

1

2 **Uniting discoveries of abundance-size distributions from soils and seas**

3 Leonard V. Polishchuk<sup>1</sup> and Julia L. Blanchard<sup>2</sup>

4 <sup>1</sup>Department of General Ecology, Biological Faculty, M.V. Lomonosov Moscow State

5 University, Moscow, 119991, Russia

6 <sup>2</sup>Institute for Marine & Antarctic Studies & Centre for Marine Socioecology, University of

7 Tasmania, 20 Castray Esplanade, Hobart, TAS 7001, Australia

8

9 Corresponding author:

10

11 Keywords: biomass equivalence rule, body mass, macroecology, size spectrum

12

13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37

Abstract: Science is a search for patterns but there are few cross-habitat patterns in ecology. We propose key questions following the findings of consistent scaling of abundance versus body mass from bacteria to earthworms and whales, based on an almost forgotten study of soils and a well-known one from the open-ocean.

Sheldon and co-authors [1] have been widely acknowledged for their pioneering work on the size spectrum, originally sampled in open oceans and later extended to lakes. Research on the empirical size spectrum across aquatic and terrestrial realms has since grown and influenced community and food web ecology, development of global and local scale modelling of systems, and indicators for environmental management [2]. Probably because of the historical origins, size spectrum studies are still more common in aquatic ecosystems than in terrestrial ones, despite some notable exceptions (e.g. [3,4]). However, they actually began in the soil rather than in the sea. An earlier and little-known description of the relationship between numerical abundance and body size was discovered 30 years before Sheldon et al.'s seminal work. Here, we tell the story of the biomass equivalence rule, according to which there is no general trend of increasing or decreasing biomass per equal log body-size bins throughout the size range from small to large creatures. In a less precise way, this may be expressed as approximately equal biomasses contained in equal log body-size bins, as revealed by M.S. Ghilarov - a Russian soil zoologist and ecologist who made the discovery back in 1944 [5]. We also show how remarkably similar the patterns are found by Ghilarov and independently by Sheldon et al. Finally, we outline outstanding questions that could be tackled by integrative studies of aquatic and terrestrial ecosystems using a size spectrum approach.

38 The war autumn of 1943, Moscow, Russia (then Soviet Union). A young man (31 years old)  
39 submits a paper to the Reports of the Academy of Sciences of the USSR, a prestigious Russian  
40 journal though not widely available internationally. The paper is brief, just 2.5 printed pages in  
41 total, and contains a single – and impressive – plot, which suggests a strong linear relationship  
42 between log numerical abundance and log body size for the most common soil organisms, in  
43 the range from bacteria to earthworms [5]. M.S. Ghilarov states: “The biomass of soil  
44 organisms of different natural body-size groups is approximately of the same order of  
45 magnitude: the product of the number of organisms belonging to a given body-size group times  
46 their linear size cubed varies very little” [5]. No statistical justification of this statement was  
47 provided, however. For one reason or another, M.S. Ghilarov’s original insight about biomass  
48 equivalence has been forgotten and lost; it would be revived, and a proper statistical treatment  
49 would be done, only much later [6,7]. M.S. Ghilarov’s paper was well ahead of its time. In soil  
50 ecology, it has long been viewed as an early piece of evidence documenting the negative  
51 correlation between numbers and size. But in a more general, cross-habitat context involving  
52 soils and seas, it can be seen as an early example of size spectra analysis where the sign and  
53 the slope of the relationship both do matter.

54

55 Here, we have rearranged M.S. Ghilarov’s [5] plot as the numerical abundance vs. body-mass  
56 spectrum. **Fig. 1a** shows that numerical abundance is inversely proportional to body mass, with  
57 the exponent of mass being  $-0.97 \pm 0.07$ . In terms of biomass, this implies that there is no  
58 general trend, either increasing or decreasing, in the biomass of the main body-size groups of  
59 soil organisms. This does not mean that the biomasses are exactly equal; in fact, they are not,  
60 though the variability does not show any monotonic trend (**Fig. 1b**). In addition, the groups  
61 span approximately equal intervals on a log body-size scale; for example, log transformed  
62 body-size ranges of myriapods, collembolans (springtails) and potworms (Enchytraeidae) are

63 0.30, 0.27, 0.30, respectively (measured in terms of  $\sigma$  for species body-size distributions, see  
64 [7] for detail). This ultimately justifies the above formulation of the biomass equivalence rule.

