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1 **Allometric scaling of faunal-mediated ecosystem functioning: a case study on two bioturbators in**
2 **contrasting sediments**

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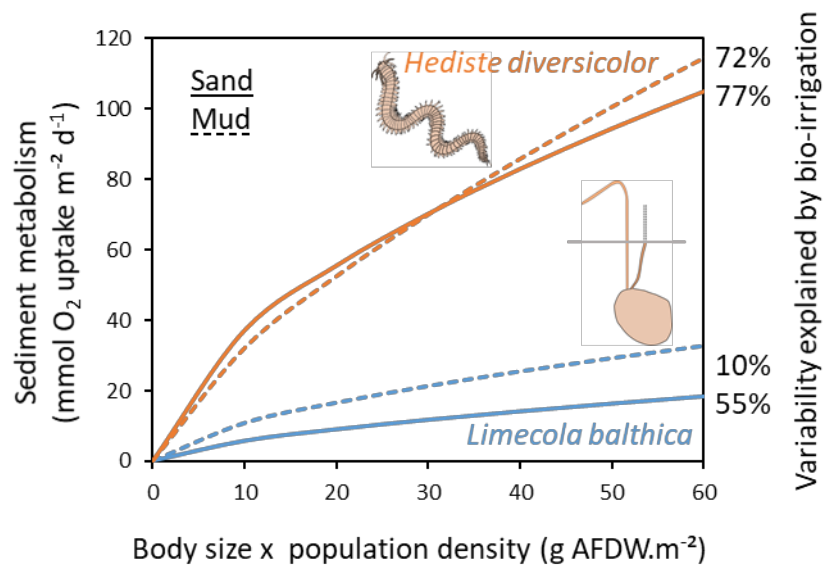
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41 **Highlights**

- 42 • Allometric scaling predicts faunal population effects on seafloor metabolism
- 43 • Stimulatory effects on sediment metabolism depend on species bioturbation traits
- 44 • Stimulatory faunal effects on sediment metabolism can vary between sand and mud
- 45 • Bio-irrigation effects on seafloor metabolism depend on species and sediment type

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65 **Abstract**

66 Soft-sediment biogeochemistry is influenced by the bioturbation activity of benthic invertebrates. We
67 investigated whether the effect of two macrobenthos bioturbators, *Limecola balthica* and *Hediste*
68 *diversicolor*, on sediment oxygen uptake can be described by allometric principles of metabolic activity
69 scaling with animal body size and population biomass. Microcosms containing reconstructed
70 populations to control density and individual body size were used to compare bioturbation effects and
71 allometric scaling principles between a sandy and muddy sediment. Both species facilitated oxygen
72 uptake in both sediment types, and a major portion of the variance in sediment metabolism (60-98%)
73 could be explained by the per capita body size and density, and total population biomass. The allometric
74 relationship with the stimulated sediment metabolism was similar in sand and mud for *Hediste* and
75 strongly related to the increasing burrow ventilation rate with population biomass. *Limecola* irrigated
76 less in mud but stimulated sediment metabolism more in mud in comparison to in sand. We discuss
77 how physico-chemical differences between both sediment types, possible changes in activity, and size-
78 dependent irrigation dynamics can explain the variable effects of *Limecola* on sediment metabolism.
79 Overall, we provide empirical evidence that allometric laws can be used to upscale bioturbation effects
80 on ecosystem functioning in marine soft sediments from the individual to the population level.

81

82 **Keywords**

83 Allometry; bioturbation; sediment biogeochemistry; Western Scheldt estuary; *Hediste diversicolor*;
84 *Limecola balthica*

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93 **1. Introduction**

94 Estuaries and coastal marine ecosystems are among the most productive biomes of the world and serve
95 as important life-support ecosystems (Costanza et al., 1997). The biogeochemical cycling of elements
96 that support these productive food webs is influenced by different seabed biota whose activities are
97 directly and indirectly involved in the burial and mineralization of the organic matter settling to the
98 seabed (Kristensen, 2000a; Levinton, 2011; Meysman et al., 2006). Whereas microbial organisms
99 directly govern a variety of biogeochemical reactions, macrobenthos are a group of large (i.e. retained
100 on a 1-mm mesh-sized sieve) sediment-dwelling animals that affect benthic metabolism via aerobic
101 respiration and indirectly via their bioturbation activities. The aerobic metabolism in the sediment
102 community that is stimulated by macrobenthos bioturbation can outweigh the direct O₂ consumption
103 by macrobenthos for respiration purposes (Glud 2008 and references therein). Bioturbation
104 encompasses two main processes: particle reworking and bio-irrigation (Kristensen et al. 2012). Particle
105 reworking results from a series of sediment mixing processes that transport particles and associated
106 living and non-living substances through faunal feeding, defaecation and burrowing activities. Bio-
107 irrigation is the ventilation of burrows with water by the fauna, providing dissolved substances for
108 respiration and particles for feeding. Bioturbation therefore redistributes reduced compounds and
109 aerates the sediment, thereby providing microbial habitats for intensified biogeochemistry (e.g.
110 Mermillod-Blondin et al., 2004; Nielsen et al. 2004; Volkenborn et al. 2012).

