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PRIMARY RESEARCH PAPER

Seasonal comparison of community-level size-spectra in southern coalfield streams of West Virginia (USA)

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Abstract Inverse scaling relationships between average body mass (*M*) and density (*D*) have been reported in many lake and marine ecosystems but are less well documented in lotic systems. We used quantitative samples of benthic macroinvertebrate and fish *D* to model the *D* versus *M* (i.e., $D \propto 1/M$) relationship in central Appalachian streams of the eastern USA. Specifically, we used the ataxic 'size-spectra' method (individuals identified only by size, not taxonomic identity, then aggregated within $\log_2$ *M* bins) to model *D* as a function of *M*. Repeat samples were collected from three study streams in March, May, August, and October, allowing us to test for seasonal differences in the slopes and intercepts of size-spectra models, using linear mixed-effects modeling. Size-spectra slopes were significantly different among months, decreasing from March (slope = − 1.73) to May (− 1.81), then increasing to August (− 1.62) and October (− 1.65). Intercepts also differed among months but showed the opposite trend: intercepts increased from March (intercept = 0.51) to May (0.91), then decreased through August (0.44) and October (0.37). Size-spectra slopes and intercepts did not differ from the overall model parameters when estimated separately for macroinvertebrate and fish data. Finally, times series data on water temperature and discharge were used to show that size-spectra parameters may respond in predictable ways to the accumulation of degree days (i.e., the growing season) and to episodic flood events.

Keywords Ataxic data · Stream fishes · Benthic macroinvertebrates · Depletion sampling · Scaling relationship · Linear mixed-effects modeling · Size-structure

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Introduction

Aquatic communities are often size-structured, such that organismal abundance is a decreasing function of body size. This fundamental, inverse relationship between abundance and size can be modeled as a power-law function (or linear function when using log-transformed abundance and size data) and has been documented in a diverse range of aquatic ecosystems (Yvon-Durocher et al., 2011a, b). For instance, Cyr et al. (1997) analyzed phytoplankton, zooplankton, and fish data from a global sample of 18 lakes and reported strong, log-linear relationships between species' population densities (*D*) and their respective mean body masses (*M*). Similarly, Schmid et al. (2000) used comprehensive samples of the invertebrate meio- and macrofauna from two European streams to demonstrate negative, log-linear relationships between species' *D* and mean *M*, both for whole assemblage data and for distinct taxonomic subsets.

A key caveat in the analysis of *D* versus *M* relationships is the decision whether to use either species-level averages (i.e., mean for a given species) or 'ataxic' data that recognize only *individual* body size, irrespective of taxonomic identity (White et al., 2007; Trebilco et al., 2013). Species' averages can mask substantial intraspecific variation in body size and feeding behavior, particularly in aquatic systems where many organisms are gape-limited, generalist predators that progress through two or more distinct feeing modes throughout their life histories. These ontogenetic shifts in feeding behavior are common among fishes (e.g., Werner & Gilliam, 1984; Mittelbach & Persson, 1998) and invertebrates (e.g., Allan, 1982; Ohba, 2009) and, if not accounted for in *D* versus *M* models, can bias one's perception of community structure (Woodward et al., 2005; Gilljam et al., 2011).

Kerr and Dickie (2001) recognized the importance of individual body size and, building upon previous work (e.g., Sheldon & Parsons, 1967; Silvert & Platt, 1978; Dickie et al., 1987; Boudreau & Dickie, 1989), compiled an ataxic, standardized method for modeling and comparing the *D* versus *M*, or 'size-spectrum,' relationship. Their method addresses co-occurring individuals within a single ecosystem and can incorporate specimens from multiple trophic levels, seeking to model *D* as a function of *M*. Notably, the ataxic size-spectra method of Kerr and Dickie (2001) uses individual-level *M* data rather than species-level *M* averages. It also utilizes the octave (doubling) scale to partition individuals among increasing $\log_2 M$ bins. Within each *M* bin, *D* is estimated as the sum of individuals within the bin.

Following the methods outlined by Kerr and Dickie (2001), researchers have reported size-spectra relationships in many different lentic systems, including the Laurentian Great Lakes (Sprules & Munawar, 1986; Yurista et al., 2014), the Bay of Fundy (Schwinghamer, 1981), Lake Constance (Germany; Gaedke, 1992), a subtropical reservoir (Chang et al., 2014), and the Atlantic Ocean (Rinaldo et al., 2002). These basic, descriptive studies are essential to develop and test ecological theory (White et al., 2007; Yvon-Durocher et al., 2011b; Trebilco et al., 2013; Sprules & Barth, 2016). But size-spectra are also being used in applied contexts, such as understanding and predicting the effects of anthropogenic perturbations on aquatic communities (e.g., Jennings & Blanchard, 2004; Petchey & Belgrano, 2010; Yvon-Durocher et al., 2011a; Dossena et al., 2012; Martínez et al., 2016).