65

66 The biomass equivalence rule was independently re-discovered by Sheldon et al. [1] for a  
67 different array of organisms living in a distinct environment, the pelagic open ocean. If  
68 presented in a way similar to that for Ghilarov's, Sheldon et al.'s data show a remarkably  
69 similar pattern (**Fig. 1c, d**). The body-mass exponent here,  $-1.04 \pm 0.04$ , is also close to  $-1$ ,  
70 implying no monotonic trend in biomass in the range from bacteria to whales. In addition, the  
71 main pelagic groups considered by Sheldon et al. occupy approximately equal intervals on a  
72 logarithmic body-size scale. The striking agreement between M.S. Ghilarov's and Sheldon et  
73 al.'s findings reinvigorates at least three outstanding questions in ecology.

74

75 *What are the mechanisms that give rise to this universal pattern?* The consistency of size  
76 spectra both for land and sea suggests that the pattern is quite universal; hence, it should be  
77 associated with rather general mechanisms and processes [8]. A range of mechanisms has been  
78 studied that could give rise to this pattern including metabolic theory which explains the minus  
79 1 slope of size spectra (numerical abundance vs. body mass) through the size-structured  
80 transfer of energy and consumer-prey interactions along a simple trophic chain [9,10].  
81 Although size-structured predation fits well in pelagic ecosystems, it may not apply to soils  
82 because many soil invertebrates, such as those representing M.S. Ghilarov's size groups  
83 (earthworms, millipedes among myriapods, some insect larvae, springtails, potworms, and  
84 nematodes; see Fig. 1a, b), are largely or entirely detritivorous and thus do not comprise a direct  
85 trophic chain. However, more detailed dynamic size spectrum theory explicitly incorporates  
86 species and size-structured networks interactions without each size class needing to consume  
87 the one directly below it [2]. Moreover, other mechanisms may be at play such as habitat

88 structure or the assembly of multiple species' power laws [11]. Whether a single general  
89 mechanism is driving this universal pattern or some set of mechanisms and processes acting in  
90 combination needs to be addressed to advance our understanding, given the pattern's cross-  
91 habitat scope.

92

93 ***At which scales does biomass equivalence apply?*** While apparently universal in terms of  
94 milieu, the biomass equivalence rule has the limits of applicability with respect to scale. Here,  
95 both on land and in the sea biomass equivalence arises on large, macroecological spatial scales.  
96 The Ghilarov data originate from several continents (Europe, Asia, North America) and  
97 climatic zones, and the Sheldon et al. data come from the vast areas of the equatorial Pacific  
98 and the Antarctic. Whether or not this pattern holds in local ecosystems such as a small patch  
99 of land, a pond or a lake remains an open question; in general, the answer seems 'no'. Biomass  
100 equivalence occurs predominantly at large spatial scales but it remains unclear where the  
101 boundary lies between the large and the small. To answer this question, we need to determine  
102 the relationship between the slope of size spectra and the magnitude of scale. We envision that  
103 the slope would vary widely at small scales (it may be even positive [12]) and converges to  $-1$   
104 at sufficiently large scales. The relationship will contribute to better understanding of the  
105 fundamental aspects of size spectra, making it possible to operationally define spatial scales  
106 where biomass equivalence normally applies. Additionally, at larger scales, inclusion of size  
107 into estimates of biomass could complement recent efforts to census the biomass distribution  
108 of all life on Earth [13].

109

110 ***How can size spectra inform environmental management on land and sea?*** Theoretical size  
111 spectra are often used as a benchmark to compare them with the observed spectra, and the shift  
112 is interpreted as due to anthropogenic pressures [14]. We suggest that this approach will

113 provide more reliable information on human impact when size spectra are examined at the large  
114 spatial scale. Moreover, the above knowledge of the appropriate spatial scale could assist in  
115 the use of ongoing monitoring programmes for comparing perturbed and unperturbed size  
116 spectra. Empirical size spectrum analyses of soils are already being used to monitor impacts of  
117 human activities [3,4]. We suggest that development of dynamic size spectrum models in  
118 terrestrial systems, while appropriately accounting for different body-size groups as shown in  
119 the Ghilarov example, could help to yield new knowledge of the combined impacts of  
120 agriculture intensity and other drivers such as climate change. The understanding that land and  
121 sea size spectra have more in common than previously thought should open new avenues of  
122 integrative research into fundamental and applied aspects of size spectra.

123

#### 124 **Acknowledgments**

125 L.V.P. was supported by the Russian Foundation for Basic Research (grant 18-04-01143).  
126 J.L.B. acknowledges Australian Research Council (Discovery Grant DP170104240 “Rewiring  
127 Marine Food Webs”). Both authors thank Iliya Kopnin for digitizing M.S. Ghilarov’s original  
128 figure and Kira Askaroff for illustrations.