111 Activity of organisms relate to their metabolism that scales with individual body size or mass (Brown et
112 al., 2004; Kooijman 2000). An allometric scaling exponent of approximately 0.75 is evidenced across
113 taxonomic groups, and this 'universal' 3/4 -power law of metabolic rate is often considered as one of
114 the fundamental principles in ecology (West et al. 1997). However, existing taxonomic, environmental
115 and phenotypic (e.g. Barneche et al., 2014; Yvon-Durocher et al., 2012; Clark et al., 2016) variability in
116 metabolic scaling exponents within and among species support ongoing debate (e.g. Glazier, 2015), and
117 other theories that allow for more dynamic body size scaling relationships in function of life stage and
118 environmental conditions have equally found their application in ecology (e.g. Kooijman, 2000). Yet if
119 the bioturbation activity of macrobenthos is proportional to its energetic requirements, the cascading
120 facilitative effect on sediment metabolism can theoretically be assumed to change proportionally to the
121 metabolic rate of the bioturbator. Cozzoli et al. (2018, 2019) support this theory by empirically
122 demonstrating that sediment resuspension can be ascribed to the overall metabolic rate of the
123 bioturbating populations. Furthermore, Wrede et al. (2018) successfully applied a scaling of 0.75 to
124 weigh the effect of body mass on bio-irrigation rates across a range of macrobenthos species
125 populations and communities. The above examples support the idea that (1) an allometric scaling of
126 macrobenthos body size on sediment metabolism can be assumed, and (2) that this metabolic body size

127 relationship can be scaled as the product of the individual metabolic rate and the population density.
128 However, species metabolic rates depend on abiotic conditions, such as temperature (Clark and
129 Johnston, 1999) and pH (Ong et al. 2017), and variable outcomes of bioturbation effects on sediment
130 metabolism can thus likewise be expected. Indeed, bioturbation activity responds quickly to changes in
131 temperature to support elevated physiological demands at higher temperature (Ouellette et al., 2004),
132 and in general bioturbation rates can respond quickly to changing environmental conditions (Levinton
133 and Kelaher, 2004; Van Colen, Ong et al., 2020, Mestdagh et al. 2020a). Besides inter- and intraspecific
134 variability in stimulatory effects on sediment metabolism related to species biological (e.g. body size)
135 and functional (e.g. sediment reworking mode) traits (Queirós et al. 2013), the local sediment habitat
136 can be important as well. For example, stimulatory effects of macrobenthos on sediment metabolism
137 were shown to be limited in permeable, well-oxygenated sediments as compared to cohesive,
138 organically enriched sediments (Mermillod-Blondin and Rosenberg, 2006). In conclusion, the
139 contribution of macrobenthos to sediment metabolism may vary between species and change
140 considerably over time and across space (Godbold et al., 2011; Needham et al., 2010).

141 Oxygen is the most favourable electron acceptor in biogeochemical reactions, and the sediment
142 community O₂ consumption (SCOC) is the most widely used measure of aerobic benthic metabolism
143 (Glud, 2008; Thamdrup and Canfield, 2011). SCOC represents a good proxy for the total benthic carbon
144 mineralization rate or sediment metabolism (Canfield et al., 1993) and integrates the re-oxidation of
145 reduced metabolites and the aerobic respiration of benthic organisms. In this study, we quantified the
146 influence of the ragworm *Hediste* (formerly *Nereis*) *diversicolor* and the Baltic tellin *Limecola* (formerly
147 *Macoma*) *balthica* (hereafter referred to as *Hediste* and *Limecola*) on the sediment metabolism of an
148 estuarine muddy and sandy sediment. Both species are common in temperate estuaries where they
149 typically constitute a significant part of the macrobenthos biomass (e.g. Ysebaert et al., 2003) and
150 bioturbate the sediment matrix (Fang et al. 2019). Microcosms with various densities and sizes of
151 animals were used to quantify the stimulatory effect of both species on sediment metabolism
152 (measured as SCOC) in both sediment types. We hypothesized that (1) allometric principles of metabolic
153 scaling with population density can be applied to quantify the faunal effects on sediment metabolism;
154 but also that (2) dissimilar porewater solute dynamics related to different bioturbation modalities of
155 both species (see 2.1), and (3) contrasting physico-chemical conditions between sandy and muddy
156 sediments, would affect faunal-mediated sediment metabolism. Finally, we evaluated whether the
157 stimulated sediment metabolism can be explained by the variability in bio-irrigation measured across
158 microcosms.