Relatively few researchers have, however, documented ataxic size-spectra in lotic systems and efforts to combine fish and invertebrate data in community-level models are even rarer. To our knowledge, only two studies have paired stream fish and invertebrate data (see Poff et al., 1993; Huryn & Benke, 2007). Most size-spectra work in lotic systems has focused exclusively on invertebrates (e.g., Cattaneo, 1993; Morin et al., 1995; Ramsay et al., 1997; Martínez et al., 2016) or fishes (e.g., Murry & Farrell, 2014; Benejam et al., 2015; Broadway et al., 2015), making it difficult to characterize size-structure at the community level (see Morin & Nadon, 1991; Schmid et al., 2000). Attempts to document seasonal or intra-annual trends in the size-spectrum for lotic communities are also rare. We are aware of only four *in situ* examples: the pioneering study of Ottawa Valley (Canada) streams (Morin et al., 1995), a longitudinal study of the Aniene River (Italy; Solimini et al., 2001), and surveys of two small streams in southeast England (Stead et al., 2005; Woodward et al., 2005). Of these, two reported clear size-spectra relationships adhering to similar intra-annual shifts (Morin et al., 1995; Solimini et al., 2001), one failed to detect strong *D* versus *M* size-spectra relationships (Stead et al., 2005), and one documented seasonal changes in the size-spectrum (and food web structure) but used taxic rather than ataxic data (Woodward et al., 2005). Furthermore, each of these seasonal studies focused exclusively on invertebrates, without incorporating fishes.

In this study, we used combined fish and invertebrate samples to characterize the community-level size-spectrum in three small, central Appalachian (USA) streams. We also used repeat samples from March, May, August, and October to test whether size-spectra model parameters differ among seasons. We hypothesized that size-spectra would exhibit seasonal variation because temperate streams are strongly influenced by seasonal changes in environmental conditions (e.g., temperature and flow) and the availability of trophic resources. For example, late spring and summer insect emergence may significantly decrease invertebrate abundance (Huryn & Wallace, 2000; Hershey et al., 2010), thereby altering *D* versus *M* relationships through the autumn and winter months. Alternatively, many temperate stream fishes spawn in the spring months (Jenkins & Burkhead, 1994; Stauffer et al., 1995), leading to predictable increases in *M* as juveniles grow through the summer and fall. Seasonal invertebrate drift and fish migration events may also drive predictable temporal changes in size-spectra models (Brittain & Eikeland, 1988; Schlosser, 1991).

Our specific objectives were to (1) quantify the community-level size-spectrum in the three study streams, using original *D* and *M* estimates for benthic macroinvertebrates and fishes; (2) test for seasonal variation in size-spectra model parameters; (3) determine whether the size-spectra parameters differ among the two taxonomic groups (i.e., macroinvertebrates vs. fishes); and (4) use time-series data on water temperature and discharge to help interpret the size-spectra results.

Materials and methods

Study sites

Site selection was guided by a secondary objective of characterizing natural fish and invertebrate size-structure within the southern coalfield streams of West Virginia, where little empirical research has been conducted. This made site selection challenging because large-scale anthropogenic disturbances, such as mountaintop removal surface mining and industrial logging, have degraded streams and instream biota throughout the region (e.g., Bernhardt et al., 2012; Johnson et al., 2013). We therefore screened candidate sampling sites with the Critical Forest Map of Maxwell et al. (2012). The Critical Forest Map is a digital representation of ecosystem health in the southern coalfields region that uses multiple indicators of landscape structure, including land use/cover type, geomorphology, and degree of forest fragmentation, to calculate an index of ecosystem integrity; forest plots (i.e., grid cells) are ranked on an ordinal scale ranging from 0 to 3, with three indicating least disturbed forest habitat. We identified stream catchments that consisted primarily of grid cells with Critical Forest scores of 2 or 3 by overlaying the Critical Forest Map on the 1:100,000 scale NHDPlus version 2 digital stream network (McKay et al., 2015) within a Geographic Information System (ArcGIS version 10.3 software, Environmental Systems Research Institute, Redlands, California, USA). Three final sample sites were then selected from this subset, with the additional constraint that each site must be located on public land to ensure accessibility.