129

130

131 **References**

132

- 133 1 Sheldon, R.W. *et al.* (1972) The size distribution of particles in the ocean. *Limnol.*  
134 *Oceanogr.* 17, 327–340
- 135 2 Blanchard, J.L. *et al.* (2017) From bacteria to whales: using functional size spectra to  
136 model marine ecosystems. *Trends Ecol. Evol.* 32, 174-186
- 137 3 Mulder, C. and Elser, J.J. (2009) Soil acidity, ecological stoichiometry and allometric  
138 scaling in grassland food webs. *Global Change Biol.* 15, 2730–2738
- 139 4 Turnbull, M.S. *et al.*(2014) Weighing in: size spectra as a standard tool in soil  
140 community analyses. *Soil Biol. Biochem.* 68, 366–372
- 141 5 Ghilarov, M.S. (1944) Correlation between size and number of soil animals. *Dokl.*  
142 *Akad. Nauk* 43, 283-285
- 143 6 Tseitlin, V.B. (1986) Energetics of Deep-SeaPelagic Communities, Nauka
- 144 7 Polishchuk, L.V. (2018) M.S. Ghilarov’s principle, or biomass equivalence rule, as one  
145 of conservation laws in ecology. *Zh. Obshch. Biol.* 79, 183-200
- 146 8 Connolly, S.R. *et al.* (2017) Process, mechanism, and modeling in macroecology.  
147 *Trends Ecol. Evol.* 32, 835-844
- 148 9 Brown, J.H. and Gillooly, J.F. (2003) Ecological food webs: high-quality data  
149 facilitate theoretical unification. *Proc. Natl. Acad. Sci. U. S. A.* 100, 1467–1468
- 150 10 Jennings, S. and Mackinson, S. (2003) Abundance-body mass relationships in size-  
151 structured food webs. *Ecol. Lett.* 6, 971–974
- 152 11 Rinaldo, A. *et al.* (2002) Cross-scale ecological dynamics and microbial size spectra in  
153 marine ecosystems. *Proc. Biol. Sci.* 269, 2051–2059
- 154 12 Trebilco, R. *et al.* (2016) The paradox of inverted biomass pyramids in kelp forest fish

155 communities. *Proc. R. Soc. B* 283 DOI: 10.1098/rspb.2016.0816

156 13 Bar-On, Y.M. *et al.* (2018) The biomass distribution on Earth. *Proc. Natl. Acad. Sci.*  
157 *U. S. A.* 115, 6506–6511

158 14 Jennings, S. and Blanchard, J.L. (2004) Fish abundance with no fishing: Predictions  
159 based on macroecological theory. *J. Anim. Ecol.* 73, 632–642