159

160 2. Materials and methods

161 2.1 Model organisms

162 *Hediste* is a highly mobile polychaete that lives in a mucus-lined gallery of semi-permanent U or Y shaped
163 burrows extending 6 to 12 cm into the sediment (Davey, 1994). Muscular movements of the body create
164 currents of oxygen-rich water and suspended food particles into the burrow; active ventilation periods
165 last about 10 minutes and are alternated with 5-minute resting periods (Riisgård 1991; Kristensen,
166 2001). *Hediste* obtains food from deposit and suspension feeding, as well as via active scavenging and
167 predation on small invertebrates (Scaps 2002 and references therein). The species' sediment reworking
168 and ventilation activities affect other benthos populations, biogeochemistry and sediment erodibility
169 (Hiddink et al., 2002; Kristensen and Mikkelsen, 2003; Widdows et al., 2009). *Limecola* is a facultative
170 surface deposit feeding tellinid bivalve, foraging on microphytobenthos, bacteria and labile organic
171 matter present on the sediment surface or suspended in the water column (Kamermans, 1994; Rossi et
172 al., 2004). The living depth in the sediment depends on the length of the inhalant siphon (Zwarts et al.,
173 1994) that is used to feed and respire on the sediment-water interface. *Limecola* intermittently irrigates
174 the sediment during feeding and respiration via the release of water and solutes through the exhalant
175 siphon just below the sediment surface (Volkenborn et al., 2012), thereby affecting sediment
176 biogeochemistry (Michaud et al., 2006). Resting periods between the irrigation bouts are short (< 2
177 minutes) and can result in an almost continuous oxygenation in permeable sediments (Volkenborn et
178 al., 2012).

179

180 2.2 Sediment and animal collection

181 Sediments were collected in May 2017 from the Paulina intertidal flat in the polyhaline reach of the
182 Scheldt estuary, SW Netherlands. There are a variety of habitats on this tidal flat, varying from mud to
183 sands almost devoid of silt (Gallucci et al., 2005; Van Colen et al. 2010). A sandy (51°21' 00.2" N, 3° 43'
184 54.9" E) and a muddy location (51° 20' 57.1" N, 3° 43' 35.4" E) were chosen. The sediment at the sandy
185 location had a higher permeability and oxygen penetration depth but a lower organic carbon content
186 as compared to the muddy location (Table 1). Sediments were collected through coring (inner diameter:
187 9 cm) and subsequently sectioned into 0-1, 1-2, 2-4, 4-6 cm sediment fractions before macrobenthos
188 and large particles were removed through wet sieving (1 mm mesh size). Each sediment section was
189 incubated at 15°C in aerated seawater collected from the sampling location and allowed to settle prior
190 to reconstruction of the vertical sediment matrix in a rectangular polypropylene box (19.4×29.4×15 cm).
191 Therefore, the 2-4 cm layer was put on top of the deepest layer (4-6 cm) followed by the subsequent
192 deposits of the 1-2 cm and 0-1 cm sediment layers. For each sampling location, two boxes with

193 reconstructed sediment without macrobenthos were acclimated in aerated seawater at 15°C for 4-5
194 weeks before the start of the experiments to maximize stabilisation of the sediment matrix and
195 restoration of biogeochemical gradients before usage in the microcosms (see 2.3).

196 *Limecola* and *Hediste* are ubiquitous and abundant in the polyhaline reach of the Scheldt estuary,
197 occupying both muddy and sandy sediments. In the polyhaline zone of the Scheldt estuary, mean
198 density of *Hediste* is 466 ind. m⁻² with maxima up to 3928 ind.m⁻² (corresponding to 13.7 g ash-free dry
199 weight (AFDW) m⁻²), while *Limecola* attains a mean density of 855 ind. m⁻² with a maximal density up to
200 5217 ind. m⁻² (corresponding to 15.9 g. AFDW m⁻²; after Ysebaert et al., 1998). Individuals of *Hediste* and
201 *Limecola* were collected on 15th June 2017 and left to acclimatize in the natural sediments at 15°C in
202 containers with aerated seawater collected from the sampling location (salinity = 20) until the start of
203 the experiments, which begun within two weeks after collection from the field.

