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Characterizing Community-level Size Spectra in Piedmont Streams of Virginia
(USA)

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science
at Virginia Commonwealth University

By Giancarlo Racanelli
B.S. College of William and Mary, 2019

Thesis Director, Dr. Daniel J. McGarvey, Center for Environmental Studies

Virginia Commonwealth University

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Preface

This thesis was organized in a format suitable for publication in the peer-reviewed journal *American Midland Naturalist*, with minor modifications to comply with Virginia Commonwealth University guidelines for thesis submission.

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Abstract

CHARACTERIZING COMMUNITY-LEVEL SIZE SPECTRA IN PIEDMONT STREAMS OF VIRGINIA (USA)

By: Giancarlo Racanelli

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University

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Many aquatic communities demonstrate an inverse scaling relationship between average body mass and density. Using quantitative samples of macroinvertebrates and fishes, we modeled this relationship in three Piedmont streams where little empirical research has been conducted. The size spectra (SS) method, in which individuals are identified by size, not taxonomic identity, was used with linear regression to model density as a function of mass. Fish and benthic invertebrate samples were collected on simultaneous days during September, then used to develop community-level SS models (combined fish and invertebrate data) for each stream. Invertebrate samples were also collected from each stream in July and August, then used to assess whether fish abundance is most strongly associated with prey availability at a prior point in time. Specifically, cross-correlation (xcorr) analysis was used to determine whether the fish SS is most closely associated with the invertebrate SS when invertebrate and fish samples are collected simultaneously, or when invertebrate samples are collected one or two months prior to the fish samples. Differences in SS slopes and intercepts were rarely significant when compared among sites. This was true for SS models that were exclusive to fish or invertebrate

samples, as well as community-level models. Collectively, the SS results indicate that fish and invertebrate size structure and density are similar in each of the three study streams. Xcorr results were variable among sites and months, and did not support the hypothesis of a time-staggered link between invertebrate SS and fish SS.

1 Introduction

2 Body mass (M) and density (D) share a characteristic, inverse relationship that is often
3 used to describe the structure of aquatic communities. This $D \propto M$ scaling relationship has been
4 demonstrated at the individual level as well as higher population and community levels (Marquet
5 *et al.*, 2005), and is generally attributed to two interrelated factors: (i) the strong relationship
6 between M and metabolism, and (ii) finite resource availability (Huryñ & Benke, 2007).

7 Size-abundance studies are often based on “taxic” data; they use individual species as
8 operational units (*i.e.*, one data point per species), with a single M estimate representing average
9 body mass across all members of a given species. (White *et al.*, 2007). For example, Cyr *et al.*
10 (1997) compiled species-level M averages and D estimates for phytoplankton, zooplankton and
11 fishes from 18 lakes, then used these data to test for a global $D \propto M$ relationship. They
12 confirmed that a clear, negative $D \propto M$ relationship exists when data for all three organismal
13 groups were combined in the same regression models.

14 An alternative to the traditional, taxic $D \propto M$ approach is the size spectrum (SS). SS
15 models are fully “ataxic”; individual specimens are recognized only by their unique size, rather
16 than taxonomic identity. The key innovation of the SS approach is that it circumvents the
17 implicit assumption of taxic models that a species’ autecology remains static throughout its life
18 history (White *et al.*, 2007). Because many fish and invertebrates experience ontogenetic shifts in
19 feeding behavior, a direct focus on individual size may better account for trophic dynamics
20 within aquatic ecosystems (Allan, 1982; Mittelbach & Persson, 1998).

21 Formalized by Kerr and Dickie (2001), SS theory began with previous size-abundance
22 research characterizing plankton community structure (Sheldon & Parsons, 1967; Parsons, 1969)
23 and the standardization of this process by Platt and Denman (1977), whereby biomass within

24 each size interval was “normalized,” or divided by the width of the respective size interval
25 (Anderson *et al.*, 2016). Following Dickie and Boudreau’s (1992) previous work, Kerr and
26 Dickie (2001) focused specifically on D as a function of individual M across multiple trophic
27 levels. The resulting SS theory is built upon three interrelated concepts: (i) the conservation of
28 biomass; (ii) the allometric link between individual body size and metabolism (i.e., energetic
29 requirements); and (iii) the foundational influence of predator-prey interactions on emergent
30 community structure (Anderson *et al.*, 2016).

31 Linear regression of log-log D and M data is most often used to model the SS. In this
32 context, ecological insights are derived through two key parameters: the SS model slopes and
33 intercepts. SS model slopes can either steepen or become shallower. Steeper model slopes imply
34 that the abundance of relatively small organisms increased or that the abundance of relatively
35 larger organisms decreased. For example, SS slopes of coral reef fish assemblages steepened
36 along an increasing gradient of fishing intensity, where there were primarily reductions in larger
37 organisms (Graham *et al.*, 2005). Alternatively, shallower model slopes imply increases in
38 numbers of larger organisms or decreases in numbers of smaller organisms. SS model intercepts
39 on the other hand reflect changes in overall abundance across multiple size classes. Higher
40 intercepts reflect greater overall abundance while lower intercepts reflect diminished overall
41 abundance.

42 SS studies have been conducted in marine and lake ecosystems (*e.g.*, Rodriguez &
43 Mullin, 1986; Gaedke, 1992; Sprules, 2008), as well as lotic ecosystems. For instance, Principe
44 (2008) examined SS variation between riffle and run habitats for benthic communities in tropical
45 streams. They observed a relatively even distribution of D among differing body sizes when
46 riffles and runs were combined, reflected by SS slopes that were close to zero. However,

47 densities were highest for intermediate-sized individuals when riffle habitat samples were
 48 examined separately. Within temperate fish communities, Arranz *et al.* (2021) examined the
 49 effects of variable nutrient concentrations and non-native species' abundances on SS model
 50 parameters. They documented D increases for smaller individuals at sites that contained higher
 51 concentrations of total phosphates, without similar increases in D of large individuals, leading to
 52 steeper SS slopes. They also noted local increases in D of relatively large individuals when
 53 relative abundances of non-native species were greater. This increase in D of large individuals
 54 resulted in shallower SS slopes and was attributed to the presence of relatively large, abundant
 55 non-native species.