Cabin Creek (37.617° latitude, − 81.454° longitude) is a third-order tributary of the Guyandotte River, located at the southern boundary of Twin Falls State Park (Wyoming County). In the surveyed reach, Cabin Creek consists of a steep series of pools, riffles, and runs with substrate dominated by large boulders and limited gravel distributed throughout the riffles and pools. Camp Creek (37.550° latitude, − 81.131° longitude) is a fourth-order tributary of the Bluestone River that flows through Camp Creek State Park (Mercer County). Within the survey reach, the stream channel is primarily riffles and runs with multiple shallow pools and one large, deep (> 1.3 m) pool. Substrate consists of medium–large boulders, flat cobbles in riffles and runs, and silt and sand deposits in pools. Slaunch Fork (37.396° latitude, − 81.889° longitude) is a fourth-order tributary of the Tug Fork River, located near the West Virginia–Kentucky state line. The upstream watershed lies entirely within the state-protected Panther Wildlife Management Area (McDowell County). Within the survey reach, substrate is primarily a mix of cobble and gravel in riffles and runs, with sand and silt in two deep pools. All three streams are covered by an extensive hardwood canopy, consisting of a diverse mix of Maple (*Acer* sp.), Oak (*Quercus* sp.), Hickory (*Carya* sp.), Walnut (*Juglans* sp.), Birch (*Betula* sp.), Elm (*Elmus* sp.), and Beech (*Fagus* sp.) trees. Cabin Creek and Slaunch Fork both lie within the Appalachian Plateau physiographic province and are underlain by sandstone, shale, coal, and limestone of Pennsylvanian age. Camp Creek lies within the Valley and Ridge physiographic province and is underlain by limestone, shale, and sandstone of Mississippian age. Maps, photos, and water chemistry summary statistics are provided for all sites in Online Resource 1.

Stream surveys

Streams were sampled in March, May, August, and October of 2014. At each site, a study reach of ca. 20× the mean wetted channel width, but no less than 100 m total length, was delineated. Channel width was measured perpendicular to the thalweg at 10-m intervals along the longitudinal profile. Channel gradient was measured at the same longitudinal intervals using a stadia rod and Abney level. Water quality measurements (pH, temperature, specific conductivity, and dissolved oxygen) were collected with a hand-held YSI Pro2030 (Yellow Springs, Ohio) meter at the beginning of each sampling event. Stream channel and water quality data are summarized in Online Resource 1.

Fish samples were collected in each of the four months using a three-pass depletion survey design and a Halltech HT-2000 backpack electrofisher (Guelph, Ontario). Closed survey reaches were established by anchoring block nets at the lower and upper ends of each reach. During each pass, a 3- to 4-person crew moved upstream collecting as many stunned fishes as possible and transporting all captured fishes to a live well. Following each pass, captured fishes were identified and measured for total body length (mm) and wet weight (g). Fish wet weights were subsequently converted to dry mass estimates using a standard conversion factor (1 g wet weight = 0.2 g dry weight; see Waters, 1977).

Six benthic macroinvertebrate samples were collected with a Hess sampler (500 µm mesh; 0.088 m^2 area) at each site, during each sampling event. Individual Hess samples were distributed among a representative mix of riffle and run habitats. For each sample, the Hess was set to ca. 2–4 cm depth beneath the substrate. Internal substrate was then agitated and scrubbed with a soft wire brush for 120 s. All Hess sample contents were preserved in 70% isopropyl alcohol and returned to the lab for visual sorting under a 10x magnification lens. Individual specimens were then identified to the genus or the lowest practical taxonomic level with a dissecting microscope. An ocular micrometer was used to measure individual head capsule widths. Published taxon-specific length–mass regressions (Smock, 1980; Benke et al., 1999) were then used to estimate individual dry mass from head capsule width.

Data analyses

Following Kerr and Dickie (2001), we used $\log_2 M$ bins to group similarly sized organisms by individual dry mass. Size bins ranged from 6.4×10^{-3} mg (lower boundary, corresponding to the smallest macroinvertebrates) to 1.07×10^{5} mg (upper boundary, corresponding to the largest fishes) for a total of 24 $\log_2 M$ size classes. Numbers of populated $\log_2 M$ bins (i.e., bins that contained at least one individual) ranged from 16 to 22 for a given dataset (see Online Resource 2). The lower boundary of the smallest size class was set at 0.0064 mg because the Hess sampler used to sample macroinvertebrates was not efficient at collecting small meiofauna specimens below this size.

