



Sediment reworking by the burrowing polychaete *Hediste diversicolor* modulated by environmental and biological factors across the temperate North Atlantic. A tribute to Gaston Desrosiers

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ABSTRACT

Particle mixing and irrigation of the seabed by benthic fauna (bioturbation) have major impacts on ecosystem functions such as remineralization of organic matter and sediment-water exchange. As a tribute to Prof. Gaston Desrosiers by the Nereis Park association, eighteen laboratories carried out a collaborative experiment to acquire a global snapshot of particle reworking by the polychaete *Hediste diversicolor* at 16 sites surrounding the Northern Atlantic. Organisms and soft sediments were collected during May – July at different geographical locations and, using a common laboratory protocol, particulate fluorescent tracers ('luminophores') were used to quantify particle transport over a 10-day period. Particle mixing was quantified using the maximum penetration depth of tracers (MPD), particle diffusive coefficients (D_b), and non-local transport coefficients (r). Non-local coefficients (reflecting centimeter scale transport steps) ranged from 0.4 to 15 yr⁻¹, and were not correlated across sites with any measured biological (biomass, biovolume) or environmental parameters (temperature, grain size, organic matter). Maximum penetration depths (MPD) averaged ~10.7 cm (6.5–14.5 cm), and were similar to the global

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average bioturbation depth inferred from short-lived radiochemical tracers. MPD was also not correlated with measures of size (individual biomass), but increased with grain size and decreased with temperature. Bio-diffusion (D_b) correlated inversely with individual biomass (size) and directly with temperature over the environmental range ($Q_{10} \sim 1.7$; 5–21 °C). The transport data were comparable in magnitude to rates reported for localized *H. diversicolor* populations of similar size, and confirmed some but not all correlations between sediment reworking and biological and environmental variables found in previous studies. The results imply that measures of particle reworking activities of a species from a single location can be generally extrapolated to different populations at similar conditions.

1. Introduction

Macrofaunal bioturbation is recognized as a major biological process controlling sediment ecosystem functions such as biogeochemical cycling and benthic material fluxes (Rhoads, 1974; Kristensen et al., 2012). Nereid polychaetes and specifically *Hediste diversicolor*, O.F. Müller, 1776 (formerly *Nereis diversicolor*) are among the species for which bioturbation activities are best documented (e.g., Davey and Watson, 1995; Kristensen, 1983a, 1983b; Riisgård et al., 1992; Kristensen and Hansen, 1999; Dupont et al., 2006; Godbold et al., 2011; Hedman et al., 2011; Lindqvist et al., 2013). Sediment reworking by *H. diversicolor* is linked to the construction and maintenance of burrow networks (Gerino and Stora, 1991; Davey, 1994; Hale et al., 2014; Hale et al., 2015) and also to its deposit-feeding activity on near-surface particles (Esnault et al., 1990). These activities generate both bio-diffusive and non-local particle transport that have been previously modelled as hybrid “gallery-bio-diffusion” (François et al., 2002). *H. diversicolor* also actively ventilates its burrow in an intermittent pattern with undulatory movements of its body to provide electron acceptors and remove metabolites (Riisgård and Larsen, 2005) and, when algal concentration is sufficient in the overlying water, to suspension-feed (Vedel and Riisgård, 1993).

It has been shown that *H. diversicolor* is able to modify the conditions of the sediment environment and influence the behavior of other species or communities (e.g., Witte and De Wilde, 1979; Reise, 1981; Ólafsson and Persson, 1986; Jensen and André, 1993; Emmerson, 2000; Gillet and Torresani, 2003; Paramor and Hughes, 2004; Wenzhöfer and Glud, 2004; Paspasyrou et al., 2006; Cuny et al., 2007; Pischedda et al., 2011; Engelsen et al., 2010; Godbold et al., 2011; Stauffert et al., 2013; Taylor and Cunliffe, 2015). Sediment reworking and ventilation by *H. diversicolor* may also partly control the fate of organic matter or pollutants (e.g.; Gilbert et al., 1994; Gilbert et al., 1997; Christensen et al., 2002; Banta and Andersen, 2003; Kristensen and Mikkelsen, 2003; Fernandes et al., 2006a; Burlinson and Lawrence, 2007; Tang and Kristensen, 2007; Cardoso et al., 2008; Bonnard et al., 2009; Mayor et al., 2009; Stomperudhaugen et al., 2009; Mouneyrac et al., 2010; Buffet et al., 2011; Buffet et al., 2013; Sun et al., 2018), sedimentary biogeochemical cycling (e.g.; Clavero et al., 1994; Gilbert et al., 1995; Banta et al., 1999; Ferro et al., 2003; Kristensen et al., 2011; Pischedda et al., 2012; Martinez-Garcia et al., 2015; Valdemarsen et al., 2018), and physical properties of the seabed (e.g.; Fernandes et al., 2006b; Fernandes et al., 2009; Widdows et al., 2009). However, the magnitude of influence, like that of many species, can depend on environmental history and context (e.g. Godbold and Solan, 2013; Murray et al., 2017; Wohlgemuth et al., 2016; Wohlgemuth et al., 2017).

H. diversicolor is broadly distributed in a ‘Northern Atlantic wide zone’, i.e. from North America to the Baltic Sea (Smith, 1977 in Röhner et al., 1997), and from the Gulf of St Lawrence south to Puerto Rico (Brunel et al., 1998). As a tribute to Prof. Gaston Desrosiers, our colleague from Institut des Sciences de la Mer (ISMER), Université du Québec à Rimouski (Québec, Canada), an internationally recognized expert in benthic ecology who passed away in 2006, the aim of this work was to acquire a regional scale perspective of sediment reworking activity of *H. diversicolor*. This work also sought to examine variation with respect to site specific biological or commonly measured environmental

parameters, although we acknowledge that causation cannot be directly and unambiguously inferred as they are confounded by location. Here we report on the findings of a set of experiments conducted at eighteen sites by research groups named here according to their respective sampling site from Europe, North America and Oceania (Nereis Park association, <http://www.nereispark.org>; Table 1).

2. Materials and methods

2.1. Sampling and experimental procedure

Sediments and polychaetes from the subfamily Nereididae were sampled in eighteen locations from May to July 2007 (Table 1 and Fig. 1). Based on a common experimental protocol, surface sediments (0–5 cm depth) were collected and sieved through a 1-mm mesh to remove macrofauna and debris, and then homogenized. *H. diversicolor*

Table 1

Code, name (code signification underlined) and location of sampling site, for the eighteen research groups involved in the Nereis Park joint-experiment carried out in Northern hemisphere Spring 2007. (*) For AS, sediments were sampled at the Venice Lagoon while polychaetes were provided (lab-reared) by the University of Modena (Italy).

