



## Upscaling river biomass using dimensional analysis and hydrogeomorphic scale-invariance

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[1] We propose a methodology for upscaling biomass in a river using a combination of dimensional analysis and hydro-geomorphologic scaling laws. We first demonstrate the use of dimensional analysis for determining local scaling relationships between *Nostoc* biomass and hydrologic and geomorphic variables. We then combine these relationships with hydraulic geometry and streamflow scaling in order to upscale biomass from point to reach-averaged quantities. The methodology is demonstrated through an illustrative example using an 18 year dataset of seasonal monitoring of biomass of a stream cyanobacterium (*Nostoc parmeloides*) in a northern California river. **Citation:** Barnes, E. A., M. E. Power, E. Foufoula-Georgiou, M. Hondzo, and W. E. Dietrich (2007), Upscaling river biomass using dimensional analysis and hydrogeomorphic scale-invariance, *Geophys. Res. Lett.*, *34*, L24S26, doi:10.1029/2007GL031931.

### 1. Introduction

[2] Several studies have related stream periphyton biomass to local physico-chemical characteristics [e.g., Lowe *et al.*, 1986; Mulholland *et al.*, 2001; Biggs and Gerbeaux, 1993; Biggs and Hickey, 1994; Biggs, 1995] as well as to local hydrologic regimes and trophic interactions [e.g., Power *et al.*, 1996; Wootton *et al.*, 1996; Power and Stewart, 1987; Clausen, 1997]. Algae and cyanobacteria that make up the autotrophic component of periphyton are heterogeneously distributed down river networks, so it remains difficult to quantify their reach or basin-wide abundance, distribution and metabolism. Good estimates of the abundance of algae and cyanobacteria (the primary producers that often dominate periphyton) in rivers and streams are critical for management and restoration of watersheds and water supplies, as well as basic understanding of major energy sources for river food webs.

[3] *Nostoc*, a genus of nitrogen-fixing cyanobacteria, is an important component of periphyton in temperate streams and rivers throughout the world [Prosperi, 1989; Dodds *et al.*, 1995]. Where abundant, it is likely a major source of biologically available nitrogen in ecosystems [Dodds *et al.*, 1995]. We demonstrate that a high percentage of the local

variability in the height of epilithic *Nostoc parmeloides* (45% to 71%) can be explained by hydrologic and geomorphic variables, appropriately grouped via dimensional analysis. We also propose a methodology for combining these local relationships with stream geometry and streamflow scaling to estimate reach-average biomass and its uncertainty. Since these hydro-geomorphic variables can be readily extracted (or computed via hydraulics) from high resolution topography, e.g., LiDaR airborne laser altimetry, the proposed framework offers an attractive way of estimating and upscaling biomass even in regions for which limited biological sampling is available.

### 2. Study System and Database

[4] An 18 year data set includes measurements of *Nostoc* height and physical stream variables at three cross-stream transects located approximately one kilometer apart along the South Fork Eel River within the Angelo Coast Range Reserve in northern California (Figure 1). The South Fork Eel River experiences a Mediterranean hydrologic regime, with winter floods and summer drought. Further description of this site is given by Power [1990, 1992]. Colonies of *Nostoc parmeloides* Kutzing grow attached to bedrock, boulder, and cobble substrates on the river bed. Our index of biomass is ‘height’ measuring the diameter of a colony if it was spherical, or the major diameter of an ear-shaped, midge-infested colony.

[5] Cross-stream transects were benchmarked at both ends with nails in trees or bedrock (nail to nail distance varied less than 1 cm over repeated surveys). At 0.5 m or 1.0 m intervals across the transect, water depth was measured, and surface velocity was estimated. The modal height of *Nostoc* colonies within an estimated 10 × 10 cm<sup>2</sup> area around each sampling point on the substrate was recorded (Power [1992] and Power and Stewart [1987] give further methodological details). *Nostoc* height and stream cross-sectional variables were measured 3 to 20 times each year from 1988–2005 during the growing season (April–August). Table 1 shows the different variables used in this study along with their definitions. It is noted that *Nostoc* biomass can be predicted from the height of the colony through empirical relationships (e.g., M. E. Power, unpublished manuscript, 2006) but these relationships are not directly used in the present study.