204 2.3 Experimental design

205 To provide mechanistic insight into the relationship between aerobic sediment metabolism, individual
206 body size, population density, and sediment type, we experimentally tested single-species treatments
207 spanning a broad range of natural body sizes and densities in a muddy and sandy sediment. For each
208 sediment type × species combination, the total sediment O₂ consumption and bio-irrigation were
209 measured in plexiglass cylindrical microcosms (height 12.2 cm, inner diameter 3.6 cm) collected through
210 coring from the boxes with macrobenthos-free sediment (depth 6 cm) and overtopped with *in situ*
211 collected 1-mm sieved seawater. Each series included in total eleven microcosms; one without
212 macrobenthos and ten with combinations of variable densities and a gradient of similarly sized
213 individuals per treatment, yielding a natural density and biomass range for both species (Table 2a, b).
214 The microcosm without macrobenthos was included to distinguish the faunal stimulatory effect by
215 *Hediste* and *Limecola* from the single contribution of microbes and meiofauna activities. The
216 microcosms were aerated, and the organisms were carefully put on top of the sediment and left to
217 acclimatize and burrow overnight into the sediment.

218 The O₂ consumption in the water column was measured using O₂ optodes (Pyroscience OXROB10)
219 connected to a FireSting O₂ meter (FSO₂-4). After a two-point calibration, each O₂ optode was inserted
220 through a rubber cap keeping the microcosms airtight during O₂ consumption measurements.
221 Microcosms were put on a platform shaker to assure homogenous mixing of O₂ in the water column;
222 the incubation lasted till O₂ concentration had dropped to 60% of the initial concentration. Sediment
223 oxygen consumption was calculated from the decline in dissolved O₂ concentrations over time,
224 considering both the sediment surface and the volume of the overlying water. Macrobenthos-mediated
225 O₂ uptake in the microcosms was calculated by subtracting the O₂ uptake measured in the microcosm

226 without macrobenthos from that experiment. This faunal-mediated O₂ uptake includes both *Hediste* or
227 *Limecola* respiration and stimulation of respiration by bacteria and meiobenthos.

228 Following the SCOC measurements, microcosms were aerated and left to acclimatise overnight. The
229 following day, seawater was replaced by an aerated solution of seawater and uranine (10 µg.L⁻¹
230 C₂₀H₁₀NaO₅⁻). Subsequently, 1.5-ml water samples were taken from the water column by Pasteur
231 pipettes at 0, 2, 4, 22.5, 24 h and the uranine concentrations were measured at 520 nm using a Turner
232 Quantech Digital Fluorometer (FM 109530-33) with 490 nm as the excitation wavelength. Uranine fluxes
233 were estimated from the linear decrease of water column tracer concentration over time and used as a
234 proxy for sediment community irrigation rates (Meysman et al. 2007), after standardization per surface
235 area.

236 Total biomass (g AFDW.m⁻²) of *Hediste* and *Limecola* individuals from each microcosm was measured at
237 the end of the irrigation measurements by loss on ignition after muffling of dried organisms for 3 h at
238 550°C. Individual body size (mg AFDW) was estimated by dividing the total biomass per treatment by
239 the number of individuals.

240 **2.4 Data analysis**

241 Following ecological scaling theory (e.g. Brown et al., 2004), the mediating effect on sediment
242 metabolism performed by a homogeneous population can be expressed as a power function $Y=aM^bA$
243 [1], where Y is the faunal-mediated O₂ uptake, and M and A are the respective individual body size (mg
244 AFDW) and the density of the examined animals; a is the coefficient quantified in the model, and b is
245 the allometric exponent relating body size to individual activity. Equation [1] can be modified to include
246 population biomass W: $Y=cW^d$ [2], where c is the quantified coefficient and d is the biomass-dependent
247 scaling exponent.

248 Analysis of covariance (ANCOVA) was conducted to compare the faunal-mediated O₂ uptake between
249 sediment types while controlling for the biomass range across treatments. Biomass of *Hediste* and
250 *Limecola* were normalized using log transformation in all experiments to meet assumptions of the
251 homogeneity of regression slopes and the homogeneity of variances. Finally, simple linear regression
252 was used to determine to what extent the variance of faunal-mediated O₂ uptake can be explained by
253 bio-irrigation of the sediment community. P-P plots and scatterplots of residuals against the explanatory
254 variable revealed that no further data transformation was needed to meet assumptions of normality
255 and homoscedasticity. The level for statistical significance was set at 0.05 in all analyses.