Site code	Sampling site	Sampling coordinates
WNS	Ythan estuary, <u>West North Sea</u> , Newburgh, Scotland, UK	57°20'05"N 2°00'12"W
ENS	Koenigshafen, <u>East North Sea</u> , Sylt, Germany	55°02'07"N 8°24'27"E
SKA	Rågårdsvik Bay, <u>Skagerrak</u> , Sweden	58°12'32"N 11°26'47"E
AS	Venice Lagoon, <u>Adriatic Sea</u> , Italy (*)	45°24'28"N 12°18'55"E
SLR	Anse à l'original, Bic, <u>Saint Lawrence River</u> , Rimouski, Québec, Canada	48°21'53"N 68°46'16"W
CS	Plage des Moulins Blancs, <u>Celtic Sea</u> , Brest, France	48°23'47"N 4°25'53"W
LIS	Flax Pond, <u>Long Island Sound</u> , Brookhaven, NY, USA	40°57'41"N 73°08'25"W
BP	Pepe Inlet, <u>Bay of Plenty</u> , Tairua, Coromandel Peninsula, NZ	37°00'12"S 175°50'51"E
TAM	St John's Ford, <u>Tamar</u> , Cornwall, UK	50°21'50"N 4°14'08"W
SBS	Schnatermann/Breitling, <u>South Baltic Sea</u> , Germany	54°10'22"N 12°08'30"E
RF	Herslev, <u>Roskilde Fjord</u> , Denmark	55°40'42"N 11°59'07"E
LG	<u>Lochgilphead</u> , Scotland, UK	56°02'08"N 5°26'13"W
OF	Kærby Fed, <u>Odense Fjord</u> , Denmark	55°27'03"N 10°29'38"E
NBS	Mörkö, Stockholm Archipelago, <u>North Baltic Sea</u> , Sweden	59°02'34"N 17°41'33"E
AB	Pointe de L'Aiguillon, <u>Arcachon Bay</u> , France	44°40'00"N 1°07'30"W
LRE	<u>Loire River estuary</u> , France	47°15'50"N 2°10'09"W
ØRE	<u>Øresund</u> , Denmark	56°02'33"N 12°36'42"E
MED	Saint-Antoine Canal, Gulf of Fos, <u>Mediterranean Sea</u> , France	43°22'31"N 4°50'17"E

was used in the experiment by sixteen research groups (Table 2). All groups obtained adult worms from their respective sampling sites, except for the reared individuals used by AS (Venice Lagoon, Italy). SLR (Québec, Canada) used individuals of *Alitta virens*, while BP (Pepe Inlet, Tairua, New Zealand) used individuals of *Perinereis vallata*. Individuals representative in size of local populations were weighed (Table 2) and maintained in homogenized, local sediments with continually aerated water, a 12:12 h dark:light cycle and at ambient temperature (Table 2).

Four PVC or Plexiglas core tubes (height: 20 cm; internal diameter: 8–10 cm) were filled with homogenized sediments (15 cm deep sediment column) and incubated in seawater for 7 days at ambient conditions (Table 2). At each location, treatments included the addition of four worms (509–796 ind. m⁻²) to each of three replicate cores, and a control without macrofauna. Worms were allowed to establish burrows for seven days before the addition of particle tracers (2 g core⁻¹, fluorescently dyed sediment particles, ‘luminophores’; 63–125 µm; Partrac Ltd., Glasgow, UK) that were suspended in seawater and distributed evenly across the sediment-water interface to achieve a visible layer of ≤1 mm thick. After 10 days, the overlying seawater was removed and the experimental cores were sectioned into 0.5-cm thick layers from the surface down to 2 cm depth, and 1-cm thick layers down to 15 cm. The sediment from each layer was freeze-dried, homogenized and luminophores were enumerated from images (Olympus C-2500 L digital camera, 1712 × 1368 pixel resolution) taken under UV-light (wavelength peak, 365 nm) using standard image analysis routines (Image-Pro Plus). Organic matter (OM) content (LOI; 400 °C overnight; Schumacher, 2002) and sediment grain size (Malvern Mastersizer 2000) were quantified from a subsample of each sieved and homogenized sediment.

2.2. Quantification of sediment reworking

Based on vertical tracer distribution depth profiles, we used the

gallery-diffusor model developed for gallery-constructing organisms such as *H. diversicolor* (François et al., 2002; Dupont et al., 2006) to quantify the intensity of sediment reworking over the 10-day experimental period. This model allows a description of both the diffusion-like mixing (bioidiffusion) of particles in the uppermost region of intense burrowing activity and non-local transport occurring across the full extent of the sediment profile (full description of the model in Gilbert et al., 2007). The bioidiffusion coefficient, D_b , and the non-local coefficient, r , were obtained for each experimental luminophore profile, and the goodness of fit between the observed distribution of luminophores and the modelled profile was achieved using the least square method (Fig. 2). In addition, the maximum penetration depth of luminophores (MPD) was used as a proxy to estimate sediment reworking depth (Lindqvist et al., 2013).

2.3. Data

As *H. diversicolor* were predominant in our study (16 of 18 sites), we present the complete dataset that includes other species, but we restrict the comparative discussion to *H. diversicolor*.

2.4. Scoring approach

We standardized the two mixing coefficients (D_b and r) using the “0–1 scaling” procedure (Sneath and Sokal, 1973; Maire et al., 2013) to generate comparable sediment reworking scores allowing ranking but not absolute comparison of the results obtained by each laboratory. Hence, each coefficient was transformed using Eq. (1):