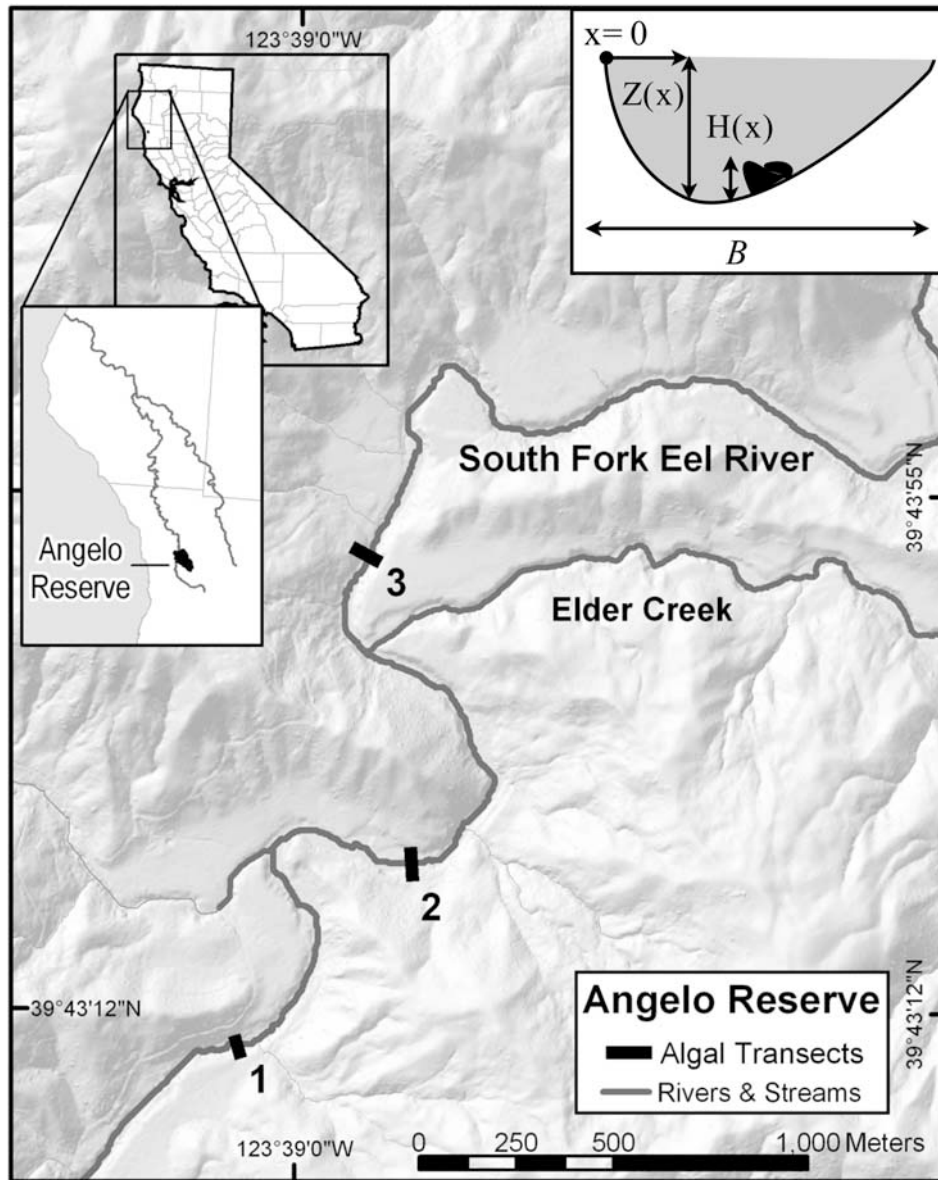
[6] Solar radiation (RAD) was measured at the ORLAND2.A weather station (operated by the University of California) approximately 80 miles from the transects. River discharge was measured at the USGS Branscomb gage (USGS 11475500), a decommissioned USGS gage that was reactivated in 1990 by Angelo Reserve researchers,