56 While SS studies of either lotic invertebrates or fishes are becoming more common,
 57 relatively few have explored community-level models that combine data from multiple trophic
 58 levels, such as invertebrates and fishes. This is important because theory predicts near-constant
 59 SS slopes within trophic levels, but differing slopes among trophic levels (Trebilco *et al.*, 2013).
 60 Within trophic groups, all individuals feed at the same trophic level and thus their energy use (E)
 61 is independent of their body size ($E \propto M^0$). As metabolic rate (MR) multiplied by abundance (N)
 62 is equal to energy use ($E = MR \times N$) and metabolic rate scales with $M^{-0.75}$ under Kleiber's law,
 63 then the size spectrum within a single trophic level is predicted to scale as $N \propto M^{-0.75}$. However,
 64 when comparing among trophic levels, steeper SS slopes are predicted because the transfer of
 65 energy from predator to prey is inefficient and will constrain growth and abundance of relatively
 66 large predators. Both transfer efficiency (TE) and predator:prey mass ratio (PPMR) affect the
 67 rate of energy transfer ($E \propto M^{(\log TE / \log PPMR)}$) from predator to prey; thusly, size spectra across
 68 multiple trophic levels is reflected differently by $N \propto M^{-0.75} \times M^{(\log TE / \log PPMR)}$. By accounting
 69 for these within and among trophic level differences, researchers can begin to assemble a more

70 complete understanding of the factors that regulate abundance within size-structured
71 communities.

72 Three notable examples of community-level SS studies in lotic ecosystems include Poff
73 *et al.* (1997), Huryrn and Benke (2007) and McGarvey and Kirk (2017). Poff *et al.* (1997)
74 assessed community size structure of a Piedmont stream in Virginia. They documented a
75 significant, negative linear relationship when data were combined among three distinct trophic
76 levels (meiofauna, macroinvertebrates, and fishes) in a single, community-level SS model.
77 However, no evidence of a negative linear relationship was detected when the three trophic
78 levels were modeled individually. Huryrn and Benke (2007) examined multi-trophic level D and
79 M relationships in four lotic systems and detected significant, negative linear relationships in all
80 systems. McGarvey and Kirk (2017) examined seasonal trends in SS model parameters within
81 southern West Virginia streams. They documented relatively steep, negative SS slopes during
82 spring months, reflecting high densities of small individuals. But in the fall, community-level SS
83 slopes became shallower indicative of high densities of relatively large individuals. These
84 community-level trends were attributed to asynchronous, annual growth rates of invertebrates
85 and fishes. McGarvey and Kirk (2017) also noted that the SS slopes were not significantly
86 different when comparing individual trophic levels with community-level models.

87 Drawing upon the approach of McGarvey and Kirk (2017), this study examined separate
88 SS models for invertebrate and fish assemblages, as well as combined community-level models,
89 in three eastern U.S., Piedmont streams. Two specific objectives were addressed. First, we aimed
90 to describe size spectra for invertebrates and fishes at three study sites along the South Fork
91 Rockfish River in Nelson County, Virginia. Specifically, we sought to determine whether within
92 and among trophic level SS patterns are comparable to other lotic systems. This descriptive

93 component of our study helps to fill a basic knowledge gap for a relatively pristine area that is
94 popular with recreational tourists, but also facing increased pressure from agricultural and
95 commercial development (Hopper & Still, 2004).

96 The second study objective was to determine whether the fish SS is most closely
97 associated with the invertebrate SS when invertebrate and fish samples are collected
98 simultaneously, or when invertebrate samples are collected one or two months prior to the fish
99 samples. In this way, three temporal comparisons were made between fish and invertebrate SS
100 models in each of the three study streams. We hypothesized that simultaneously collected fish
101 and invertebrate data would be less closely associated than time-staggered data (i.e.,
102 invertebrates collected prior to fishes) because the transition from ingestion of invertebrate prey
103 to fish growth is not an instantaneous phenomenon. Time is needed to digest and assimilate food.
104 It is therefore logical to predict that fish size and abundance at a given moment will be more
105 closely associated with prey availability at a prior point in time. However, if simultaneously
106 collected fish and invertebrate data produce the most strongly correlated SS models, it may be
107 indicative of a near constant, time-invariant predator-prey mass ratio (see Barnes *et al.*, 2010;
108 Mehner *et al.*, 2018). To our knowledge, this is the first study to test for a time-staggered
109 association between fish and invertebrate SS. It therefore has potential to add an important,
110 temporal dimension to the SS literature.

111

112 **Materials and Methods**

113 *Study Sites*

114 Three sample sites were selected in Nelson County, Virginia, where anthropogenic
115 impacts are modest and little prior stream research has been conducted (Hopper & Still, 2004).

116 Stoney Creek (1-SC) is an intermittent first order tributary to the South Fork Rockfish River, at
117 419 m elevation (Figure 1A). Physical habitat within the 1-SC study reach included an even mix
118 of pools, riffles and runs, with substrate dominated by cobbles, large boulders, and exposed
119 bedrock. Canopy cover was extensive, shading the entire wetted channel along most of the study
120 reach. The Upper South Fork Rockfish River (2-USF) study site is a perennial, second order
121 stream that underwent restoration (armoring of stream banks and installation of several plunge
122 pools) in 2005 (Figure 1B). Physical habitat consisted of riffles, runs, and pools, with substrate
123 dominated by cobbles and pebbles. Canopy cover was also extensive, with complete to near-
124 complete shading along the entire study reach. Elevation at the 2-USF site was 230 m. The
125 Lower South Fork Rockfish River (3-LSF) site is a perennial, third order tributary to the James
126 River, located at 171 m elevation, ~6.5 km downstream of the 2-USF site (Figure 1C). Habitat
127 consisted of riffles and runs, with substrate dominated by pebbles and cobbles. Canopy cover
128 was limited to partial riparian shading along the channel banks.

129 Descriptive statistics for each study site, including basic measures of local
130 geomorphology, annual water temperature, landcover and anthropogenic activity, were
131 downloaded from the National Hydrography Dataset Plus version 2 attribute tables (McKay *et*
132 *al.*, 2015) and the StreamCat database (Hill *et al.*, 2016). Notably, the extent of forest cover
133 decreased along an elevation gradient, moving from 1-SC to the lower sites, while the extent of
134 urban development and agricultural activity, including fertilizer and pesticide application,
135 increased (Table 1).