$$X_{stand} = \frac{X - X_{min}}{X_{max} - X_{min}} \quad (1)$$

where X_{stand} is the coefficient X (X : D_b or r ; mean value for each

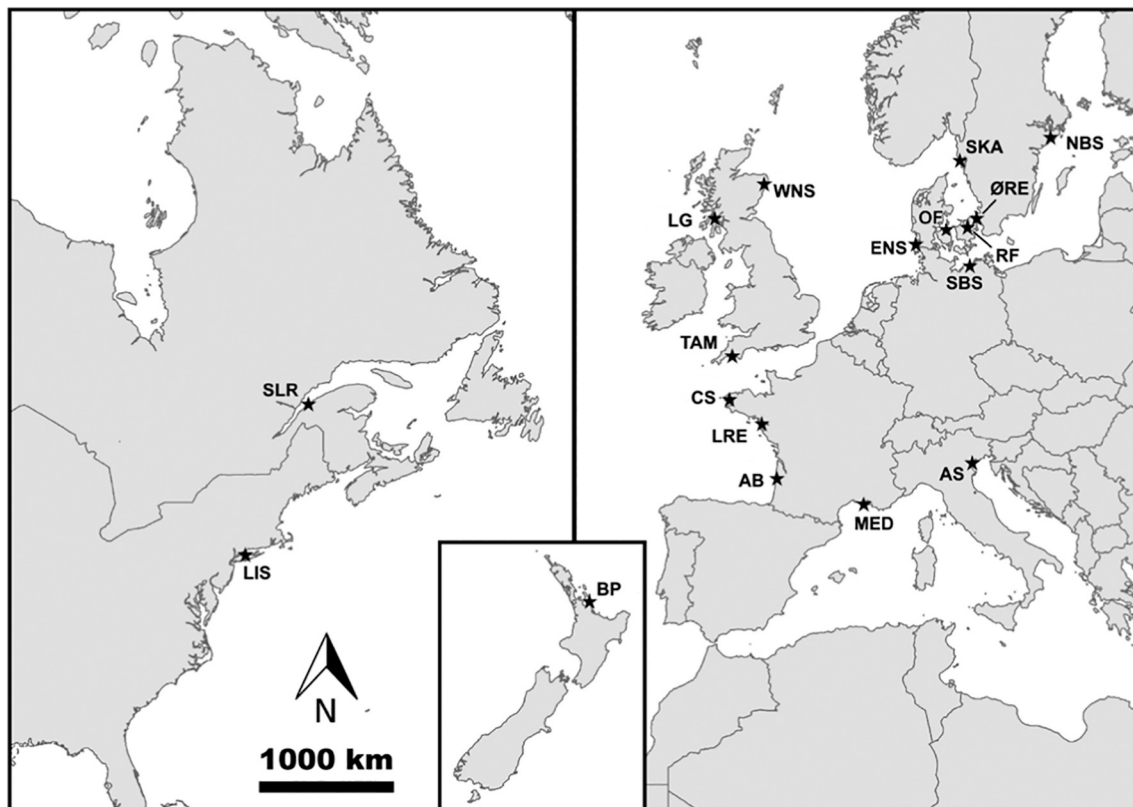


Fig. 1. Location of sampling sites, for the eighteen research groups involved in the Nereis Park joint-experiment carried out in the Northern hemisphere spring 2007. Site codes are indicated. For site coordinates, see Table 1.

Table 2

Polychaete species, experimental biological and environmental parameters for the eighteen research groups involved in this study. Wet biomass and biovolume data are mean ± SD for triplicate cores, excepted for TAM and AB (n = 4) and SKA (n = 6). *A. virens*: *Alitta virens*, *H. diversicolor*: *Hediste diversicolor*, *P. vallata*: *Perinereis vallata*. For the location of each site, refer to Fig. 1 and Table 1.

Site code	Species	Density	Wet biomass	Wet biovolume	Temp.	Grain-size (µm)	OM
		(ind. m ⁻²)	(g; per core)	(cm ³ ; per core)	(°C)	(median/mode)	(%)
WNS	<i>H. diversicolor</i>	509	0.87 ± 0.05	1.05 ± 0.10	13	46/58	6.00
ENS	<i>H. diversicolor</i>	629	1.62 ± 0.22	1.09 ± 0.07	18	357/340	0.38
SKA	<i>H. diversicolor</i>	530	0.50 ± 0.03	1.18 ± 0.20	15	61/122	1.77
AS	<i>H. diversicolor</i>	576	0.80 ± 0.03	3.17 ± 0.25	20	26/70	0.55
SLR	<i>A. virens</i>	509	13.5 ± 0.59	89.71 ± 3.46	5	296/282	1.95
CS	<i>H. diversicolor</i>	615	3.15 ± 0.12	2.68 ± 0.22	14	391/494	2.45
LIS	<i>H. diversicolor</i>	564	1.80 ± 0.00	3.30 ± 0.00	15	32/76	3.79
BP	<i>P. vallata</i>	509	1.89 ± 0.01	2.77 ± 0.06	20	154/161	2.47
TAM	<i>H. diversicolor</i>	509	3.07 ± 0.06	7.07 ± 0.77	13	32/63	10.24
SBS	<i>H. diversicolor</i>	509	1.75 ± 0.03	2.60 ± 0.28	14	140/161	0.28
RF	<i>H. diversicolor</i>	509	1.37 ± 0.19	2.53 ± 0.34	16	246/310	0.85
LG	<i>H. diversicolor</i>	509	1.49 ± 0.08	2.31 ± 0.20	12	101/134	3.34
OF	<i>H. diversicolor</i>	796	1.14 ± 0.09	3.78 ± 0.46	16	246/234	0.95
NBS	<i>H. diversicolor</i>	796	2.40 ± 0.07	3.39 ± 0.05	10	224/257	0.10
AB	<i>H. diversicolor</i>	576	1.65 ± 0.19	2.90 ± 0.52	13	63/70	2.25
LRE	<i>H. diversicolor</i>	509	1.49 ± 0.17	2.76 ± 0.63	17	35/134	5.91
ØRE	<i>H. diversicolor</i>	553	0.85 ± 0.05	3.56 ± 0.24	15	325/340	0.58
MED	<i>H. diversicolor</i>	615	2.07 ± 0.03	4.64 ± 0.07	21	35/111	3.19