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**Figure 1.** Three transects (1, 2, 3) in the South Fork Eel River, Mendocino County, CA. Transect 1 is the southern most (farthest upstream), while transect 3 is the northern most (farthest downstream) transect. The inset shows a cross-section with relevant variables.

97 and is located just south of transect 1. Gaps in the hydro-  
 98 logic record from this station were filled with a scaling  
 99 relationship between discharge at USGS Elder Creek gaging  
 100 station (USGS 11475560) 4 km away from the Branscomb  
 101 gage on a major tributary of the South Fork Eel.

102 **3. Terminology and Framework of Analysis**

103 [7] All variables considered in this study are referenced  
 104 by a location along the river network ( $s$ ), a location ( $x$ )  
 105 across the considered transect (stream cross-section) and  
 106 time ( $t$ ) (see Figure 1). If we denote such a generic variable  
 107 by  $\xi(s, x, t)$ ,  $s$  can be an indexed variable representing the  
 108 transects 1, 2, and 3;  $x$  varies between zero (at the left most  
 109 position of the cross-section of the transect) and  $B(t)$ , where  
 110  $B(t)$  represents the cross-section wetted channel width at  
 111 time  $t$ .

[8] Given the limited data available to quantify environ- 112  
 113 mental controls, a representative quantity for the whole  
 114 transect is defined as the arithmetic average over all data  
 115 across the transect. We denote the cross-sectional-averaged  
 116 quantity with an overbar,

$$\bar{\xi}(s, t) = \frac{1}{B(t)} \int_0^{B(t)} \xi(s, x, t) dx. \quad (1)$$

We relate cross-sectional averaged *Nostoc* colony height, 118  
 119  $\bar{H}(s, t)$ , to groups of key geomorphic, hydrologic, and other  
 120 environmental variables which can be observed or esti-  
 121 mated. In general, at any transect

$$\bar{H}(s, t) = f_1 [V_g(s^\pm, t^-), V_h(s^\pm, t^-), V_e(s^\pm, t^-)] \quad (2)$$

t1.1 **Table 1.** Definitions of Variables

t1.2	Variable	Dimensions	Units	Range <sup>a</sup>	Description
t1.3	$\bar{H}(t)$	$L$	m	0.001–0.10 (0.005) [0.005]	transect-average <i>Nostoc</i> height at time t
t1.4	$\bar{Z}(t)$	$L$	m	0.06–0.70 (0.28) [0.26]	transect-average water depth at time t
t1.5	$\bar{U}(t)$	$LT^{-1}$	m/s	0.05–1.61 (0.45) [0.42]	transect-average velocity at time t
t1.6	$B(t)$	$L$	m	3.00–27.0 (13.5) [8.31]	width of transect at time t
t1.7	$RAD$	$MT^{-3}$	kg/s <sup>3</sup>	186–715 (260) [303]	average solar radiation (past 45 days)
t1.8	$\rho(t)$	$ML^{-3}$	kg/m <sup>3</sup>	992–998 (996.33) [995.51]	water density ( $\propto$ temp) at time t
t1.9	$\bar{U}_{\max}$	$LT^{-1}$	m/s	0.04–6.88 (1.32) [0.48]	transect-maximum velocity (past 45 days)

t1.10 <sup>a</sup>Spring median in parentheses, summer median in brackets.

