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**Depth and vertical hydrodynamics constrain the size-
structure of a lowland streambed community**

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This article does not present research with ethical considerations

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It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:

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This paper has multiple authors and our individual contributions were as below

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IPM, DP and ALR conceived the study. IPM, DP carried out the statistical analysis. Finally, IPM wrote the manuscript with a significant contribution from DP and ALR.

1 **Title:** Depth and vertical hydrodynamics constrain the size structure of a lowland
2 streambed community

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6

7 **Abstract:** Abundance-body mass (N–M) relationships are prominent macroecological
8 patterns and provide an integrated measurement of the structure and energy flow
9 through natural communities. However, little is known about how N–M relationships
10 are constrained by local environmental conditions. Here we quantify how sediment
11 depth and direction of surface–groundwater exchange (vertical hydrodynamics), two
12 major drivers of the streambed ecology, determine N–M scaling in a sandy lowland,
13 European stream. Streambed assemblages included flagellates, ciliates, meiofauna and
14 macroinvertebrates, and spanned five orders of magnitude in body mass. We detected a
15 significant interaction of body mass with depth and vertical hydrodynamics with a sharp
16 reduction in N–M slopes in the hyporheic zone and under upwelling conditions. These
17 results revealed that streambed assemblages become more size–structured as
18 environmental constraints increase with direct implications for the metabolic capacity
19 and functioning of the system.

20

21 **Keywords:** Metabolic scaling theory, benthos, hyporheos, body size, freshwater
22 communities

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26 out the statistical analysis. Finally, IP–M wrote the manuscript with a significant
27 contribution from DP and ALR.

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36 **1. Introduction**

37 Abundance-body mass relationships are one of the most extensively studied patterns in
38 ecological research [1,2,3] both in terrestrial and aquatic realms [4]. The distribution of
39 the abundance (N) of organisms within body mass classes (M) on a logarithmic scale,
40 known as the size spectrum (N–M relationship *henceforth*), provides an integrated
41 measure of community size structure [5,6]. A gathering body of evidence demonstrates
42 interactions between environmental stressors and N–M scaling coefficients [7], with N–
43 M slopes typically becoming steeper following disturbances (e.g. [8,9]) – i.e. there is a
44 relative increase in the number of small versus large organisms. This has led to the use
45 of N–M scaling coefficients as a quantitative measure of deviation of a natural
46 community from a reference status as a result of anthropic stressors [7]. However, little
47 is known about how N–M scaling coefficients (intercept and slope) vary with persistent
48 environmental gradients within natural systems, such as the availability of metabolic
49 substrates and resources. These environmental factors are widely recognised as major
50 selecting forces that determine which organisms survive and persist within a given
51 habitat [9] and thus we might expect them to impact N–M scaling relationships.

52 In streams and rivers, empirical studies quantifying N–M relationships in the
53 streambed have been limited to the upper sediment layer (benthic zone; e.g. [10, 11]).
54 However, depth below the surface, and the direction of the surface–groundwater
55 exchange (here as vertical hydrodynamics), have been widely recognised as primary
56 ecological constraints shaping streambed communities and driving the ecological
57 functioning of the streambed system at a micro–scale (see [12]). This is mainly because
58 the reduction of oxygen and nutrient availability with increasing depth and under
59 upwelling conditions limits the vertical colonization of organisms with larger body size
60 and high metabolic requirements [13, 14, 15, 16]. Surprisingly little is known about
61 how these environmental factors constrain N–M scaling in streambed systems but
62 investigation into this question could provide important insights into the role of resource
63 supply on community size structure [17].

64 Here we quantify for the first time how depth and surface–groundwater
65 exchange (as vertical hydrodynamics) govern N–M scaling in streambed communities.
66 We analysed data from a multi-disciplinary project in which community structure and
67 magnitude of the surface–groundwater exchange were determined at a very fine spatial
68 resolution (5 cm intervals) across a depth gradient in the streambed [12]. Streambed

69 assemblages included unicellular flagellates and ciliates, meiofauna (body length ranges
70 between 0.45 and 500 μ m) and macroinvertebrates. We hypothesize that increasing
71 streambed depth and upwelling groundwater exchange constrain the abundance of
72 organisms, especially among large-size fractions as a result of reduced resource supply
73 (i.e. oxygen) under these conditions. Thus we expect N–M intercepts (as a proxy of the
74 carrying capacity of the community) to decrease, and N–M slopes (as a measure of
75 energy flow and the trophic transfer efficiency) to become steeper, with depth and
76 vertical hydrodynamics. Our findings shed light on how important environmental
77 constraints may shape the structure, metabolic capacity and energy flow through
78 streambed communities.