136

137 *Field Sampling*

138 Benthic invertebrates were sampled at each of the three study sites, in each of three months: July,
139 August, and late-September or early-October 2020 (all September and October sampling dates
140 are hereafter labeled as “September”). During each sampling event, five replicate samples were
141 collected at each site (total no. benthic samples among all sites and months, $n = 45$). At USF and
142 LSF, a Hess sampler (0.088 m² area; 500 μm mesh) was used to collect the benthic samples
143 (Figure 1E). For each sample, the lower edge of the Hess was inserted 2-4 cm beneath the
144 channel substrate to create a rough seal with the stream bottom. All substrate within the Hess
145 was then scrubbed and agitated with a soft wire brush for 120 seconds. At 1-SC, where bedrock
146 and boulder substrate made it difficult to seat the Hess, a modified, large frame Surber sampler
147 (0.25 m² area; 500 μm mesh; 120 second scrub per sample) was used to collect benthic samples
148 (Figure 1D). For all sampling events, the locations of the five replicate samples were chosen to
149 represent the range of physical habitats observed at a given site. All invertebrate samples were
150 preserved in 70% isopropyl alcohol and returned to the lab for processing.

151 Fish surveys were conducted at each of the three study sites in September, on the same
152 day that September invertebrates were sampled. During each survey, a closed study reach (~100-
153 150 m longitudinal distance) was first created by securing block nets at the lower and upper ends
154 of the reach. Fish samples were then collected with a three-pass depletion survey design and a
155 Halltech HT-2000 backpack electrofisher. In each pass, a 3-5 person crew moved upstream,
156 sweeping laterally between the left and right banks. Stunned fishes were captured with dip nets
157 and transferred to aerated holding pens. At the conclusion of each pass, all collected fishes were
158 identified to species, measured for total body length (mm) and wet weight (g), then released
159 downstream of the closed study reach to prevent recapture. Field measured wet weights were
160 later converted to dry mass estimates with a standard conversion factor (1 g wet = 0.2 g dry;

161 Waters, 1977). For additional information regarding either invertebrate or fish sampling
162 methods, see McGarvey *et al.* (2019).

163

164 *Estimating fish and invertebrate densities within log₂ dry mass bins*

165 In the lab, the contents of each macroinvertebrate sample were sorted in a white tray with
166 a 10x magnification lens. All specimens were identified to family-level with a dissecting
167 microscope and measured for total body length or head capsule width (depending on specimen
168 condition) using an ocular micrometer. Individual dry mass was then estimated from the size
169 measurement using taxon-specific length-mass regressions (Benke *et al.*, 1999). Prior to data
170 analysis, the five replicate samples collected at each site, during each of the three sampling
171 events, were pooled into a single collection.

172 Following the original SS method of Kerr and Dickie (2001), all invertebrates and fishes
173 were partitioned by size among log₂ dry mass bins. Specifically, we used the standardized list of
174 25 log₂ size bins of McGarvey and Kirk (2017). Invertebrate abundances within log₂ dry mass
175 bins were estimated directly for each sample by partitioning individuals among size bins and
176 summing the number of individuals within each bin. Each of the summed abundance estimates
177 was then converted to a *D* estimate by dividing abundance by the total sampled area (i.e., Hess or
178 Surber surface area × 5).

179 For fishes, we began by sorting individuals captured in the first depletion pass among
180 log₂ dry mass bins, then summing the total numbers of individuals within each bin. Note that the
181 summed counts within log₂ size bins did not account for species' identities; we only accounted
182 for the number of individuals within a given size class, irrespective of taxonomy. This process
183 was repeated for the second and third depletion passes. Next, we used the Zippin maximum

184 likelihood method (Zippin, 1958; Carle & Strub, 1978) to estimate total abundance within each
 185 \log_2 size bin. The Zippin method first calculates an intermediate statistic X :

186

$$187 \quad X = \sum_{i=1}^k (k - i)C_i, \quad (\text{Eq. 1})$$

188

189 where i is i th sampling pass, k is the total number of passes, and C_i is the total number of fish
 190 caught in the i th pass. For example, if 100, 50, and 20 individuals are captured in the first,
 191 second, and third passes, respectively, then $X = 250$. An iterative process is then used to solve
 192 for the maximum likelihood estimate of n using the equation:

193

$$194 \quad n = \left[\frac{n+1}{n-T+1} \right] \prod_{i=1}^k \left[\frac{kn-X-T+1+(k-i)}{kn-X+2+(k-i)} \right]_i \leq 1.0, \quad (\text{Eq. 2})$$

195

196 where n is the total abundance estimate, T is the total number of fish caught in k passes, and all
 197 other variables are as shown above. Equations 1 and 2 were solved independently for each of the
 198 \log_2 dry mass bins. Finally, the n estimates were divided by the total surveyed surface area at
 199 each site to estimate D within each \log_2 size bin. For additional information on using the Zippin
 200 method with ataxic, size-structured data, see McGarvey *et al.* (2019).

201

202 *Size spectra modeling*

203 Separate SS models were built for invertebrate samples collected in each of the three
 204 sample months (July, August, and September) and for the September fish samples. Invertebrate
 205 and fish D estimates within each of the \log_2 size bins were calculated as described above. For
 206 \log_2 size bin, the point estimate of dry mass was calculated as the arithmetic mean of the lower

207 and upper boundaries of the respective bin. Empty size bins (i.e., no invertebrates or fishes
208 collected within a given size bin) were treated as “NA” values and excluded from SS models.
209 Inferred zero values were not used to represent empty size bins because zeroes imply that
210 specimens are "missing" (vs. natural size gaps within ecological communities) and have undue
211 leverage on linear regression models (Blanco *et al.*, 1994; White *et al.*, 2008). Invertebrate
212 specimens weighing < 0.0064 mg dry mass were also removed prior to SS analysis, as the
213 methods used to collect and process invertebrate samples (i.e., collection within 500 μm mesh
214 nets, followed by manual sorting) were not efficient in retaining these very small specimens.
215 Community-level SS models were also built from combined September invertebrate and fish data
216 by combining the invertebrate and fish D estimates within a common set of \log_2 size bins. If fish
217 and invertebrates were observed in the same size bin, their respective densities were summed to
218 obtain an overall D estimate for the bin.

219 All D estimates were normalized to account for the non-uniform intervals among \log_2
220 size bins (Blanco *et al.*, 1994; White *et al.*, 2008). To normalize the data, each D estimate was
221 divided by the width (i.e., upper boundary - lower boundary) of its respective size bin (Vidondo
222 *et al.*, 1997; Kerr & Dickie, 2001). All normalized D and dry mass values were \log_{10} transformed
223 to improve normality. Ordinary least squares regression was then used to build SS models,
224 predicting \log_{10} normalized D as a function of $\log_{10} M$ (as dry mass).