123 where  $f_1$  is a function,  $V_g$  denotes a vector of geomorphic  
 124 variables,  $V_h$  a vector of hydrologic variables, and  $V_e$  a  
 125 vector of other environmental variables such as light,  
 126 temperature and nutrient concentration. In the above  
 127 relationship,  $s^{\pm}$  denotes a location in the vicinity of location  
 128  $s$  (it would be mostly upstream although a dependence on an  
 129 immediately downstream junction might be possible), and  
 130  $t^-$  denotes time t and previous times, e.g. dependence on  
 131 maximum flow in the previous week or dependence on light  
 132 not only during the specific day of measurement, but during  
 133 a previous period of time. A dependence on a vector of  
 134 biotic variables,  $V_b(s^{\pm}, t^-)$ , such as grazing could also be  
 135 added in the above equation but it is not considered in this  
 136 study.

137 [9] We assume the geomorphic vector  $V_g$  to be composed  
 138 of  $B$  (channel width) and  $\bar{Z}$  (channel-averaged depth)  
 139 (Figure 1); the hydrologic vector  $V_f$  to be composed of  $Q$   
 140 (cross-section average flow) and  $Q_{\max}$  (maximum flow over  
 141 a pre-specified antecedent period), and the environmental  
 142 vector  $V_e$  to be composed of  $RAD$  (daily global radiation in  
 143  $W/m^2$ ) and water density as a function of temperature ( $\rho$ ).  
 144 From this point on, the time dependence of each variable is  
 145 implicitly assumed in each equation.

#### 146 4. Dimensional Analysis

147 [10] The theory of dimensional analysis is elaborated in  
 148 many textbooks [e.g., *Potter et al.*, 2002]. The purpose of  
 149 the analysis is to formulate useful dimensionless groups of  
 150 variables to describe a process and to establish a basis for  
 151 similarity between the processes on different time and space  
 152 scales [*Warnaars et al.*, 2007]. In this paper we use this  
 153 technique to determine dimensionless groups that provide a  
 154 basis for explaining *Nostoc* height at different years and  
 155 transects. The variables chosen for our relationship and their  
 156 dimensions are given in Table 1. Our generic scaling  
 157 function takes the following form:

$$\bar{H} = f_2(\bar{Z}^a, B^b, \bar{U}^c, RAD^d, \bar{U}_{\max}^e, \rho^h). \quad (3)$$

159 Although a multivariate regression that includes all  
 160 variables in (3) is possible, the use of dimensional analysis  
 161 has the advantage of reducing the number of independent  
 162 variables and resulting in dimension-free parameters.

163 [11] Inserting the corresponding dimensions (Table 1)  
 164 into (3), and combining equal dimensions, we obtain:

$$L = L^{a+b+c-3h+e} M^{d+h} T^{-c-3d-e} \quad (4)$$

where  $L$  is the dimension of length,  $M$  is the dimension of  
 166 mass and  $T$  is the dimension of time. Solving for the above  
 167 exponents, we derive the dimensionless model to be  
 168

$$\left(\frac{\bar{H}}{\bar{Z}}\right) = k \left(\frac{B}{\bar{Z}}\right)^{\alpha} \left(\frac{\bar{U}}{\bar{U}_{\max}}\right)^{\beta} \left(\frac{RAD}{\rho \bar{U}^3}\right)^{\gamma}. \quad (5)$$