256

257 3. Results and discussion

258 Sediment O₂ consumption by microbial and meiobenthos communities alone was 8.8 ± 2.3 SD mmol m⁻² d⁻¹ (n = 2) and 1.9 ± 0.3 SD mmol m⁻² d⁻¹ (n = 2) in muddy and sandy sediments, respectively, which was
259 marginal in comparison to the SCOC rates in microcosms with macrobenthos (Figure 1a,b). *In situ*
260 measurements and experimental data show that faunal respiration typically accounts for 10-40% of the
261 faunal-mediated O₂ consumption (e.g. Glud et al. 2003; Glud, 2008; Dunn et al. 2009; Kristensen 1985);
262 the remaining portion is than ascribed to the stimulated microbial activity related to the bioturbation
263 activity, i.e. particle mixing and bio-irrigation. Bio-irrigation rates by meiobenthos alone were 12.7 ± 0.2
264 SD L.m⁻².d⁻¹ (n = 2) and 2.7 ± 1.0 SD L.m⁻².d⁻¹ (n = 2) in muddy and sandy sediments, respectively. The
265 additional irrigation by *Hediste* and *Limecola* explained a significant portion of the faunal-mediated O₂
266 uptake ($R^2 = 0.55 - 0.77$, $p < 0.01$) in all experimental series, except for the stimulated sediment
267 metabolism by *Limecola* in the muddy sediments ($R^2 = 0.10$, $p = 0.37$) (Figure 2a,b). Irrigation rates for
268 *Limecola* across body size × density combinations in the muddy sediments were generally lower as
269 compared to the sandy sediments, and in the same order of magnitude as for irrigation by meiobenthos
270 alone. Irrigation by *Limecola* mainly occurs when the water that is inhaled during feeding is injected into
271 the sediment via the exhalent siphon (Volkenborn et al. 2012). It is therefore likely that *Limecola*
272 individuals reduced feeding (and irrigating) events in organically enriched muddy sediment as compared
273 to the food poor sandy sediment. We furthermore hypothesize that limited porewater advection (e.g.
274 Hedman et al., 2011) reduced the relative importance of bio-irrigation for organic matter mineralisation
275 in the muddy sediment. Despite the limited contribution of bio-irrigation, the *Limecola*-mediated
276 sediment O₂ uptake was significantly higher in muddy as compared to sandy sediments when
277 considering the population biomass variation across treatments (0.9 ± 0.3 mmol O₂ gAFDW⁻¹ d⁻¹ and 0.4
278 ± 0.2 mmol O₂ gAFDW⁻¹ d⁻¹ in muddy and sandy sediments respectively; ANCOVA: Sediment type $p <$
279 0.001 , Table 3), which might be explained by the higher availability of reduced metabolites in muddy
280 sediments (e.g. Kristensen et al. 2000b). In comparison, the stimulated O₂ uptake by *Hediste* was higher
281 than that of *Limecola* (2.6 ± 1.8 mmol O₂ gAFDW⁻¹ d⁻¹ and 2.5 ± 0.9 mmol O₂ gAFDW⁻¹ d⁻¹ in muddy and
282 sandy sediments respectively), but did not vary between sediment types (ANCOVA: Sediment type $p =$
283 0.678 , Table 3). The stronger enhancement of aerobic sediment metabolism by gallery-burrowing
284 polychaetes in comparison to biodiffusing bivalves corroborates earlier findings by Michaud et al. (2005)
285 for populations from the St. Lawrence estuary. The periodic ventilation of the deep *Hediste* gallery
286 burrow system (Kristensen, 1981; Pischedda et al., 2012) in comparison to the more continuous
287 diffusion that is limited to the surface sediment by *Limecola* (Volkenborn et al. 2012) can explain this
288 species effect. The creation of the gallery burrow system expands the sediment – seawater interface for
289 solute exchange several-fold, and redox oscillations such as those generated through periodic
290

291 ventilation activities are known to strongly stimulate microbial organic matter mineralisation (e.g. Aller,
292 1994). Indeed, *Hediste* was detected as a key irrigator in intertidal sediments along the Scheldt estuary
293 (Fang et al., 2019), where irrigation contributed significantly to the sediment metabolism (Mestdagh et
294 al., 2020b). The fact that oxygen dynamics generated by *Hediste* irrigation are restricted to the burrow
295 lumen and a few mm in the burrow wall (Pischedda et al. 2012; Nielsen et al. 2004) may explain why
296 cascading effects on sediment metabolism did not differ between sediments despite differences in
297 sediment permeability and organic matter content (Table 1). However, longer incubations could have
298 yielded different results because sediment type can affect body condition, which in turn influences
299 burrowing depth (Esselink and Zwarts, 1989). Furthermore, the increasing depth and complexity of
300 burrow structures with incubation time is known to increase oxygen uptake in marine sediments (e.g.
301 Michaud et al. 2005, Gilbert et al. 1994, 1995).