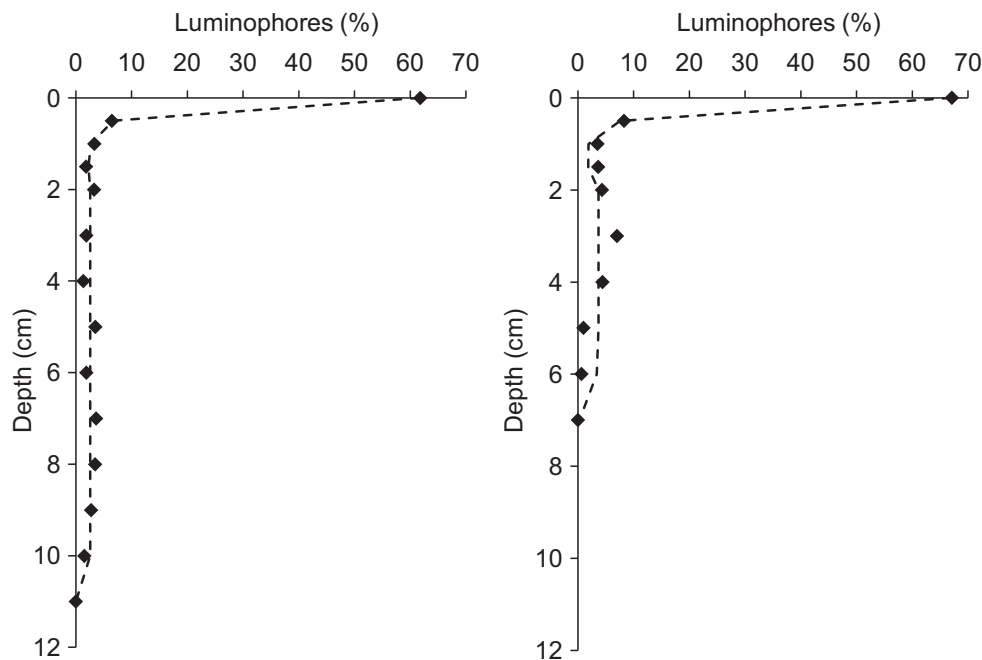


Fig. 2. Two examples of experimental luminophore profiles (diamonds) and corresponding modelled profiles (dotted lines) obtained with the gallery-diffuser model (François et al., 2002; Dupont et al., 2006). They either produced a relatively good (6.3% error; PLM_2; left) or poor (14.8% error; RUC_3; right) fit between experimental and modelled data. For the location of each site, refer to Fig. 1 and Table 1.

laboratory) after standardization, and X_{min} and X_{max} are the minimum and maximum mean values of the coefficient X within the whole set of experiments, respectively. The value of each standardized coefficient consequently ranged from 0 (lowest mixing) to 1 (highest mixing). Then, the two standardized coefficients ($D_{b-stand}$ and r_{stand}) were summed to produce a unique sediment reworking score combining both elements of reworking for each experiment Eq. (2). This dimensionless sediment reworking score ranged from 0 to 2.

$$Sediment\ reworking\ score = D_{b-stand} + r_{stand} \tag{2}$$

2.5. Statistical analyses

As the observations in our study are confounded by location specific

differences in environmental conditions, it is inappropriate to perform standard factorial regression analysis. Whilst we recognize that care must be taken in inferring causality from correlations, we correlated mixing coefficients (D_b and r), MPD and our experimental parameters (biomass, biovolume, temperature, grain size distribution, organic matter content) using non-parametric correlation analyses (Spearman correlation).

3. Results

In the sixteen experiments with *H. diversicolor*, the abundances in core microcosms were restricted to 509–629 m⁻², with total biomasses varying across the different sampling sites between 0.5 and 3.15 g wet

weight (Table 2). Thus, sizes of *H. diversicolor* measured as biomass (wet weight) per individual ranged between 0.13 and 0.79 g wet wt ind⁻¹, averaging 0.41 ± 0.19 (median 0.39 g). Median grain size and organic matter contents at the multiple locations were 26–391 µm and 0.1–10.2 wt% respectively, with mean 2.6 ± 2.6 wt% (median 2.1 wt%). Most of the variation in organic matter content characterized sediment sites with a median grain size <50 µm (0.5–10.1% wt). For median grain sizes above 50 µm, organic matter otherwise averaged 1.4 ± 1.1 wt% (median 1.4 wt%). There were no discernable relationships (correlations) across the sampling locations between the biomass of individuals (~size) and either average/median grain size or organic matter content of sediments.

The sixteen experiments with *H. diversicolor* revealed that the maximum penetration depth (MPD) of luminophores ranged from 6.5 ±

1.0 (AS, Italy) and 6.5 ± 2.2 (RF, Denmark) to 14.5 ± 0.0 cm (ENS, Germany) (Fig. 3A). Overall, biodiffusion (D_b) and non-local (r) mixing coefficients ranged from 0.2 to 1.89 cm² y⁻¹ and from 0.4 to 15.0 y⁻¹, respectively. Both the mean D_b and r coefficients differed among locations. Mean coefficients varied from the lowest: $D_b = 0.8 ± 0.1$ cm² y⁻¹, $r = 2.4 ± 0.4$ y⁻¹, LG, Scotland; to the highest: $D_b = 1.7 ± 0.1$ cm² y⁻¹, AS, Italy, and $r = 11.0 ± 3.3$ y⁻¹, WNS, Scotland (Fig. 3B and C).

Sediment reworking scores that integrated biodiffusion (D_b) and non-local (r) particle transport allowed ranking of the sediment reworking intensity by *H. diversicolor* populations between the different locations (Fig. 4). Scores ranged from 0 for LG, Scotland (i.e., the lowest values of both D_b and r for the whole study) to 1.42 for AB (France) (Fig. 4). Correlations between sediment mixing proxies (MPD, D_b and r) and the registered experimental, biological and environmental parameters (Table 2) indicated that MPD is positively correlated with an increase in median grain size (Spearman correlation test; $\rho = 0.56$; $p = 0.00017$) and inversely with temperature ($\rho = -0.33$; $p = 0.018$). D_b is positively correlated with temperature ($\rho = 0.37$; $p = 0.008$) but negatively correlated with an increase in biomass (size) ($\rho = -0.29$; $p = 0.042$) (Fig. 5). We found no significant correlation between MPD or D_b and density or OM content ($\rho > 0.2$; $p > 0.05$). r was not significantly correlated with any measured environmental parameters ($\rho > 0.2$; $p > 0.05$).