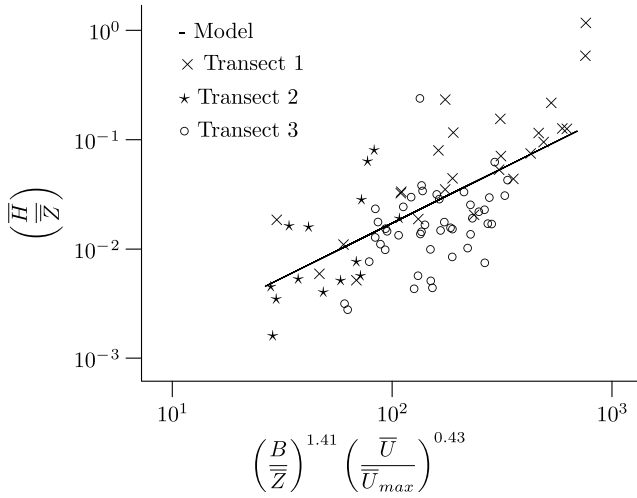
The first dimensionless group to the right of the equal sign  
 170 represents an important geomorphic characteristic of the  
 171 stream cross-section: width ( $B$ ) to depth ( $\bar{Z}$ ) ratio. As the  
 172 width to depth ratio of the channel increases, light becomes  
 173 more available to *Nostoc*, which, as a nitrogen-fixing  
 174 autotroph, has a high demand for photosynthetically derived  
 175 carbon energy. The next dimensionless group captures the  
 176 cyanobacterium's dependence on moderate (numerator) and  
 177 high (denominator) stream velocities. Under moderate flow  
 178 velocities, *Nostoc*, like other attached stream autotrophs,  
 179 benefits from increasing velocities (increasing flows  
 180 increase delivery of nutrients and removal of waste  
 181 products) up to a certain threshold, beyond which scouring,  
 182 detachment and export occur [*Whitford and Schumacher*,  
 183 1964; *Hondzo and Wang*, 2002]. The final dimensionless  
 184 group is the ratio between solar power ( $RAD$ ) and stream  
 185 power per unit stream bed area ( $\rho \bar{U}^3$ ). The exponents  $\alpha$ ,  $\beta$ ,  
 186  $\gamma$  and constant  $k$  must be determined by fitting (5) with our  
 187 data.  
 188

#### 189 5. Scaling of *Nostoc* Height

[12] During spring, *Nostoc* colonies re-establish follow-  
 190 ing winter flood scour, and colonies grow, then senesce,  
 191 during summer. We separated the analysis into two groups:  
 192 biomass establishment in the spring (April–May) and  
 193 growth accrual in the summer (June–August). We estimated  
 194 the parameters of (5) using a weighted linear regression on  
 195 the logs, with the best fit defined as the minimum sum of  
 196 squares of the errors and weights inversely proportional to  
 197 the number of measurements that season. Different time  
 198 lags were investigated for the definition of  $\bar{U}_{\max}$  (see Table 1  
 199 for definition), and the highest  $R^2$  was obtained for a time  
 200 lag of 45 days.  
 201

[13] Comparing our data and the proposed scaling rela-  
 202 tionship (5), we found that the third dimensionless group  
 203 ( $RAD/\rho \bar{U}^3$ ) contributed an insignificant amount to explain-  
 204 ing the variability of the data and it was eliminated from the  
 205 model. Figure 2 shows the results for transects 1, 2 and 3  
 206 over the two seasons. Table 2 shows the results of six other  
 207 scaling relationships for various seasons and transect  
 208 combinations. It appears that transects 1 and 2 behave quite  
 209





**Figure 2.** *Nostoc* height over three transects in the spring and summer (April–August) over the 18 years of record. Weighted least squares results in the scaling relationship  $\left(\frac{\bar{H}}{\bar{Z}}\right) = 1.7 \times 10^{-4} \left(\frac{\bar{B}}{\bar{Z}}\right)^{1.41} \left(\frac{\bar{U}}{\bar{U}_{max}}\right)^{0.43}$  with an  $R^2 = 0.45$ .

210 similarly, for 71% of their variability over all seasons was  
 211 accounted for. *Nostoc* height at transect 3 did not follow  
 212 the trend depicted by transects 1 and 2, and there are two  
 213 possible reasons for this. First, transect 3 is located down-  
 214 stream of a major tributary. Second, while transects 1 and 2  
 215 have similar valley geometries (symmetric with a slope of  
 216 approximately 1:8) and thus receive comparable amounts of  
 217 direct sunlight each day, the flat topography flanking the  
 218 western shore of transect 3 increased its daily period of  
 219 insolation. The RAD variable was not able to account for  
 220 these differences as it was not transect specific and our results  
 221 show that this radiation variability is not explainable via  
 222 channel geometry alone (see Table 2 where a lower  $R^2$  was  
 223 found especially in the summer for transect 3).