302 For both species the faunal-mediated O₂ consumption followed an allometric power law as a function
303 of body size and density in both sediment types, supporting the metabolic theory of ecology (Brown et
304 al. 2004) (Table 4). For both sediment types, the model based on population biomass explained the
305 variability in *Hediste*-mediated O₂ uptake better (adjusted R² > 0.95) as compared to the allometric
306 model that considers the scaled body size component and population density (adjusted R² < 0.85). This
307 suggests that for this species, non-linear density effects on solute exchange may exist, such as e.g. space
308 limitation for burrow construction (Aller, 2004). The biomass size scaling exponents for *Hediste* (0.58 -
309 0.71, Table 4) are in accordance with the quantified relationships between oxygen consumption and
310 body weight in eight marine polychaetes (0.61-0.69; Shumway, 1979), further supporting the metabolic
311 basis of the stimulatory effect on sediment metabolism. In contrast, the predictive power of both
312 allometric models for *Limecola* was similar, suggesting that density-dependent interference amongst
313 *Limecola* individuals is less important than for a more mobile species like *Hediste*. On the other hand,
314 the stimulated sediment metabolism in function of body size and density or population biomass of
315 *Limecola* was clearly better explained for the muddy (adjusted R² > 0.88) than for the sandy sediments
316 (adjusted R² < 0.64)(Table 4). This may result from constraints on depth distribution set by body size,
317 and from environmental constraints on how metabolic activity and bioturbation affect sediment
318 metabolism. That is, as shorter siphon lengths in small individuals decrease burrowing depth (Zwarts et
319 al., 1994), the shallow advective irrigation flows generated by smaller individuals might not have
320 contributed importantly to sediment metabolism in the sandy sediment that is characterized by a
321 deeper diffusive oxygen penetration (Table 1).

322

323

324 4. Conclusion

325 We demonstrate that ecological scaling laws based on body size allometry can be applied to predict
326 sediment metabolism based on the bioturbation effect of two macrobenthos species with different
327 sediment particle reworking and ventilation traits. Similarly, Cozzoli et al. (2019) found that allometric
328 principles of metabolic activity scaling and population size explained the bioturbation impact of different
329 macrobenthos species on sediment resuspension. Allometric laws based on body size and population
330 density can thus be used to upscale species effects on ecosystem functioning in marine soft sediments
331 from the individual to the population level. However, this work also corroborates earlier findings that
332 sediment texture can modify bioturbation effects on ecosystem functioning (e.g. Li et al., 2017;
333 Joensuu et al., 2018; Van Colen et al., 2013), depending on how species interact with their
334 environment. This demonstrates that insights into how environmental conditions can modify organism
335 activity and metabolism (e.g. Halsey et al. 2015; Cornwell et al. 2020), and the cascading effects this
336 may have on ecosystem functioning, are needed before allometric extrapolations can be applied to
337 larger spatial (e.g. the entire estuary) and temporal scales, encompassing e.g. gradients in salinity,
338 temperature and sediment composition.

339

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345

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525 **Tables**

526 **Table 1.** Physico-chemical sediment characteristics for the two sampling locations: median grain size (in
527 μm), mud content (in % < 63 μm), total organic carbon (in %), permeability (in m^2) and oxygen
528 penetration depth (in mm). Data were derived from a seasonal survey in the Scheldt estuary in 2015-
529 2016 (Mestdagh et al. 2020b). All values are means \pm standard deviations for characteristics obtained
530 in September 2015, December 2015, March 2016, and June 2016. The total organic carbon (TOC) (FLASH
531 2000 NC Analyzer, Thermo Scientific, Wilmington, DE, United States), sediment grain size and mud
532 content (Mastersizer 2000 particle analyser, Malvern Panalytical, Malvern, United Kingdom) were
533 analysed by homogenising a 10 cm deep sample. Permeability was calculated based on Eggleston and
534 Rojstaczer (1998): $\text{KH} = 1.1019 \times 10^3 \text{ m}^{-2} \text{ s} * d_{10}^2 * v$, where KH is the permeability (in m^2), d_{10} is the first
535 decile of the grain size distribution (in m), and v is kinematic viscosity (in $\text{m}^2 \text{ s}^{-1}$) calculated from water
536 temperature and salinity. Oxygen penetration depths were derived from the vertical oxygen profiles
537 using Unisense oxygen microsensors (type OX100) in vertical increments of 250 μm .

538 **Table 2:** Overview of macrofaunal density (Ind.m^{-2}), biomass (g AFDW.m^{-2}) and individual body size (mg
539 AFDW ind^{-1}) in the different treatments. Several combinations of densities and individual body sizes of
540 the target organisms (a) *H. diversicolor* and (b) *L. balthica* were tested according to their natural density
541 range in sandy and muddy sediments in the polyhaline zone of the Scheldt estuary.