4. Discussion

The abundances of *H. diversicolor* utilized in experiments were fixed at 4 individuals per core, equivalent to 509–620 ind. m⁻². In contrast, total biomass and biovolume differed substantially across locations; averaging 0.41 ± 0.39 g wet weight ind⁻¹ and 0.75 ± 0.37 mL ind⁻¹ respectively (Table 2). Assuming a conversion factor for *H. diversicolor* ash free dry weight to wet weight of ~0.15 (AFDW/WW) (Rumohr et al., 1987; Ricciardi and Bourget, 1998), and an average allometric relationship between individual length, L, and AFDW of AFDW = 0.32 L^{2.3} as measured over 3 years in Dutch Wadden Sea tidal flats by Esselink and Zwarts (1989), the characteristic lengths of *H. diversicolor* in experiments averaged ~10 cm and ranged roughly from 6 to 14 cm. Widths of individuals, and thus burrow diameters, are also directly related to the length of *H. diversicolor* according to $L = 1.67(\text{width})^{1.47}$ (Esselink and Zwarts, 1989; White, 2005). Based on previous studies with *H. diversicolor* and other infauna, these size scales (biomass, length, width), along with species specific behavior and local environmental conditions, are expected to be closely related to the biogenic transport

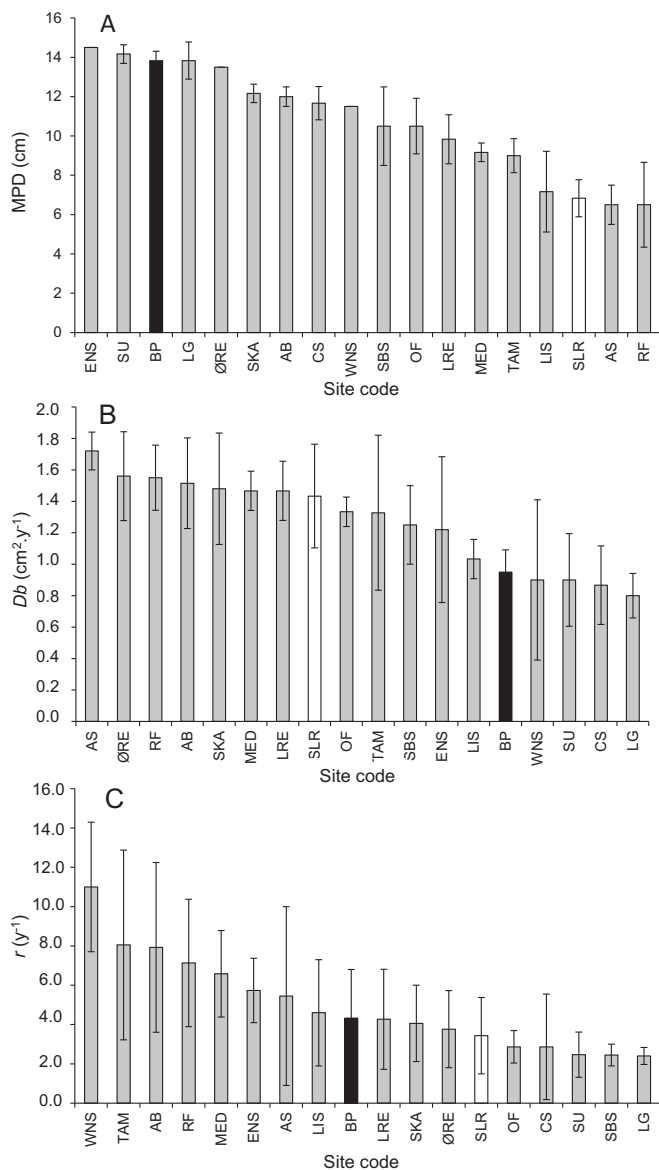


Fig. 3. Luminophore maximal depth (A, Maximum penetration depth = MPD), Biodiffusion-like coefficient D_b (B) and non-local coefficient r (C) obtained for the eighteen laboratory experiments involved in the Nereis Park joint-experiment carried out in the Northern hemisphere spring 2007. Values are mean ± SD for triplicate cores, except for PLM and UB ($n = 4$) and GOT ($n = 6$). The species studied was *Hediste diversicolor* except for ISMER (*Alitta virens*; white column) and NIWA (*Perinereis vallata*; black column). Sites are sorted in descending value order. For the location of each site, refer to Fig. 1 and Table 1.

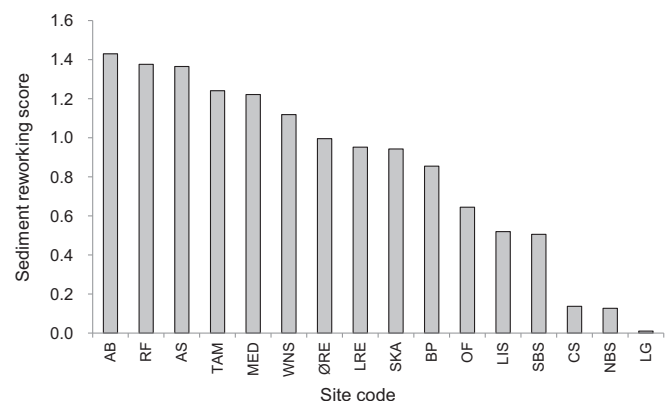


Fig. 4. Sediment reworking score integrating the values of both the biodiffusion-like coefficient D_b and non-local coefficient r obtained for the sixteen *Hediste diversicolor* laboratory experiments involved in the Nereis Park joint-experiment carried out in the Northern hemisphere spring 2007. Sites are sorted in descending value order. For the location of each site, refer to Fig. 1 and Table 1.