## 226 6. A Framework for Upscaling Local Biomass

227 [14] Consider a hypothetical stream reach of 10 km  
 228 length for which *Nostoc* height observations are available  
 229 only at a few locations. How is one to estimate the *Nostoc*  
 230 biomass along the entire stream from the available  
 231 observations?

232 [15] Suppose that the *Nostoc* cross-sectional average  
 233 colony height is scaled by the previously discussed local  
 234 relationship (5):

$$\bar{H}(s) = k \cdot B(s)^\alpha \cdot \bar{Z}(s)^{1-\alpha} \cdot \left(\frac{\bar{U}(s)}{\bar{U}_{max}(s)}\right)^\beta \quad (6)$$

236 The reach-averaged biomass over a stream reach of length  
 237  $\Delta s$ ,  $\langle \bar{H}(\Delta s) \rangle$ , is defined as

$$\langle \bar{H}(\Delta s) \rangle = \frac{1}{\Delta s} \int_{s_0}^{s_0+\Delta s} \bar{H}(s) ds. \quad (7)$$

239 Due to the nonlinearity of (6),  $\langle \bar{H}(\Delta s) \rangle$  cannot be estimated  
 240 from (6) and (7) by substituting in the reach-averaged  
 241 quantities  $\langle B(s) \rangle$ ,  $\langle \bar{Z}(s) \rangle$ , etc. Instead, one must perform

integration of (7) by properly acknowledging how each of  
 the variables varies along the stream.

[16] *Leopold and Maddock* [1953] demonstrated that  
 $B(s)$ ,  $\bar{Z}(s)$  and  $\bar{U}(s)$  relate to streamflow  $Q(s)$  at location  $s$   
 via the so-called hydraulic geometry (HG) relationships:

$$B(s) \propto Q(s)^{m_1} \quad (8)$$

$$\bar{Z}(s) \propto Q(s)^{m_2} \quad (9)$$

$$\bar{U}(s) \propto Q(s)^{m_3} \quad (10)$$

where  $m_1 + m_2 + m_3 = 1$ . These relationships apply to a  
 specific location for varying flows (at a station HG) or at  
 several locations along a stream for a flow of specific  
 frequency (downstream HG). Since our interest is in  
 integration along a stretch of the stream at a specific instant  
 of time, the downstream HG is relevant for all quantities  
 except for the maximum velocity  $\bar{U}_{max}(s)$  which is  
 considered to result from an extreme flood (e.g., of a  
 specified exceedance probability) at each location and thus  
 at a station HG,  $\bar{U}_{max}(s) \propto Q_{max}(s)^{m'_3}$  needs to be  
 employed. The exponents  $m_1$ ,  $m_2$ ,  $m_3$  and  $m'_3$  can be  
 estimated locally (if high resolution topography data are  
 available) or determined using regional relationships [e.g.,  
 see *Singh*, 2003]. Substituting these scaling relationships  
 into (6), one obtains,

$$\bar{H}(s) = k' \cdot Q(s)^{M_1} Q_{max}(s)^{-M_2} \quad (11)$$

where  $M_1 = m_1\alpha + m_2(1 - \alpha) + m_3\beta$  and  $M_2 = m'_3\beta$ . By  
 further introducing the known discharge-drainage area  
 scaling relationships [e.g., see *Gupta and Dawdy*, 1995]

$$Q(s) \propto A(s)^{\theta_1} \quad (12)$$

$$Q_{max}(s) \propto A(s)^{\theta_2} \quad (13)$$

where  $\theta_1$  and  $\theta_2$  are exponents dependent on flood  
 frequency and watershed characteristics, we obtain

$$\bar{H}(s) = k'' \cdot A(s)^p \quad (14)$$

where  $p = \theta_1 M_1 - \theta_2 M_2$ . Equation (14) is an approximation  
 of *Nostoc* height at a single transect as a function of