79

80 **2. Methods**

81 *Data acquisition* – Here we used open-access published data from Peralta–Maraver et
82 al. [12], which included measurements of the vertical hydrodynamics quantified at the
83 same spatial resolution as the community sampling. The assemblage of organisms and
84 vertical hydrodynamic conditions in the streambed were sampled in six sites along a 3.5
85 km river stretch in the sandy river Erpe (northeast Germany). Even though the local
86 scale of this study might limit the scope of our results, it allowed us to test the effects of
87 depth and vertical hydrodynamics under natural conditions whilst controlling for other
88 factors such as substrate type, community composition, stream temperature etc.
89 Previous analyses using these data have focussed on the taxonomic composition,
90 productivity and community delineation between benthic and hyporheic zones [12];
91 here we leverage these data, and a theoretical framework (abundance-body mass
92 scaling), to assess, for the first time, the constraints of streambed depth and vertical
93 hydrodynamics on community size structure and the transference of energy through the
94 food web. A detailed description of the studied system and the sampling sites is
95 available in the Supplementary methods.

96 Samples were collected weekly between 16th May and 16th June 2016. Using a
97 modified Kajak corer, the assemblage of protists (flagellates and ciliates), meiofauna
98 and macroinvertebrates inhabiting the sediments was sampled by slicing 5–cm layers
99 down to 35 cm (7 depth-layers). Vertical hydrodynamics at each sampling site were
100 characterised by coupling averaged measurements of the thermal extinction depth,
101 vertical flux, and indirect analysis of redox conditions during the whole study period.
102 Vertical flux was determined applying the Hatch amplitude method [18] and using

103 constant measures of streambed thermal depth profiles. These values ranged from
104 negative values (upwelling conditions) to positive values (downwelling conditions), the
105 value of 0 indicated no surface–groundwater interchange. In the laboratory, organisms
106 were identified, counted and measured (length and width). Then, individual density
107 (ind/L) was calculated and body dimensions of all counted organisms were converted to
108 body mass ($\mu\text{g C}$). Additional details are provided in Supplementary methods and
109 abundance and body mass values are available as Supplementary data.

110

111 *Statistical analysis* – We constructed N–M relationships for each sampling unit ($n =$
112 168: 6 sites \times 4 sampling occasions \times 7 depths). Size bins were created within the \log_{10}
113 body mass range for each site and sampling occasion (variables fitted as random effects
114 in the statistical models) and the abundance of organisms were summed within each size
115 bin and regressed against the midpoint of each bin [19]. We used the logarithmic
116 binning method for constructing size spectra [20], with equal bin widths on a log-scale.
117 The number of bins ($n = 5$) was used as it maximized the number of size bins, while
118 minimizing the number of empty size bins in the analysis [11,21]. The effects of
119 streambed depth and hydrodynamics on N–M scaling was assessed by adding depth and
120 vertical water flux as continuous covariates, as well as the interaction between them and
121 with body mass, in the model equation. Detailed explanations of the binning method,
122 model fitting and model validation is provided in the Supplementary methods.

123

124 **3. Results and discussion**

125 Over 5 orders of magnitude in body mass from flagellates to macroinvertebrates,
126 abundance declined linearly (Fig 1a) with an average size spectra slope of -1.5 (Table
127 1). This slope [$N \sim M^{-1.5}$ (95% CI: -1.6,-1.4)] is much steeper than the generally assumed value
128 of -0.75 or -1 within and across trophic levels, respectively [17]. Even when restricting
129 our analysis to the top 5-cm depth and under downwelling conditions (the least
130 constricting conditions), this observation was consistent (slope = -1.4, 95%CI: -1.5, -
131 1.3). Therefore, our results support the notion that streambed and groundwater habitats
132 are characterised by strongly size–structured communities [3,22].

133 As predicted, N–M intercept (carrying capacity) and slope (energy flow and the
134 trophic transfer efficiency) were dependent upon depth and vertical hydrodynamics
135 (Table 1). We found that the N–M intercepts were higher and slopes were indeed
136 shallower under downwelling conditions (Fig 1a) and in the top sediment layers

137 (benthic zone; Fig 1b), while intercepts decreased and spectrum slopes exhibited a sharp
138 decline under upwelling conditions and at deeper sediment layers (hyporheic zone).
139 Moreover, both predictors showed a synergic interaction (i.e., the combined effect was
140 more than the sum of its parts), on the N–M slope (Table 1). These results are consistent
141 with the reduction in resource supply (e.g. oxygen) with depth and under upwelling
142 conditions, which exert a greater selective constraint on large body–size classes [12,13].
143 We also verified whether our results were independent of the truncation of size spectra
144 with depth – i.e. the largest body size organisms were not present at deeper sediment
145 layers. For this purpose, we repeated the analysis including only communities from the
146 upper 15 cm of the sediment – communities that spanned the full range of body size
147 bins (Table S1) – obtaining similar results (Table S2). Given that metabolic rates scale
148 with body size [25], and in the light of the decline in N–M intercepts with depth, the
149 streambed assemblage also tends to be metabolically less active with increasing
150 sediment depth. Crucially, our study shows that this is offset to some extent under
151 down–welling conditions where the greater supply of resources allows larger organisms
152 to persist [12,13,16,26].