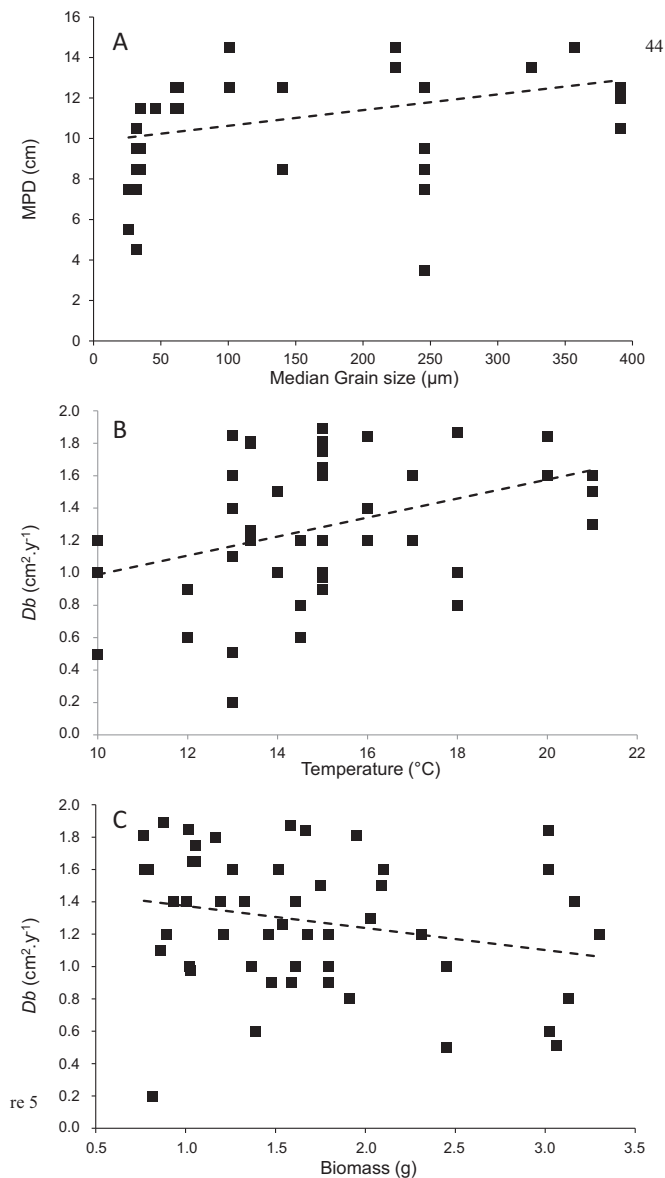


Fig. 5. Luminophore maximal depth MPD vs Grain size (Median) (A), Biodiffusion-like coefficient D_b vs Temperature (B) or Biomass (C) for the sixteen *Hediste diversicolor* laboratory experiments involved in the Nereis Park joint-experiment carried out in the Northern hemisphere spring 2007.

activities represented by D_b , r , and MPD (e.g., Cammen, 1980; Kudenov, 1982; Esselink and Zwarts, 1989; Duport et al., 2006; Wohlgemuth et al., 2017).

4.1. Depth scaling of particle reworking: MPD

Due to the defined network of burrow galleries constructed by *H. diversicolor* (Gerino and Stora, 1991; Davey, 1994; Hale et al., 2014; Hale et al., 2015), the maximum penetration depth of luminophores (MPD) may be considered a surrogate for maximum burrow and mixing depths. Our estimated mean *H. diversicolor* burrow depth of 10.7 ± 2.6 cm (mean \pm SD) based on average MPD is similar to but slightly shallower than previously reported typical depth ranges (1–29 cm; mean \sim 12 cm for a size class of $L = 10$ cm; Esselink and Zwarts, 1989). It is also similar to the \sim 10 cm global average mixing depth estimated from short-lived radiochemical tracer distributions (e.g., ^{234}Th , ^{210}Pb) in bioturbated deposits (Boudreau, 1998; Teal et al., 2008).

Although burrowing depth can directly reflect size of individuals up

to an asymptotic depth range, no obvious correlation between estimates of size (biomass ind^{-1}) and MPD is evident in the pooled data of the present study. Avoiding predation is one factor determining burrowing depth, and a depth of \sim 10 cm provides at least a partial refuge from a range of fish, crabs, and birds. However, some birds such as curlews and bar-tailed godwit can probe at least to \sim 16 cm, consistent with burrowing depth being an optimized balance of multiple factors such as food acquisition, environmental conditions, and predation rather than any single factor (Esselink and Zwarts, 1989).

With respect to environmental conditions, burrowing depths of *H. diversicolor* are known to be closely associated with and to vary inversely with temperature in European coastal waters. Burrowing depths are usually $<$ 40 cm, but can extend to 50–60 cm during cold winters (e.g. Muus, 1967; Beukema, 1979), perhaps as a way for the worms to escape from freezing surface temperatures. An overall inverse correlation between MPD of luminophores and sampling site temperature is also evident in our grouped, between site data (Fig. 6). The slope of the regression for these data, \sim 0.4 cm/ $^{\circ}\text{C}$, is quite similar to the \sim 0.6 cm/ $^{\circ}\text{C}$ dependence reported for *H. diversicolor* populations of the Dutch Wadden Sea (Esselink and Zwarts, 1989).

H. diversicolor burrowing depths can also respond to sediment granulometry, at least for localized populations, with deeper burrows found in sandy than muddy deposits (Esselink and Zwarts, 1989). The positive, albeit weak, correlation between MPD and grain size in our pooled data (Fig. 5A) reflects variation in burrow depth, indicating that burrow construction can depend more generally (globally) on sediment mass properties. However, there is some evidence that fine and medium sands are more conducive for deep burrowing by polychaetes, including *H. diversicolor*, than smaller grain sizes (Davey, 1994; François et al., 2002; Rees et al., 2005; Hale et al., 2015). Regardless of the underlying factors, the variation in reworking depth among locations confirms the ability of this species to occupy a wide range of sediment types (Alexander et al., 1993).

4.2. Transport rate measures: biodiffusion and nonlocal exchange

The analysis of particle transport by *H. diversicolor* was based on biodiffusion and non-local mixing processes as described by the gallery-diffusor model (François et al., 2002; Duport et al., 2006). The magnitudes obtained for both model reworking modes were within the range typically found for *H. diversicolor* populations at single locations at similar densities (François et al., 2002; Duport et al., 2006; Fernandes et al., 2006a); however, higher biodiffusive mixing values have occasionally been observed (i.e., $4\text{--}5 \text{ cm}^2 \text{ y}^{-1}$; François et al., 2002; Mermillod-Blondin et al., 2004; Solan et al., 2008). Surprisingly, Nogaro et al. (2008) did not observe any diffusion-like activity, rather only non-local transport, in their experiment with *H. diversicolor* at low densities

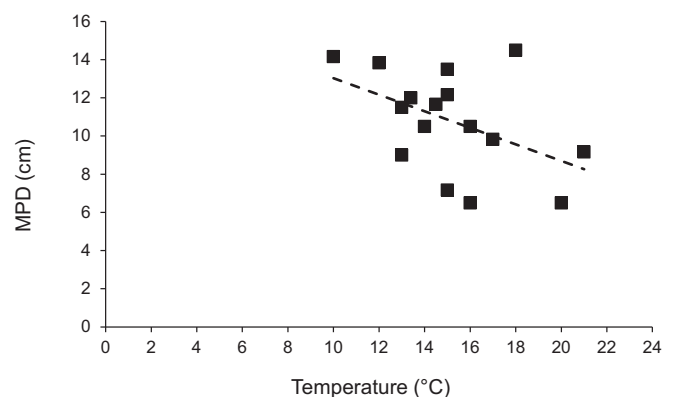


Fig. 6. Luminophore maximal depth MPD vs Temperature. Average values for the sixteen *Hediste diversicolor* laboratory experiments involved in the Nereis Park joint-experiment carried out in the Northern hemisphere spring 2007.

(i.e., down to 260 ind. m^{-2}). Part of these differences may reflect variations in dominant feeding mode as a function of experimental conditions (e.g., abundance; water column suspended matter, Biles et al., 2003).