**Table 2.** Scaling Relationships With  $R^2$  Values for Combinations  
 of Transects and Seasons<sup>a</sup>

Transects and Seasons	$\alpha$	$\beta$	$k$	$R^2$
T-1,2,3 spring & summer	1.41	0.43	$1.7 \times 10^{-4}$	0.45
T-1,2 spring & summer	1.54	0.54	$1.8 \times 10^{-4}$	0.71
T-3 spring & summer	0.90	0.47	$6.9 \times 10^{-4}$	0.21
T-1,2 spring	1.70	0.69	$0.6 \times 10^{-4}$	0.83
T-3 spring	0.14	0.40	$172.8 \times 10^{-4}$	0.57
T-1,2 summer	1.79	0.62	$0.8 \times 10^{-4}$	0.71
T-3 summer	0.61	0.52	$18.0 \times 10^{-4}$	0.22

<sup>a</sup>Functions are of the form  $\left(\frac{\bar{H}}{\bar{Z}}\right) = k \left(\frac{\bar{B}}{\bar{Z}}\right)^\alpha \left(\frac{\bar{U}}{\bar{U}_{max}}\right)^\beta$ . The amount of  
 variability accounted for by scaling is determined by the  $R^2$  value, as  
 defined by *Draper and Smith* [1981].

279 upstream drainage area  $A(s)$  only, which is easy to extract  
 280 from maps or digital elevation models. As such, it  
 281 represents a derived “biological” scaling relationship akin  
 282 to the hydrologic scaling relationships discussed above,  
 283 which have found extensive use in hydrology (prediction in  
 284 ungauged basins and regionalization).

285 [17] Equation 14 can be further explored for upscaling  
 286 purposes by noting that  $A(s)$  can be related to length  $L(s)$   
 287 (from the watershed divide to location  $s$ ) using a variant of  
 288 Hack’s law [e.g., *Rigon et al.*, 1996] for nested basins,  $A(s)$   
 289  $\propto L(s)^\delta$ . Combining this with (14) and inserting it into (7),  
 290 we obtain

$$\langle \bar{H}(\Delta s) \rangle = k^* \cdot \frac{[L^{m+1}(s_0 + \Delta s) - L^{m+1}(s_0)]}{(m+1)\Delta s} \quad (15)$$

291 where  $m = \delta(\theta_1 M_1 - \theta_2 M_2)$ .

293 [18] The above relationship quantifies the dependence of  
 294 reach-averaged biomass on reach length  $\Delta s$ , where the  
 295 reach starts at an arbitrary location  $s_0$ . Assuming without  
 296 loss of generality that  $s_0 = 0$  (i.e.  $L(s_0) = 0$  and  $L(\Delta s) = \Delta s$ ),  
 297 and considering two reaches of lengths  $\Delta s_1$  and  $\Delta s_2$ , the  
 298 above relationship results in

$$\frac{\langle \bar{H}(\Delta s_1) \rangle}{\langle \bar{H}(\Delta s_2) \rangle} = \left( \frac{\Delta s_1}{\Delta s_2} \right)^m \quad (16)$$

299 As an illustrative example, let  $m_1 = 0.5$ ,  $m_2 = 0.4$ ,  $m_3 = 0.1$   
 301 and  $m'_3 = 0.3$  (as defined by *Leopold and Maddock* [1953];  
 302 see also *Singh* [2003]),  $\theta_1 = 1$  and  $\theta_2 = 0.7$  [see *Gupta and*  
 303 *Dawdy*, 1995, Table V],  $\delta = 0.58$  (as extracted by us for the  
 304 Eel River basin using LiDaR data),  $\alpha = 1.41$  and  $\beta = 0.43$   
 305 (spring and summer *Nostoc* in Table 1); then the final scaling  
 306 exponent is  $m = 0.3$ . Thus, if  $\Delta s_1 = 10$  km and  $\Delta s_2 = 1$  km  
 307 the above equation implies that *Nostoc* biomass per unit  
 308 stream length scales by a factor of  $10^{0.3} = 2.0$ . In other  
 309 words, starting from a given reference point and going  
 310 downstream, a stream reach 10 times longer has total *Nostoc*  
 311 biomass not 10 times, but 20 times larger. Of course,  
 312 biomass cannot grow unbounded and a physically-imposed  
 313 upper limit will constrain the range of applicability of the  
 314 above scaling relationship. Determining this upper limit  
 315 (empirically or mechanistically) is an issue that requires  
 316 careful study.