225

226 *Cross-correlation analysis*

227 In each of the three study streams, cross-correlation (xcorr) was used to assess whether
228 the SS for fishes collected in September was more closely associated with the SS for
229 invertebrates collected in the same month, or with invertebrates collected one or two months

230 prior. Specifically, we compared a single SS for fishes (September samples) in each stream with
 231 three invertebrate SS (July, August, and September samples). In traditional applications, xcorr is
 232 a measure of association between two time series, x_i and y_i , where i is an integer representing a
 233 discrete time step within the series. Repeated correlation (r) values are calculated between x_i and
 234 y_i at staggered time intervals or lags (l). The basic equation for r is:

235

$$236 \quad r = \frac{\sum_i [(x_i - \bar{x}) \times (y_{i-l} - \bar{y})]}{\sqrt{\sum_i (x_i - \bar{x})^2} \times \sqrt{\sum_i (y_{i-l} - \bar{y})^2}}, \quad (\text{Eq. 3})$$

237

238 where \bar{x} and \bar{y} are the mean averages of x and y , respectively, and l can be any integer value
 239 between 0 and the maximum length of the series (Bourke, 1996; Kohn, 2006). By calculating r at
 240 multiple l values, one can quantify the overall strength of association between two time series
 241 and determine if one series tends to lag or track the other at a characteristic interval. For
 242 example, Croke *et al.* (2015) used xcorr to study the lagged response of river discharge to
 243 precipitation in southeast India.

244 We used xcorr for two reasons. First, the normalized SS is analogous to a time series; the
 245 standardized series of size bins creates a uniform progression of size intervals that can, in effect,
 246 be substituted for uniform time intervals. The normalized D values also tend to be autocorrelated.
 247 Indeed, the observation that D within a given size bin is often a strong predictor of D within
 248 adjacent size bins is central to SS theory (Kerr & Dickie, 2001). Second, xcorr directly addresses
 249 the two research questions that we were most interested in: (i) how strong is the association
 250 between the invertebrate and fish SS; and (ii) at what lag interval is correlation between the fish
 251 SS and invertebrate SS strongest?

252 Prior to xcorr analyses, we expanded the standardized list of 25 \log_2 size bins to 45 bins
253 by adding 10 unsampled or “pseudo” size bins to the left of the smallest invertebrate bin and 10
254 additional pseudo bins to the right of the largest fish bin. We then calculated the mean
255 normalized D for each invertebrate and fish data series (i.e., separate means for the July, August,
256 September invertebrate data at each sample site and separate means for the September fish data
257 at each site) and used these means as default D values in each of the respective pseudo bins. This
258 was necessary to ensure that invertebrate and fish data series of equivalent length (i.e., same
259 numbers of size bins) would be available in xcorr analyses at different lag intervals (see
260 explanation of xcorr lags in next paragraph); equal length data series are required in xcorr
261 analysis. In effect, we created flatlines or uninformative segments in the invertebrate and fish
262 data series that extended the series without “corrupting” the empirical SS signals. An example of
263 this process is shown in Figure 2A for invertebrate (July samples) and fish (September samples)
264 data from 2-USF.

265 When the above process was completed for all normalized invertebrate and fish data, we
266 used xcorr to compare the fish data from each study stream with invertebrates collected from the
267 same stream in July, August, and September. For each comparison (September Fish vs. July,
268 August, or September invertebrates), correlation between the invertebrate and fish data was
269 calculated at $l = 0$ (i.e., no lag or horizontal shift among the two data series) following Eq. 3. We
270 then recalculated r for 20 incremental lags ($l = 1, 2 \dots 20$). In effect, we used the xcorr lags to
271 identify the point at which the normalized fish densities most closely resembled the normalized
272 densities of their invertebrate prey, denoted hereafter as r_{max} . An example of the shifting size
273 intervals is shown for July invertebrates and September fishes from 2-USF in Figure 2B & C.

274 To further test the generality of the xcorr results from the three study streams, we
275 repeated the xcorr analysis using seasonally staggered SS data from McGarvey and Kirk (2017).
276 McGarvey and Kirk (2017) collected invertebrate and fish samples from three central
277 Appalachian streams (Cabin Creek, Camp Creek, and Slaunch Fork) that were physically similar
278 to the present study streams (*see* Online Resource 1 in McGarvey & Kirk, 2017), using field
279 sampling and data analysis procedures that were identical to the present study. Thus, the
280 McGarvey and Kirk (2017) data, which were collected at approximately quarterly intervals
281 (March, May, August, October), provide a unique opportunity to bolster our xcorr results. We
282 performed xcorr comparisons for adjacent sampling periods at each stream. For instance, xcorr
283 between March invertebrates and May fishes was compared with the xcorr results for May
284 invertebrates and fishes in each of the three additional streams. The remaining xcorr comparisons
285 were as follows: May-August vs. August-August, August-October vs. October-October. Xcorr
286 tests for each pair followed the same process described above for the Nelson County streams
287 data.

288

289 **Results**

290 All community-level SS models (September data only) exhibited negative, highly
291 significant relationships between M and D . The community-level SS slopes decreased from -1.61
292 at the upstream site (1-SC) to -1.77 at the downstream site (3-LSF; Figure 3). Community-level
293 SS intercepts exhibited the opposite trend: intercepts decreased from 1.61 at 3-LSF to 0.50 at 1-
294 SC. However, differences among the community-level SS model parameters were generally not
295 significant, as indicated by overlapping 95% confidence intervals (Table 2). Among all
296 community-level slope and intercept comparisons, only the intercept at 1-SC was significantly

297 different (lower) than at the other sites. Community-level SS slopes were consistently,
298 significantly steeper than the monthly invertebrate-only SS slopes for each month, with the
299 exception of the August and September invertebrate models at 1-SC. Comparisons of fish-only
300 SS slopes and community SS slopes revealed only one significant difference: the community-
301 level SS slope at 1-SC was significantly steeper than the fish-only SS slope. Community-level
302 SS intercepts at 1-SC and 3-LSF were significantly greater than the fish-only SS intercepts at the
303 respective sites. Notably, none of the community-level SS intercepts differed significantly from
304 the monthly invertebrate-only SS intercepts, with the exception of the 1-SC community and 1-SC
305 July invertebrate models.