542 **Table 3:** ANCOVA results in species subsets: (a) *H. diversicolor* and (b) *L. balthica*. Faunal-mediated O_2
543 uptake is the dependent variable, sediment type is the factor, and biomass is the covariate. Once the
544 significant effect of sediment type was found in the *L. balthica* dataset, the estimated marginal means
545 were analysed.

546 **Table 4:** Summary of allometric models to predict faunal-mediated O_2 uptake ($\text{mmol m}^{-2} \text{ d}^{-1}$).

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555 *Table 1*

Property	Sandy	Muddy
Median grain size (μm)	226 ± 3	46 ± 1
Mud content (%)	$3,7 \pm 1,2$	$64,8 \pm 1,7$
TOC (%)	$0,2 \pm 0,1$	$1,2 \pm 0,1$
Permeability (m^2)	$8,17 \cdot 10^{-11} \pm 1,1 \cdot 10^{-10}$	$7,17 \cdot 10^{-14} \pm 1,9 \cdot 10^{-14}$
Oxygen penetration depth (mm)	$7,7 \pm 3,2$	$3,9 \pm 0,4$

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(a) <i>Hediste diversicolor</i>	Sandy			Muddy		
Treatment	Density	Biomass	Body size	Density	Biomass	Body size
1	0	0	0	0	0	0
2	943	7.6	8.1	943	2.7	2.8
3	943	28.5	30.2	943	14.6	15.5
4	943	43.1	45.7	943	45.4	48.1
5	1887	17.3	9.2	1887	27.8	14.7
6	1887	3.2	1.7	1887	21.7	11.5
7	2830	105.6	37.3	2830	71.3	25.2
8	3774	114.2	30.3	2830	46.7	16.5
9	4717	61.5	13.0	3774	99.3	26.3
10	4717	42.4	9.0	3774	43.1	11.4
11	5660	127.9	22.6	5660	32.7	5.8
(b) <i>Limecola balthica</i>	Sandy			Muddy		
Treatment	Density	Biomass	Body size	Density	Biomass	Body size
1	0	0	0	0	0	0
2	943	7.1	7.6	943	4.8	5.1
3	943	24.2	25.9	943	16.0	17.0
4	943	29.3	31.4	943	21.1	22.4
5	1868	48.9	26.2	1887	32.7	17.4
6	2802	9.5	3.4	2830	11.8	4.2
7	2802	49.5	17.7	2830	18.9	6.7
8	2802	67.1	23.9	2830	51.4	18.2
9	4670	27.8	6.0	4717	17.6	3.7
10	4670	67.5	14.4	4717	40.3	8.5
11	5604	36.5	6.5	5660	11.2	2.0

(a) <i>Hediste diversicolor</i>	Type III Sum of Squares	df	Mean Square	F	p-level
Corrected Model	36660.8	2	18330.4	52.8	<0.001
Intercept	4416.7	1	4416.7	12.7	<0.001
Biomass	36228.7	1	36228.7	104.4	<0.001
Sediment type	61.8	1	61.8	0.2	0.678
Error	5897.8	17	346.9		
Total	197874.5	20			
Corrected Total	42558.6	19			
R Squared = 0.86 (Adjusted R ² = 0.85)					
(b) <i>Limecola balthica</i>	Type III Sum of Squares	df	Mean Square	F	p-level
Corrected Model	991.2	2	495.6	50.4	<0.001
Intercept	67.5	1	67.5	6.9	0.018
Biomass	934.4	1	934.4	95.1	<0.001
Sediment type	344.1	1	344.1	35.0	<0.001
Error	167.1	17	9.8		
Total	5886.0	20			
Corrected Total	1158.4	19			
R Squared = 0.86 (Adjusted R ² = 0.84)					

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587 **Table 4**

Faunal-mediated O ₂ uptake		=a(Bodysize) ^b Density					=c(Biomass) ^d				
Species	Sediment type	a	b	R ²	Adj. R ²	p	c	d	R ²	Adj. R ²	p
<i>Limecola balthica</i>	Sandy	0.10	0.69	0.64	0.6	0.005	1.29	0.65	0.63	0.59	0.006
	Muddy	0.37	0.83	0.88	0.87	<0.001	2.58	0.62	0.93	0.92	<0.001
<i>Hediste diversicolor</i>	Sandy	0.39	0.58	0.75	0.72	0.001	9.75	0.58	0.96	0.95	<0.001
	Muddy	0.90	0.78	0.86	0.85	<0.001	6.25	0.71	0.99	0.98	<0.001

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607 **Figures**

608 **Figure 1:** Faunal-mediated O₂ uptake (mmol.m⁻².d⁻¹) measured in each microcosm as a function of
609 *Hediste* (a) and *Limecola* (b) biomass (gAFDW.m⁻²). Allometric model fits $Y = cW^d$ (see Table 3) are
610 presented in blue (muddy sediment) and red (sandy sediment).