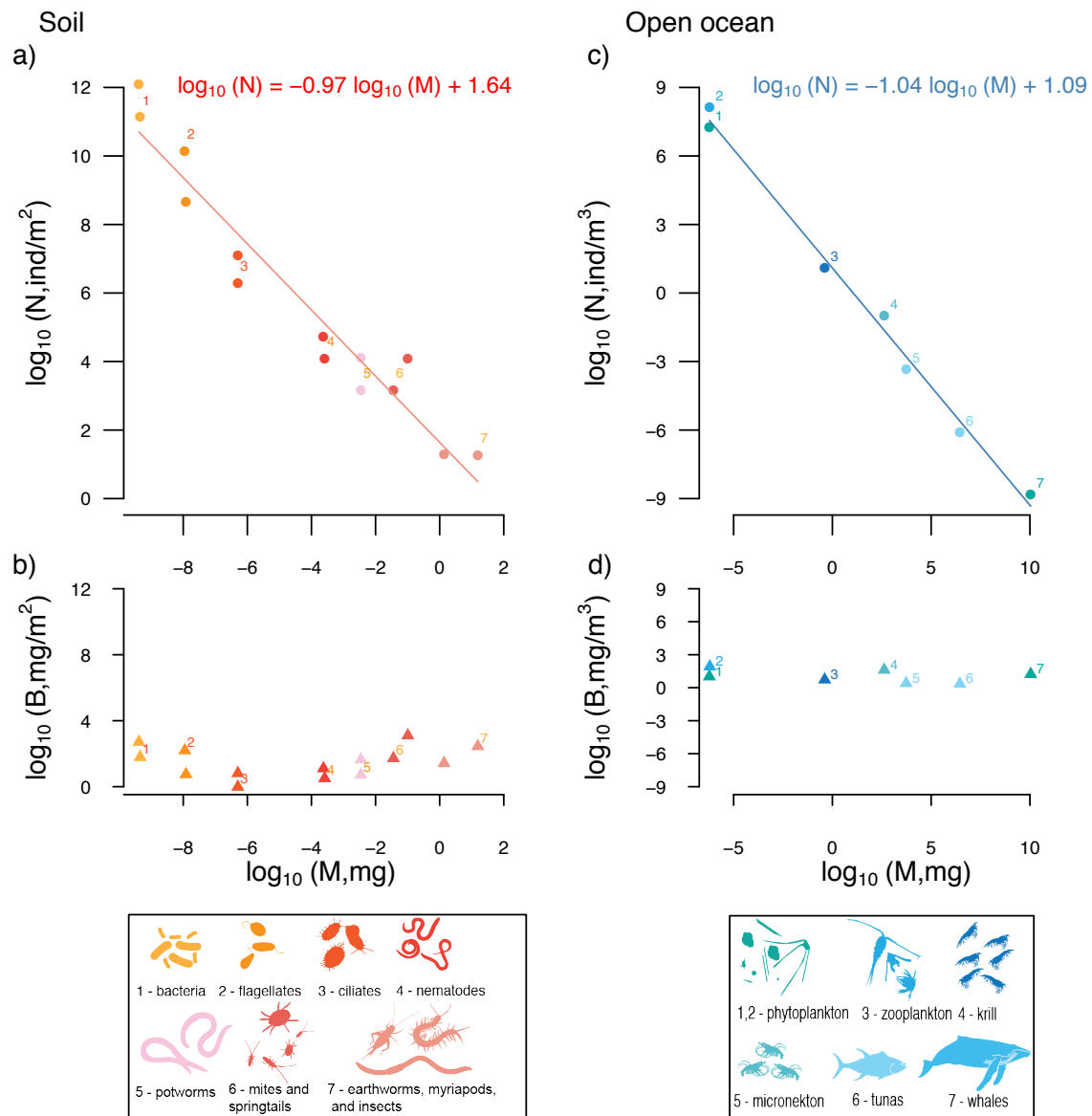
160

161

162



163 **Figure 1. Size spectra in soils and seas demonstrate biomass equivalence.** The relationships  
164 between numerical abundance  $N$  and biomass  $B$  vs. body mass  $M$  of body-size or taxonomic  
165 groups for soil (**a**, **b**) and open ocean pelagic (**c**, **d**) organisms based on Ghilarov's [5] and  
166 Sheldon et al.'s [1] data, respectively. The  $\log_{10}(N) - \log_{10}(M)$  relationships are highly  
167 significant ( $r^2$  is 0.94 and 0.99 for **a** and **c**, respectively;  $P < 0.001$  in both cases). The  $\log_{10}(B)$   
168 is calculated as the sum of  $\log_{10}(N)$  and  $\log_{10}(M)$  and presented here by way of illustration.  
169 The scale of the Y-axis in panels **b** and **d** is made the same as the scale of the Y-axis in panels  
170 **a** and **c**, respectively, to visualize the variation in biomass as compared with the variation in  
171 numerical abundance; the former is much smaller than the latter. For panels **a** and **b**, the data  
172 were taken from Ghilarov's figure, a single one in the paper, which was digitized using the  
173 program ImagePro. The original figure depicts the groups' numerical abundance vs. body  
174 length; the former was used directly while the latter was transformed to body mass using a  
175 mass-length relationship from Tseitlin [6]. Here, as well as in the original data, each group is  
176 represented by a pair of points to characterize the variability within the group. The abundance  
177 and biomass refer to the 0-~25 cm soil layer. For panels **c** and **d**, the data were taken from  
178 Sheldon et al.'s Figure 12, which was digitized. The original figure shows the groups' biomass  
179 vs. body-size range where body size is expressed as equivalent spherical diameter. The mean  
180 diameter found from the body-size range was transformed into body volume and body mass,  
181 given the organisms' body density of  $1\text{ g}\cdot\text{cm}^{-3}$ ; numerical abundance was calculated as the ratio  
182 of the groups' biomass over body mass. Note that Sheldon et al.'s figure presents data for the  
183 equatorial Pacific and the Antarctic separately; here we combine them on one plot. Data points  
184 2, 4 and 7 refer to the Antarctic, and 1, 3, 5 and 6 to the Pacific.



185

186 **Figure 1**

187