaunal community is dominated by detrivores (Engelsen et al., 2008).

Porosity was measured at the sampling occasion by weight loss after drying the sediment at 70 °C until constant weight. Solid phase organic carbon (TOC) and organic nitrogen (TON) were determined by an elemental analyzer NA 1500 NC, Fison instruments. Grain size was determined by sieving and re-weighing a known amount of dry sediment through a stack of sieves with progressively decreasing mesh size. The analysis on dry sediment may have underestimated the silt and clay fraction due to particle aggregation during the drying process.

Sediment and fauna were transported to temperature-controlled (15 °C) facilities at the Lovén Centre Kristineberg. The sediment was dry-sieved (1 mm) to remove macrofauna and larger debris, homogenized, and placed in large (75 × 55 × 45 cm) plastic containers. Animals were placed in sediment from the sampling location. Sediment and animal aquaria were continuously supplied with unfiltered seawater from the Gullmarsfjord ($S = 31$, $T = 15$ °C) for a period of 11 days to stabilize biogeochemical characteristics and chemical

Table 1
Overview of experimental activities.

Day	*Activity*
−23/24	Sampling of animals and sediment
−14	Plexiglass cores inserted into the sediment and thin aquaria filled with sediment
−7	Additions of *Hediste diversicolor* to the experimental microcosms
0–1	Additions of luminophores and start of sediment–water incubations
1–11	Capture of images
10–11	Termination of incubation