A general positive correlation between D_b and r was, however, observed in the present study (Fig. 7), suggesting that these measures are not entirely independent for *H. diversicolor* and, perhaps, other gallery-diffusers. One explanation for coherence of the two measures is functional and based on burrow architecture, whilst another is computational and reflects fitting an imperfect transport model to tracer profiles. During our experiment (10 days), *H. diversicolor* was able to build complex galleries with U- or Y-shaped burrows (see Davey, 1994; Hale et al., 2015) which increased tracer mixing in the surface zone (D_b), including cementation of tracer into multiple, bifurcating burrow walls, but also promoted the passive infilling of underlying burrow sections and transfer of particles to depth (r). Computationally, the rapid loss of particles from the surface region where the tracer is initially emplaced, decreases the measured tracer concentration gradient near the sediment-water interface and may enhance the calculated D_b . The simultaneous transfer of particles to distal burrow locations at depth requires increased r . The exact relationship between these two measures is likely not strict and requires additional investigation. There is sufficient variability in the relationship between D_b and r that correlations of each with other variables can differ. The sediment reworking score (2) incorporates both transport modes in a relative estimate of overall activity.

The positive correlation between D_b and temperature (Fig. 5B) agrees well with the previous results for various reworking species as assessed by different field, experimental (e.g., Bender and Davis, 1984; White et al., 1987; Hollertz and Duchêne, 2001; Maire et al., 2007; Valdemarsen et al., 2011; Bernard, 2013), and modelling approaches (Shull, 2001), although the temperature range within our study did not incorporate possible seasonal extremes (Ouellette et al., 2004). Indeed, the impact of temperature on sediment mixing may depend on the range of temperature investigated if temperatures deviate from optimal physiological conditions for a species. For example, Przeslawski et al. (2009) demonstrated a positive temperature effect on *Capitella* sp.1 burrowing between 13°C and 21°C , but above this range no further increase was observed, presumably due to physiological stress. Similarly, Ouellette et al. (2004) observed for the polychaete *Alitta virens* that the biodiffusion coefficient increased with temperature up to $\sim 13^\circ\text{C}$, after which the values declined with increasing temperature. The reduction in biodiffusive mixing by *A. virens* at higher temperature was attributed to a reduced food searching and surface particle collection activity and

enhanced ventilation activity demanded by respiratory requirements. The intensity of food searching by *H. diversicolor* is known to be temperature dependent, for example, in coastal Brittany, its searching activity ceased below 8°C , increased relatively rapidly between 13 and 18°C , and continued to increase at a slower rate at least up to 23°C (Lambert et al., 1992). Such seasonal variation in species responses were explicitly factored out of the present study as our objective was to determine the variation between populations spatially, rather than within populations at single locations (Wohlgemuth et al., 2017). The mean temperature of locations in the present study of *H. diversicolor* was 15°C (median 15°C), with a range of 10 – 21°C , and thus within the mid-to upper range experienced across the seasonal cycle at each sampling site. The regression slopes between D_b and T or $\ln(D_b)$ and $1/T$ are consistent with a temperature dependence model Q_{10} of ~ 1.7 or an Arrhenius apparent activation energy of $\sim 39 \text{ kJ mol}^{-1}$ (Fig. 8). The variation of D_b with temperature observed across environments is therefore quite similar to that observed for multiple activities with populations in manipulative experiments or in situ seasonally at single sites (e.g., 29 kJ mol^{-1} respiration dependence: (Kristensen et al., 1992); $Q_{10} \sim 1.8$ filtration dependence; Vedel et al., 1994).

We found a negative correlation between D_b and *H. diversicolor* biomass, which in the present study is equivalent to the size of individuals (Fig. 5C). Inverse dependence of reworking activity with size of individuals (biomass ind^{-1}) has been found in single populations of *H. diversicolor* (as D_b ; Duport et al., 2006), as ingestion rates in other species of polychaetes (e.g. Kudenov, 1982), and sediment ingestion rates by deposit feeders generally (e.g., Cammen, 1980). The exact

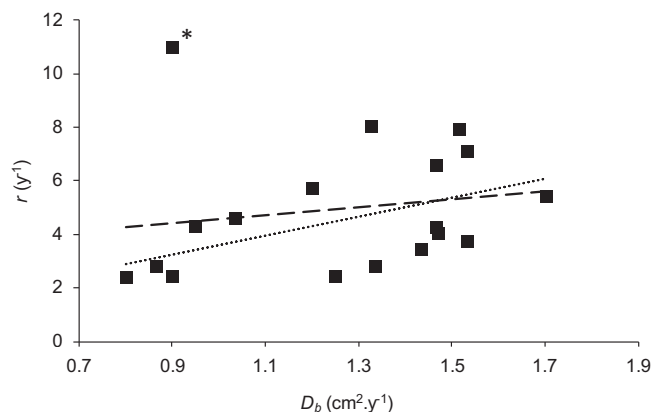


Fig. 7. Non-local coefficient r vs biodiffusion-like coefficient D_b . Average values for the sixteen *Hediste diversicolor* laboratory experiments involved in the Nereis Park joint-experiment carried out in the Northern hemisphere spring 2007. Linear regressions are indicated either with the complete dataset considered (long dashes) or excluding the outlier value (*); short dashes).

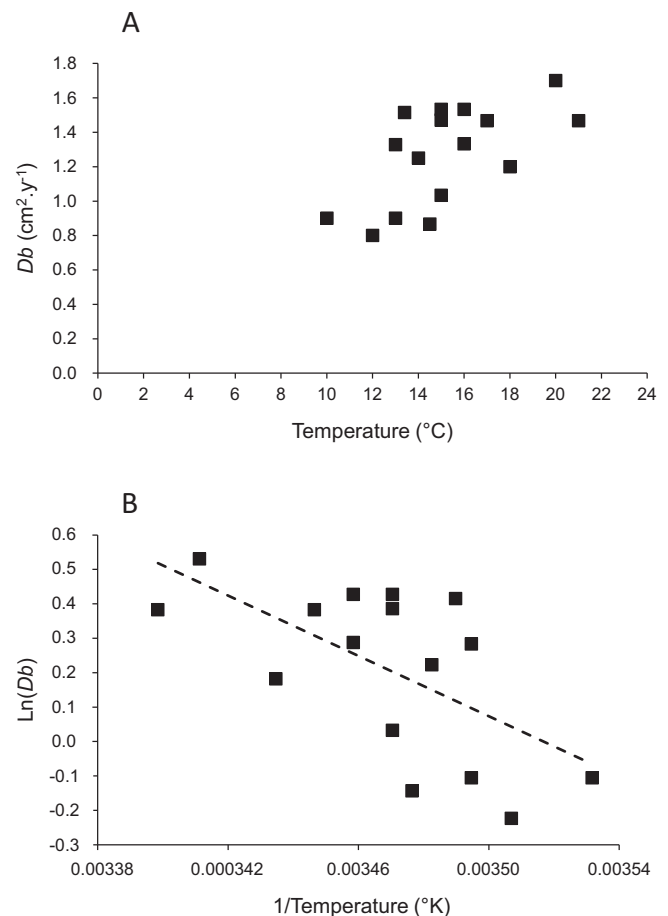


Fig. 8. Biodiffusion-like coefficient D_b vs Temperature (A) and $\ln(D_b)$ vs $1/\text{Temperature}$. Average values for the sixteen *Hediste diversicolor* laboratory experiments involved in the Nereis Park joint-experiment carried out in the Northern hemisphere spring 2007.