After processing and estimating individual dry mass, macroinvertebrates were pooled among the six Hess samples from each site × month sampling event and then partitioned by individual dry mass among the $\log_2 M$ bins. Notably, the size-based partitioning of individual macroinvertebrates was entirely ataxic; each specimen was assigned to its corresponding $\log_2 M$ bin without further consideration of taxonomic identity. Macroinvertebrate abundance within each of the $\log_2 M$ bins was then summed to estimate D (per m^2). M values were estimated as the arithmetic means of the upper and lower bounds of each $\log_2$ size interval ($M \approx$ [lower bound + upper bound] ÷ 2; see Blanco et al., 1994).

Fish abundances (n) were estimated with the maximum likelihood depletion method (Zippin, 1958; Carle & Strub, 1978), but we did not calculate n for fish species. Rather, we calculated ataxic n estimates for unidentified populations of individuals within the $\log_2 M$ bins. These ataxic calculations, where fish specimens were characterized only by their individual body mass, were logically consistent with the traditional 'individual particles' method of Kerr and Dickie (2001). For each $\log_2 M$ bin, we first calculated the intermediate statistic X as

$$X = \sum_{i=1}^{k} (k - i)C_i, \tag{1}$$

where i is the ith sampling pass ($i = 1, 2,$ or 3), k is the total number of passes ($k = 3$), and C_i is the total number of fish caught (of a given $\log_2 M$ interval) in the ith pass. The maximum likelihood estimate of n was then calculated iteratively by substituting decreasing n values until

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

where T is the total number of individuals (in a given $\log_2 M$ interval) caught in k passes and all other variables are as defined above for Eq. 1. For example, we captured 75, 54, and 22 individuals ($T = 151$) within the 838.9–1,677.7 mg $\log_2 M$ interval (average $M = 1{,}258.3$ mg). Following Eq. 1, X for this series was 204. Equation 2 was then solved as above, resulting in $n = 183$. If zero counts occurred in the first, second, or third pass for a given $\log_2 M$ bin, we used the total observed abundance (i.e., summed count among the three passes) as the n estimate.

Equations 1 and 2 were applied independently to each of the $\log_2 M$ size classes. Fish n estimates for each of the $\log_2 M$ size bins were then converted to D estimates by dividing each n value by the surveyed channel surface area of the respective study site, then standardizing the results to per 1 m^2 values for direct comparison with macroinvertebrate D estimates. Among all sites and months, size disparities between macroinvertebrates and fishes were large enough to preclude overlap within the same $\log_2 M$ bins; smaller bins (< 30 mg M) were populated entirely by macroinvertebrates, while larger bins (> 50 mg M) were populated exclusively by fishes. Empty $\log_2 M$ bins, in which no individuals occurred, were excluded from NSS models as they can unduly influence regression model outputs (Blanco et al., 1994; White et al., 2008).

Next, all D estimates were 'normalized' to account for the differing widths of the $\log_2 M$ bins. Because $\log_2$ bins become incrementally wider with increasing M (i.e., ΔM is not uniform among bins), statistical procedures designed for continuous data, such as linear regression, will be biased (see Blanco et al., 1994; White et al., 2008). Normalization scales D to ΔM by dividing each D estimate by the width of its respective $\log_2 M$ bin (Vidondo et al., 1997; Kerr & Dickie, 2001). This reveals the true exponential shape of the continuous size-spectrum and is necessary to obtain unbiased size-spectrum parameter estimates (White et al., 2008; Edwards et al., 2017).

Linear mixed-effects modeling was then used to build normalized size-spectra (NSS) models after $\log_{10}$-transformation of all M and normalized D estimates. We began with a simple model that included M as a covariate and *sample site* as a random effect. Next, we built a series of more complex models, including *month* and *taxonomic group* (macroinvertebrates vs. fishes) as fixed effects, with and without M interactions (see Martínez et al., 2016). Pairwise likelihood ratio tests were then used to assess the significance of the following model components: *month* (intercept), *taxonomic group* (intercept), a *month* $\times$ M interaction (slope), a *taxonomic group* $\times$ M interaction (slope), a 3-way *month* $\times$ *taxonomic group* $\times$ M interaction, and a *month* $\times$ *site* interaction (random slopes; see Bolker et al., 2009). Linear mixed-effects models were fit using the *lmer* function in R package 'lme4' (Bates et al., 2015) and pairwise likelihood ratio tests were performed with the *anova* function in base R (R Core Team, 2016). All M and D data used in the NSS models are provided in Online Resource 2.