306 Negative, highly significant relationships between M and D were also detected for each
307 of the invertebrate-only and fish-only SS models. Slopes of the monthly invertebrate SS models
308 varied by site: 1-SC slopes became less steep from July to September while 2-USF slopes
309 became steeper (Table 2). At 3-LSF, invertebrate SS model slopes exhibited neither an
310 increasing nor decreasing trend from July to September. Intercepts of invertebrate-only SS
311 models were variable among months at all sites. Slopes of fish-only SS models ranged from -
312 0.87 at 1-SC to -1.25 at 2-USF, while intercepts ranged from -1.92 at 1-SC to -0.41 at 2-USF.
313 However, none of the SS slopes were significantly different (overlapping 95% confidence
314 intervals) when compared among sites, months, or trophic levels (i.e., fish vs. invertebrates) for
315 fish-only and invertebrate-only models. For invertebrate-only models, no significant differences
316 in SS intercepts were detected among months or sites. Similarly, no significant differences in SS
317 intercepts were detected among sites for fish-only models. But in all comparisons (3 fish-only
318 estimates vs. 9 invertebrate-only estimates), the SS intercepts were significantly lower for the
319 fish-only models than the invertebrate-only models.

320 Xcorr analyses showed that the invertebrate and fish SS were most strongly associated
321 during the same sampling period at 1-SC (in September; see Table 3). At 3-LSF, r_{max} was
322 greatest when comparing the August invertebrate SS with the September fish SS. At 2-USF, r_{max}
323 was equivalent for two comparisons: July invertebrates compared with September fish, and
324 September invertebrates compared with September fish. Overall, monthly differences in the r_{max}
325 values among Nelson County streams were modest and did not reveal a consistent pattern.
326 Similarly, no consistent temporal pattern was observed for the McGarvey and Kirk (2017) data
327 (Table 4). r_{max} values were sometimes greatest for staggered samples (*e.g.*, March invertebrate
328 and May fish samples at Cabin Creek) but in other cases, r_{max} values were greatest for
329 simultaneously collected samples (*e.g.*, August invertebrate and August fish samples at Camp
330 Creek).

331

332 **Discussion**

333 Across all three sites, significant differences in community-level SS intercepts or slopes
334 were not detected. Thus, size structure and overall abundance appear similar across and within
335 trophic groups. Among the invertebrate model slopes and intercepts, 95% confidence intervals
336 overlapped for all sites. Thus, we found no evidence of significantly different slopes or intercepts
337 among months. This suggests that all sites share similar size distribution and overall abundance
338 of invertebrates across all months. Furthermore, no significant differences in fish-only SS model
339 slopes or intercepts were detected, suggesting that all sites share similar size distribution and
340 overall abundance of fish.

341

342 *Invertebrate-only and fish-only size spectra*

343 Monthly changes in the SS slopes for invertebrate-only models were driven by
344 differential changes in the densities of key invertebrate families. At the 1-SC site, increasing
345 densities of relatively large Heptageniidae, Perlidae, and Psephenidae were responsible for
346 increasing (i.e., less steep) SS slopes among the July, August, and September models. The
347 decreasing SS slope trend at 2-USF is due in part to increased density of Hydropsychidae within
348 larger \log_2 size bins during September. While 3-LSF SS slopes did not consistently decrease nor
349 increase across months, invertebrate densities within the larger size bins were lower in August
350 than in July or September. This change contributed to a steeper SS slope in August.

351 Estevez *et al.* (2020) performed a similar study of invertebrate SS in temperate, forested
352 streams along the Cantabrian Mountains in Spain. Their summer SS models had more shallow
353 slopes and higher intercepts than our SS invertebrate models. These differences reflect lower
354 densities of relatively large invertebrates in the Nelson County study streams. Overall
355 invertebrate densities were, however, lower in our study streams, as indicated by the lower
356 intercepts. Interestingly, the shallowest SS slopes were consistently observed in streams with the
357 most extensive adjacent forest cover (~80% in Estévez *et al.*, 2020; 100% in the present
358 streams). This may reflect increases in larger scraper and shredder taxa (*e.g.*, Heptageniidae,
359 Psephenidae, and Tipulidae), as increased adjacent forest cover would result in more coarse
360 particulate organic matter within the stream.

361 No significant differences in fish-only SS slopes or intercepts were detected among sites,
362 suggesting that size structure and overall abundance of fish were similar. Modest differences
363 among sites were exhibited among the larger \log_2 size bins. 3-LSF and 2-USF contained lower
364 densities of fish in larger bin sizes compared to 1-SC. Thus, the shallower slope at 1-SC can be
365 partially attributed to the increased presence of larger individuals such as Brook Trout

366 (*Salvelinus fontinalis*). The 95% confidence intervals did, however, overlap among each of the
367 fish-only SS models, for both slopes and intercepts.

368 Preliminary comparisons of SS slopes suggest that densities of large fishes, relative to
369 smaller fishes, may be higher in Nelson County streams than in some other temperate streams.
370 For example, Arranz *et al.* (2021) examined nutrient concentration and abundance of non-native
371 species effects on SS model parameters along the Iberian Peninsula. Across 118 reaches from
372 2003 to 2009, they documented a mean SS slope of -2.90; a value much lower than the fish-only
373 SS slopes reported here. However, our results were more similar to the SS results of Perkins *et*
374 *al.* (2018), who studied the effect of allochthonous prey subsidies on SS parameters. After
375 surveying 31 streams across the United Kingdom, they reported a mean SS slope of -0.79; this
376 value was close to the fish-only SS slopes detected in the Nelson County streams, suggesting that
377 large fishes in our study streams may also benefit from allochthonous subsidies. This variability
378 in SS slopes for stream fishes suggests that further research is needed to identify factors that
379 regulate the growth and density of relatively large fishes in streams

380

381 *Community size spectra*

382 Community-level SS models are useful because they link individual trophic level models
383 together in one continuous function, reflecting predator-prey relationships and the transfer of
384 energy between them (Kerr & Dickie, 2001). In general, the community-level (i.e., among
385 trophic level) SS slopes were consistently steeper than the slopes from invertebrate and fish-only
386 (i.e., within trophic level) models (Table 2). This observation is consistent with the theoretical
387 prediction that the inefficient transfer of resources among trophic levels will constrain growth