relationships between ingestion (\sim reworking) rate or D_b and the size of individuals can be confounded by organic matter availability (Hargrave, 1972; Cammen, 1980), and also opportunistic changes in feeding mode; for example, increased filter feeding relative to surface deposit feeding in the case of *H. diversicolor* (Vedel and Riisgård, 1993; Vedel et al., 1994). We did not find any correlation between D_b and total sediment organic matter in our data, perhaps reflecting a dominant mode of filter feeding during the experimental period, or possible inaccuracies in the estimation of available organic matter content. For example, at smaller grain sizes dominated by clay minerals, mineral-bound water can contribute to the weight loss at 400 °C, resulting in mineral-dependent overestimates of organic matter per se (e.g. Dean, 1974; Sun et al., 2009). In addition, total measures of organic matter may or may not relate closely to reactivity or quality of food source.

With respect to total benthic biomass, theoretical (Che and Dorgan, 2010) and empirical studies have generally demonstrated a positive relationship between sediment reworking and benthic biomass (e.g., Reible et al., 1996; Rice et al., 1986; Reible and Mohanty, 2002; Queiros et al., 2013). However, these investigations were performed using individuals of similar sizes or, in the case of models, an equivalent assumption, and the results may reflect changes in abundance in addition to total biomass. Here, our experimental design factored out the effects of abundance, allowing us to conclude that variation in bio-diffusion mixing is attributable to body size, although we are unable to distinguish other confounding effects. This dependence of bioturbation rates on size may imply, in contrast to what was recently suggested in the Baltic Sea (Norkko et al., 2013), that individuals of small body size of certain infaunal species (e.g. *H. diversicolor*) are more important than individuals of large body size for maintaining sediment reworking and related organic matter mixing processes.

Correlative evidence from sediment reworking descriptors applied here suggests that deep burrowers may rework less intensively (in a bio-diffusive manner) and/or that the influence of any particle reworking is spread over a wider depth range (Fig. 9; $\rho = -0.469$; $p = 0.049$). Interestingly, the expected positive correlation between r and MPD was not observed ($\rho = -0.322$, $p = 0.192$), which may suggest that bio-diffusion is sufficient to describe reworking and that non-local transport is somehow minimized under the experimental conditions. The mechanism leading to non-local transport could be less dependent on active particle movement and, instead, predominantly reflect the passive relocation of particles that occurs because of the existence of burrows into which particles can fall/sink (Powilleit et al., 1994). Our use of quiescent incubation conditions without sediment resuspension and lateral transport by currents, likely minimized infilling events of burrows and thus the role of non-local transport. Irrespective of the mechanism, it is noteworthy that D_b correlated with most experimental and environmental parameters (see below) and that the non-local mixing parameter did not relate strongly to environmental parameters.

5. Conclusions

We have investigated patterns of activity for a functionally important species across a number of environmental settings and at a spatial scale that ordinarily could not be achieved within a single study. Whilst our approach could not distinguish specific local biological and environmental parameters that may influence faunal activity (e.g. Emmerson et al., 2001; McKie et al., 2008; Wohlgemuth et al., 2017), both the magnitudes of the transport activities observed across sampling locations and the correlations of those magnitudes with variables such as individual size and temperature, were consistent with findings from localized studies. These results imply that measures of particle mixing activities of a species from single locations and their relationships to local biological and environmental properties can be more generally extrapolated to different populations at similar conditions. Such extrapolations are often made implicitly, for example in reviews of bioturbation, but have not been explicitly tested until now. Our study also

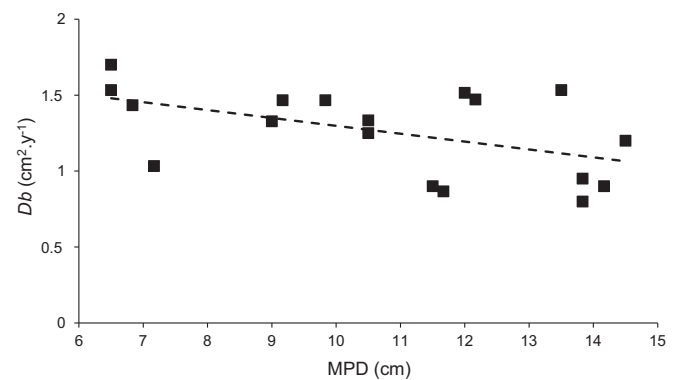


Fig. 9. Bio-diffusion-like coefficient D_b vs luminophore maximal depth MPD for the sixteen *Hediste diversicolor* laboratory experiments involved in the Nereis Park joint-experiment carried out in the Northern hemisphere spring 2007.

confirms a great need for research on the role of environmental context, body size and life stage, and physiological condition in determining species contributions to ecosystem properties.

Authors' complementary list and contributions

Have also contributed to this work: Josephine Y. Aller, Valérie Bélanger, Lucienne Caines, Frédérique François-Carcaillet, Mauro Frignani, Silvia Giuliani, Britta Gribsholt, Jenny Hedman, Aleya Kaushik, Pascal Lecroart, Claude Manté, Marie Morineaux, Mohammed Mouloud, Catherine Mouneyrac, Cristian Mugnai, Hazel Needham, Jean-Christophe Poggiale, Stefania Romano, Göran Samuelsson, Sabine Schmidt, Annie Seguin, Pablo Simo, Min Tang, Emily Widdicombe and Lewis Widdicombe. FG designed the study; all authors contributed to data collection or analysis; FG, EK, GB and RCA contributed to the preparation of the manuscript; all authors read and approved the final version.

Declaration of Competing Interest

None.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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