317 [19] There is uncertainty associated with each HG and  
 318 flow scaling exponent, and this uncertainty is separate from  
 319 the errors associated with the model’s biomass predictions.  
 320 To better understand the effects of HG related uncertainties,  
 321 we performed first order analysis of variance [see *Benjamin*  
 322 *and Cornell*, 1970] on (15) with respect to the HG  
 323 exponents  $m_1$ ,  $m_2$ ,  $m_3$ ,  $m'_3$ . Using the values given above,  
 324 and letting  $\Delta s = 1$  km, we find that a 5% uncertainty  
 325 (standard deviation) in each scaling exponent leads to a 17%  
 326 uncertainty in the reach-averaged biomass. Of course, as in  
 327 any uncertainty analysis, it is expected that considering the  
 328 uncertainty of all variables involved in the model will  
 329 reduce the power of the predictive relationship.

## 330 7. Conclusions and Caveats

331 [20] We have demonstrated that cyanobacterial biomass  
 332 scales with hydrologic and geomorphic local variables in a  
 333 river network (5). Moreover, combining this scaling rela-

334 tionship with hydraulic geometry and other geomorphic and  
 335 hydrologic scaling laws resulted in a simple nonlinear  
 336 scaling relationship of transect-averaged biomass with up-  
 337 stream drainage area (14) and stream-averaged biomass  
 338 with stream length (16). The proposed methodology, which  
 339 can be further refined in its assumptions, e.g., to consider  
 340 spatial inhomogeneity in the scaling of HG [see *Dodov and*  
 341 *Foufoula-Georgiou*, 2004], can potentially be implemented  
 342 across different drainage basins and abundances of biota.  
 343 Being able to upscale local relationships aids in the  
 344 understanding of the impacts of organisms on ecosystems  
 345 (e.g. nitrogen loading to river ecosystems by *Nostoc*) as well  
 346 as how populations are affected by landscape dynamics and  
 347 heterogeneity. It also aids in efforts to improve (target) field  
 348 sampling to develop mechanistically-based predictive  
 349 models of biota at the reach or basin-wide scale by  
 350 empirically determining the key controlling variables.

351 [21] In our upscaling example, the HG scaling exponents  
 352 were assigned “mean regional” values for illustration  
 353 purposes only. Values specific to each reach should be used  
 354 to obtain more accurate estimates and thus increase the  
 355 overall power of the predictive relationships, where the  
 356 uncertainty can be quantified within the proposed frame-  
 357 work.

358 [22] The distribution and abundance of any species reflect  
 359 not only whether the environment provides essential resour-  
 360 ces and tolerable conditions (Fundamental Niche), but also  
 361 potentially limiting ecological interactions (Realized Niche)  
 362 [*Hutchinson*, 1957]. *Nostoc* may be more predictable from  
 363 physical features of its environment than more edible  
 364 periphyton, because toxic secondary compounds and a  
 365 tough, mucilaginous sheath deter grazing on this cyano-  
 366 bacterium [*Dodds et al.*, 1995]. Future field work in our  
 367 system will estimate *Nostoc* biomass over larger areas of the  
 368 river bed, and relate reach-level biomass to hydraulic  
 369 scaling parameters and to per-area rates of biological  
 370 activity (e.g., nitrogen fixation).

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