611 **Figure 2:** Scatterplots of faunal-mediated O₂ uptake (mmol.m⁻².d⁻¹) against *Hediste* (a) and *Limecola* (b)
612 – mediated uranine flux (L.m⁻².d⁻¹) measured in muddy (blue) and sandy (red) sediments. Linear fits and
613 regression statistics are presented in the figure legend.

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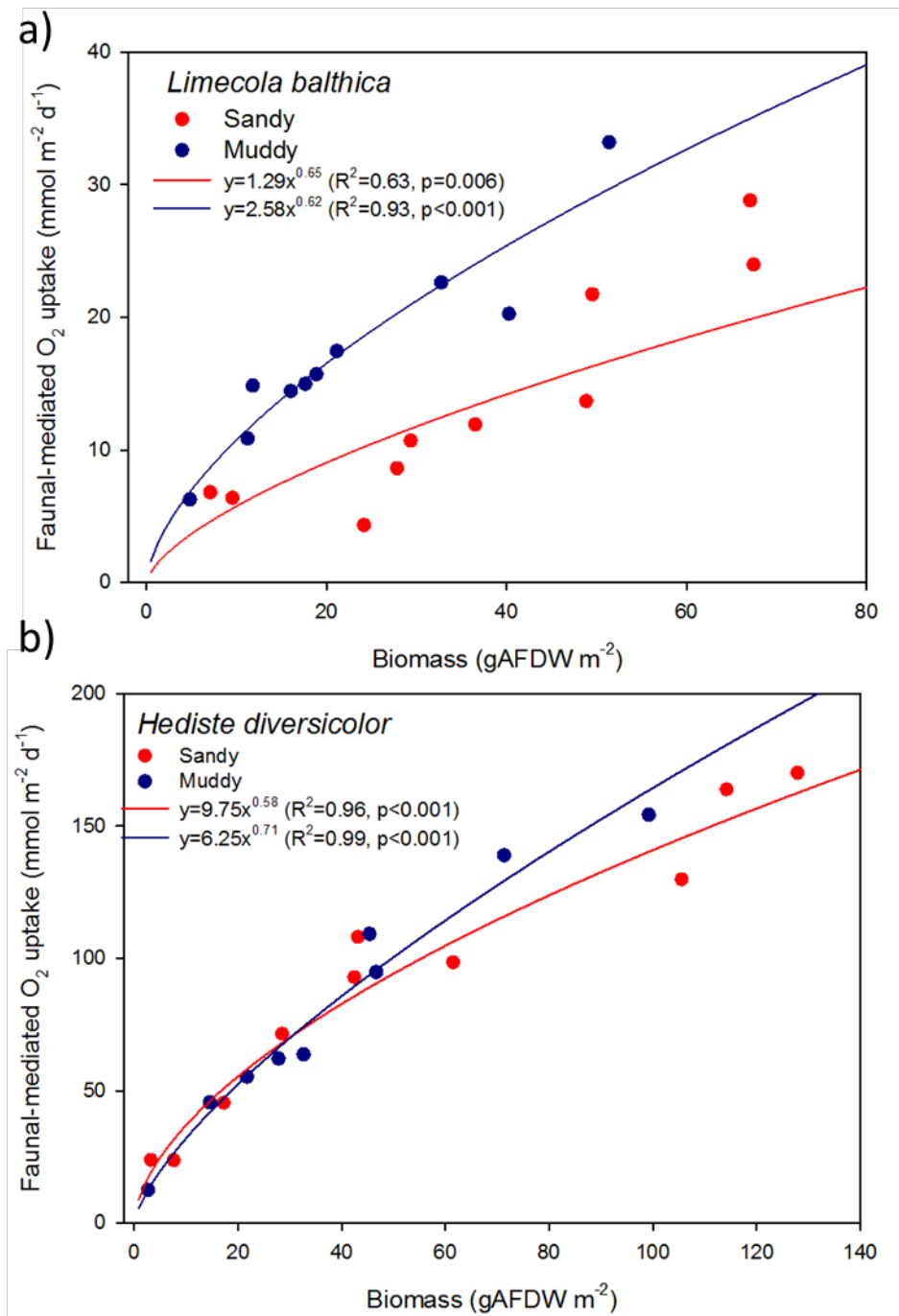
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