388 and abundance of relatively large predators, thus steepening community-level SS slopes
389 (Trebilco *et al.*, 2013)

390 One community-level study that used identical methods and is therefore directly
391 comparable with our results is McGarvey and Kirk (2017). The reported community slope and
392 intercept for their streams during August was -1.62 and 0.44, and during October were -1.65 and
393 0.37, respectively. The slopes of the September SS models from Nelson County streams were
394 similar to the slopes of the West Virginia streams in August and October. Intercepts of both 2-
395 USF and 3-LSF were markedly higher compared to West Virginia streams; however, the low
396 intercepts at West Virginia were attributed to an early-June flood event that likely reduced both
397 invertebrate and fish D (McGarvey & Kirk, 2017). Another useful benchmark for our results is
398 Poff *et al.* (1993). They sampled 3 trophic levels (meiofauna, macroinvertebrates, and fishes) in a
399 Piedmont stream and reported a community-level SS slope of -1.82 (reported biomass was
400 converted to D following Sprules & Barth, 2016). Collectively, the similarities among SS slopes
401 suggest that variation in community-level size structure is minimal within temperate, eastern
402 U.S. streams.

403

404 *Cross-correlation*

405 Cross-correlation tests did not consistently support the hypothesis of a time-staggered
406 link between invertebrate (i.e., prey) and fish (i.e., predator) SS models in the Nelson County or
407 West Virginia streams. r_{max} values were higher for simultaneous tests than for time-staggered
408 tests in one-half of the Nelson County stream comparisons (Table 3) and in 5 of 9 West Virginia
409 stream comparisons (Table 4). However, two other observations from the xcorr results were
410 notable. First, the r_{max} values themselves were consistently high. In Nelson County streams, the

411 minimum observed r_{max} (regardless of the staggered vs. simultaneous rankings) was 0.65 and in 7
412 of 9 tests, r_{max} was ≥ 0.70 . Second, the observed r_{max} values tended to occur at similar l values.
413 Xcorr l values in the Nelson County streams ranged from 8 to 13 with a clear central tendency
414 around 10 (mean $r_{max} = 10.11$). Similarly, xcorr l values in the West Virginia streams ranged
415 from 10 to 14. Taken together, these xcorr results may indicate that size-structure within benthic
416 invertebrate and fish assemblages is a highly conserved phenomenon that exhibits only modest
417 change among seasons.

418 High r_{max} values, irrespective of their associated l values, reflect similar size-structure
419 among invertebrate and fish assemblages and may be particularly suited to SS analysis. This is
420 because the within-trophic level SS models did not exhibit strictly linear relationships. Rather,
421 they exhibited slight curvature (Figure 3). This tendency towards curvilinear SS models was
422 predicted by Kerr and Dickie (2001) and is important because direct comparisons of linear model
423 slopes may not fully characterize similarity in size structure among trophic levels. Instead, a
424 means to account for similarity between SS, without a strict assumption of linearity, may be
425 necessary. r_{max} values can accommodate the curvature when comparing two SS models and may
426 reflect close associations between specific size bins in two SS models. For example, the r_{max}
427 value of 0.968 at 2-USF for July invertebrates and September fishes (when $l = 12$; Figure 2C)
428 may indicate that fish density within the 9.8304 mg dry mass size bin is strongly associated with
429 invertebrate density within the 0.0096 mg dry mass size bin (i.e., the 9.8304 mg bin is $12 \log_2$
430 intervals larger than the 0.0096 mg bin). Fish density within the 19.6608 mg bin may be strongly
431 associated with invertebrate density within the 0.0192 mg bin, and so on. These types of close
432 associations between specific size bins may in turn reflect consistent, size-selective predation by
433 fishes in the study streams. Indeed, size-selective predation has been demonstrated for some fish

434 predators (*e.g.*, Gilson & Benson, 1979; Grant & Noakes, 1986) and if it is a germane foraging
435 strategy in lotic ecosystems, its recognition will greatly enhance SS research in these systems.

436 Similar or near-constant l values at r_{max} may imply that invertebrate and fish SS are
437 linked through a consistent predator-prey mass ratio. Within the context of \log_2 size bins, the
438 ratio between the average mass of any given bin and a bin that is 10 steps larger is always
439 1:1,024. Thus, a lag of 10 implies a PPMR of 1:1,024, while a lag of 14 implies a PPMR of
440 1:16,834. In a meta-analysis of empirical PPMR estimates in lotic ecosystems, Brose *et al.*
441 (2006) confirmed that the average PPMR for fishes is \sim 1:10,000. This average PPMR is notable
442 because it is bracketed by the implied PPMR values from our xcorr analyses. The r_{max} lag for
443 West Virginia streams ($l = 14$) implies a PPMR that is nominally larger than the average value of
444 Brose *et al.* (2006), while the implied PPMR in the Nelson streams ($l = 10$, PPMR = 1:1024) is
445 about one order of magnitude smaller. This difference in implied PPMR values may indicate that
446 fishes in the Nelson County streams are consuming larger prey (*i.e.*, the PPMR is relatively
447 small) than similar size fishes in other lotic systems. We therefore suggest that fish and
448 invertebrate ecology in Nelson County streams may be unique and in need of further study.

449

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Tables

Table 1 Descriptive statistics for the three study streams.

Variable	Stoney Creek	Upper South Fork Rockfish River	Lower South Fork Rockfish River
Longitude (dd)	-78.913	-78.916	-78.849
Latitude (dd)	37.920	37.877	37.904
Strahler stream order	1	2	3
Slope	0.059	0.017	0.006
Surveyed channel length (m)	96	142	151
Mean wetted channel width (m)	7.2	6.0	11.1
Elevation (m)	419	230	171
Basin area (km ²)	8.1	25.8	88.9
Mean annual stream temp (C)	10.6	12.4	12.9
% forest cover in catchment	100	66	67
% urban cover in catchment	0	6	11
% crop or hay cover in catchment	0	28	22
Nitrogen fertilizer application (kg/km ² /yr)	0	424	332
Pesticide application (kg/km ² /yr)	0	4	7

Table 2 Summary of macroinvertebrate, fish, and combined community size spectra models. Each model was a linear regression between M (independent variable) and D (dependent variable). For each model, the degrees of freedom (df), slope, intercept, r^2 , significance level (p), and F statistic (f) are shown. 95% confidence intervals are shown in parentheses for each of the model slopes and intercepts. Modeling results are specific to datasets that included only invertebrates (I), only fish (F), and combined community-level samples (I + F).