153 Under equilibrium conditions, the slope of the size spectrum is expected to be
154 described by the model: $N = M^\lambda \times M^{\log(\text{TE}) / \log(\text{PPMR})}$, where N is abundance of a given
155 size class, M is body mass, λ is abundance–body mass scaling exponent within trophic
156 levels, TE is transfer efficiency and PPMR is the predator–prey mass ratio [23].
157 Therefore an alternative explanation for the generally steep size spectra slopes observed
158 in this study could be related to the trophic structure of the streambed community and
159 changes in PPMR. Given the mean slope [$N \sim M^{-1.5}$ (95% CI: -1.6,-1.4)] we observed and a
160 TE and λ value of 0.1 and -0.75, respectively [24], predator–prey mass ratios would be
161 on average approximately 10:1 for this system. Such values are much lower than that
162 observed for stream invertebrates [11] and lower than those expected from known
163 predator–prey pairs in this study [e.g. Nematoda (mean = $3.5 \pm \times 10^{-1}$ mg/C) feeding on
164 ciliates (mean = 2.3×10^{-5} mg/C)]. We propose therefore that differences in the trophic
165 structure of streambed communities is unable to fully explain the steep N–M scaling in
166 this study, but instead the reduction of resources with depth and upwelling conditions
167 play a pivotal role in constraining the size structure of the streambed community.

168 The strong patterns reported here highlights that streambed communities become
169 strongly size–structured as a consequence of the interplay between depth and negative
170 vertical hydrodynamics, at least in lowland streams with sandy sediments. This

171 reduction in the number of large organisms also implies a concomitant reduction in the
172 metabolic capacity of the system. These findings therefore highlight important
173 constraints that govern the functioning of the sediments in streams and rivers that are
174 key sites of intense biochemical turnover (including nutrients and pollutants) sustained
175 and maintained by the metabolisms of the communities inhabiting them (see [16]). Our
176 findings might therefore help explain why the biochemical turnover rates decrease
177 markedly with depth [27], however, future research considering large-scale approaches
178 is needed to extrapolate our findings to a more global context.

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181 5. References

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271 **Table 1.** Summary table of the fitted abundance-body mass regression (fixed
 272 coefficients). Fixed coefficients (*Coef*), standard errors (*SE*), degrees of freedom (*DF*),
 273 *t*-values and P-values (*P*). Significance codes (*Sig*): 0 (***), 0.001 (**). A
 274 Satterthwaite approximation was used to calculate the effective degrees of freedom.

Fixed equation terms	Coef	SE	DF	t-value	P-value	Sig
Intercept	3.41	0.07	4.60	51.74	> 0.001	***
Log ₁₀ Body mass	-1.52	0.04	391.07	-37.74	> 0.001	***
Depth	-0.57	0.04	393.20	-13.78	> 0.001	***
Hydrodynamics (UW)	-0.33	0.09	3.89	-3.48	0.02	*
Log ₁₀ Body mass × Depth	-0.34	0.04	391.42	-10.06	> 0.001	***
Log ₁₀ Body mass × Hydrodynamics (UW)	-0.16	0.06	392.76	-2.51	> 0.02	*
Depth × Hydrodynamics (UW)	-0.16	0.07	394.10	-2.35	> 0.02	*

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296 **Figure caption**

297 **Fig 1:** Multi-panel showing the results from the multiple linear regression of Log_{10} total
298 abundance on Log_{10} body mass bin, and the effects of vertical water flux (a) and depth
299 (b). In panels 'a' and 'b', each data point ($n = 457$) denotes the abundance of a given
300 size class for each sampling unit. The fitted lines in panel 'a' represent the average N-M
301 slope for upwelling (UW) and downwelling (DW) conditions, derived from the linear
302 mixed effect model. Note that the four obvious groups of data points in the panel
303 correspond to flagellates, ciliates and invertebrates meiofauna and macroinvertebrates.
304 The fitted lines in panel 'b' represent the average N-M slope in the upper sediment
305 layers (marked as BZ: benthic zone), and deeper sediment layers (marked as HZ:
306 hyporheic zone). The median value of depth (10 cm) was used as the midpoint between
307 BZ and HZ to simplify interpretation. Note that depth is a continuous covariate with a
308 three-dimensional relationship with the N-M intercept and slope (3d plot insert at the
309 top of panel b).