Site	Month	Taxa	df	slope	intercept	r^2	p	f
1-SC	July	I	10	-1.08 (-1.42, -0.73)	1.10 (0.72, 1.48)	0.79	1.17E-04	37.09
	Aug	I	12	-0.94 (-1.20, -0.68)	0.93 (0.52, 1.33)	0.80	1.33E-05	49.75
	Sep	I	11	-0.88 (-1.20, -0.55)	1.06 (0.61, 1.52)	0.72	2.65E-04	27.76
	Sep	F	7	-0.87 (-1.39, -0.35)	-1.92 (-3.43, -0.41)	0.60	1.36E-02	10.70
	Sep	I + F	18	-1.61 (-1.83, -1.40)	0.50 (0.05, 0.95)	0.92	1.60E-11	219.30
2-USF	July	I	13	-0.89 (-1.12, -0.65)	1.50 (1.13, 1.87)	0.81	4.82E-06	55.52
	Aug	I	11	-0.93 (-1.28, -0.57)	1.69 (1.19, 2.18)	0.70	3.33E-04	26.23
	Sep	I	12	-1.22 (-1.48, -0.97)	1.54 (1.21, 1.87)	0.88	6.98E-07	88.31
	Sep	F	9	-1.25 (-1.70, -0.81)	-0.41 (-1.83, 1.01)	0.77	3.74E-04	30.38
	Sep	I + F	20	-1.68 (-1.83, -1.53)	1.36 (1.01, 1.72)	0.96	1.85E-15	480.90
3-LSF	July	I	12	-0.94 (-1.19, -0.70)	1.57 (1.24, 1.89)	0.82	7.09E-06	56.48
	Aug	I	13	-1.07 (-1.35, -0.80)	1.49 (1.21, 1.76)	0.89	1.79E-07	100.10
	Sep	I	16	-0.93 (-1.13, -0.73)	1.62 (1.28, 1.95)	0.84	1.08E-07	81.94
	Sep	F	8	-1.11 (-1.65, -0.57)	-1.52 (-3.27, 0.23)	0.67	3.69E-03	16.40
	Sep	I + F	20	-1.77 (-1.96, -1.59)	1.61 (1.18, 2.04)	0.95	3.38E-14	354.80

Table 3 Cross correlation test results for the Nelson County study streams. Lag (l) values indicate the number of shifted intervals (\log_2 size bins) at which the maximum correlation coefficient (r_{max}) was observed for each comparison between invertebrate and fish data.

Site	Invert month	Fish month	r_{max}	l
1-SC	July	Sept	0.761	9
	Aug	Sept	0.716	9
	Sept	Sept	0.869*	10
2-USF	July	Sept	0.968*	12
	Aug	Sept	0.937	13
	Sept	Sept	0.968*	11
3-LSF	July	Sept	0.700*	11
	Aug	Sept	0.676	8
	Sept	Sept	0.648	8

Table 4 Cross correlation test results for the three additional streams (Cabin Creek, Camp Creek, and Slaunch Fork) from McGarvey & Kirk (2017). Lag values (l) indicate the number of shifted intervals (\log_2 size bins) at which the maximum correlation coefficient (r_{max}) was observed for each comparison between invertebrate and fish data.

Site	Invert month	Fish month	r_{max}	l
Cabin	March	May	0.934	14
	May	May	0.740	11
	May	Aug	0.486	10
	Aug	Aug	0.552	14
	Aug	Oct	0.692	14
	Oct	Oct	0.807	13
Camp	March	May	0.902	13
	May	May	0.701	11
	May	Aug	0.631	10
	Aug	Aug	0.736	11
	Aug	Oct	0.623	10
	Oct	Oct	0.578	12
Slaunch	March	May	0.844	12
	May	May	0.974	14
	May	Aug	0.790	12
	Aug	Aug	0.562	10
	Aug	Oct	0.680	11
	Oct	Oct	0.910	13

Figures

Fig. 1 - Photos of the three study sites, including Stoney Creek (panel A), Upper Southfork Rockfish (panel B), and Lower Southfork Rockfish (panel C). Panels D and E show the modified Surber sampler and standard Hess sampler, respectively.

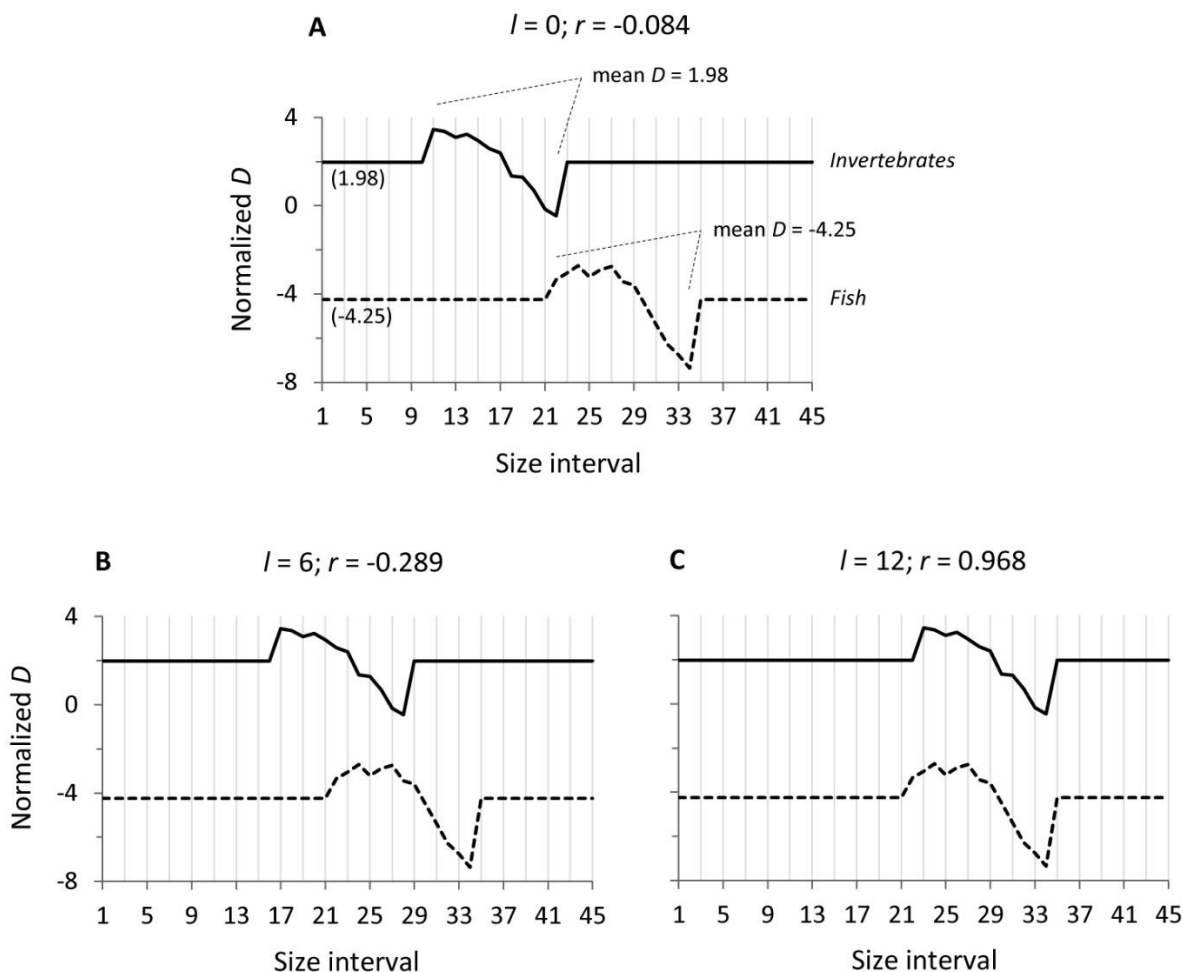


Fig. 2 - Exemplar plots demonstrating the use of cross-correlation (xcorr) analysis to assess similarity between size spectra data series for benthic macroinvertebrates and fishes. Normalized density (D ; y-axis) data are shown for July invertebrates and September fishes from the Upper South Fork Rockfish River study site. The original \log_2 dry mass size bins (x-axis) have been replaced with uniform size intervals ranging from 1-45 (*see* main text). Flatline regions to the left and right of the invertebrate and fish plots are the means of the observed normalized D values (1.98 and -4.25, respectively). Panel A shows invertebrate and fish data series with a xcorr lag (l) of 0; at $l = 0$, the invertebrate and fish data series are weakly, negatively correlated (Pearson correlation coefficient r). Panel B shows the same two data series when the invertebrate data have been shifted 6 size intervals to the right ($l = 6$); r is negative because the descending trend for relatively large invertebrates is now aligned with the ascending trend for relatively small fishes. Panel C shows a shift of 12 intervals ($l = 12$); the maximum xcorr r value occurs here, as the invertebrate and fish data series are now closely aligned. Size intervals can be converted to the original \log_2 dry mass bins with the following benchmarks: interval 11 = 0.0096 mg dry mass; interval 21 = 9.8304 mg dry mass; interval 31 = 10,006.3296 mg dry mass. Identical axes are used in each plot to aid in comparison.

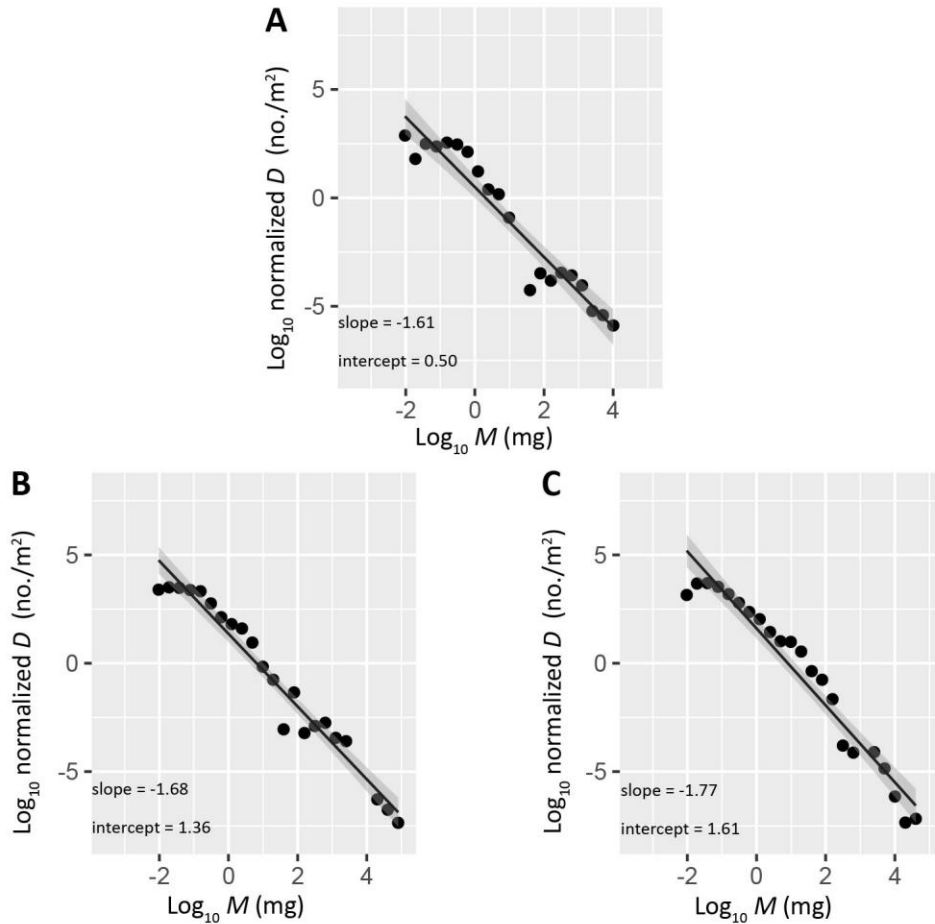


Fig. 3 - Normalized density (D) community size-spectra plots for benthic invertebrates and fishes collected during September in Nelson County, Virginia streams. Panels A, B, and C show SS plots for Stony Creek, the Upper South Fork Rockfish River, and the Lower South Fork Rockfish River, respectively. Size-spectra model coefficients (from Table 2) are shown in each plot. In each plot, points to the left of the $\text{Log}_{10} M = 1$ mark are invertebrates and points to the right are fishes. To facilitate direct comparison, all plots are shown with identical axes and gridlines.