Finally, to aid in interpreting NSS results within the context of major environmental influences, we collected annual time-series data on water temperature and discharge at Slaunch Fork. This site was chosen to represent intra-annual variation in temperature and discharge because a U.S. Geological Survey gauging station (No. 03213500) was present in the immediate vicinity, ca. 5 km downstream from the sample site and just below the Slaunch Fork confluence with Panther Creek. Comparable, continuous discharge records were not available for the other two study sites. Mean daily discharge was calculated and plotted throughout the calendar year of the study (2014), then superimposed on long-term discharge records (1946–2014) including daily means and the 5th–95th percentile range of daily discharge over the period of record. To incorporate the potential effects of winter flood events prior to our first sampling event, we added discharge records from November and December 2013 to the 2014 calendar year discharge data. Water temperature data were collected in Slaunch Fork at 15-min intervals, using a Hobo® Pendant data logger (Onset Computer Corporation, Bourne, Massachusetts, USA). Mean daily water temperatures were calculated and plotted throughout the 2014 calendar year. Cumulative degree days were also calculated and plotted for the 2014 calendar year using two threshold values: a lower threshold of $\geq$ 10°C, which is commonly used to model macroinvertebrate growth (Corkum, 1992; Lawrence et al., 2010), and a higher threshold of $\geq$ 14°C, which is applicable to many temperate freshwater fishes (Murphy et al., 2011; Chezik et al., 2013).

Results

All NSS models exhibited negative, highly significant relationships between *M* and normalized *D*, beginning with the simplest model that included only *M* ($F_{1,\,231} = 8156.5$) and the random effect of *sample site* as predictors. Likelihood ratio tests then revealed two key aspects of the NSS within our study streams. First, they confirmed a significant effect of *month* (χ^2 *P* value ≤ 0.05), relative to models that did not include *month* as a fixed effect (Table 1). This significant *month* effect was expressed by model intercepts increasing from March to May, then decreasing through August and October (Fig. 1). Second, likelihood ratio tests revealed a significant *month* $\times$ *M* interaction, relative to models that included only an additive effect (Table 1). This interaction was expressed by model slopes that decreased (i.e., became steeper) from March to May, then increased to a nearly constant value in August and October (Fig. 1). However, our tests did not provide evidence of a significant additive or multiplicative effect of *taxonomic group* on the NSS (χ^2 *P* values > 0.05 in Table 1), indicating that neither the intercepts nor the slopes of independent invertebrate and fish NSS models would deviate significantly from the overall model parameters for combined data. Nor did we find evidence of a random *month* $\times$ *sample site* interaction (Table 1). Thus, NSS models did not exhibit random slopes (i.e., differing slopes among unique combinations of *month* and *sample site*). Random intercepts, which were assumed in the mixed models, were highest for Slaunch Fork (intercept = 0.76), intermediate for Camp Creek (0.50), and lowest for Cabin Creek (0.27).

Table 1 Summary of linear mixed-effects size-spectra model comparisons

Model	*df*	*AIC*	χ^2 (*df*)	*p*
1 + *M* + (1 ǀ site)	4	437.87		
Month + *M* + (1 ǀ site)	7	431.95	11.92 (3)	0.01
Month + *M* + (1 ǀ site)	7	431.95		
Month × *M* + (1 ǀ site)	10	421.48	16.47 (3)	< 0.01
Month × *M* + (1 ǀ site)	10	421.48		
Month × *M* + **Taxa** + (1 ǀ site)	11	420.55	2.92 (1)	0.09
Month × *M* + (1 ǀ site)	10	421.48		
Month × *M* + **Taxa × *M*** + (1 ǀ site)	12	421.77	3.71 (2)	0.16
Month × *M* + (1 ǀ site)	10	421.48		
Month × Taxa × *M* + (1 ǀ site)	18	425.67	11.81 (8)	0.16
Month × *M* + (1 ǀ site)	10	421.48		
Month × *M* + (1 + **Month** ǀ site)	19	433.96	5.52 (9)	0.79

In each of the pairwise model comparisons, the specific model component being tested (e.g., multiplicative interaction between Month and Body Mass [*M*] vs. an additive function) for significance is shown in bold text. Significance levels (*P* values) were obtained using likelihood ratio tests. The random effect of study site is indicated by '(1 ǀ Site)' notation and is assumed in all mixed models. The model including Month in the random effect term is a random slopes model. Degrees of freedom (*df*) and Akaike information criterion (*AIC*) values are shown for individual models. Chi-square (χ^2) statistics (*df* in parentheses) and *p* values are shown for pairwise comparisons. Significance of a given model component is inferred at $p \leq 0.05$

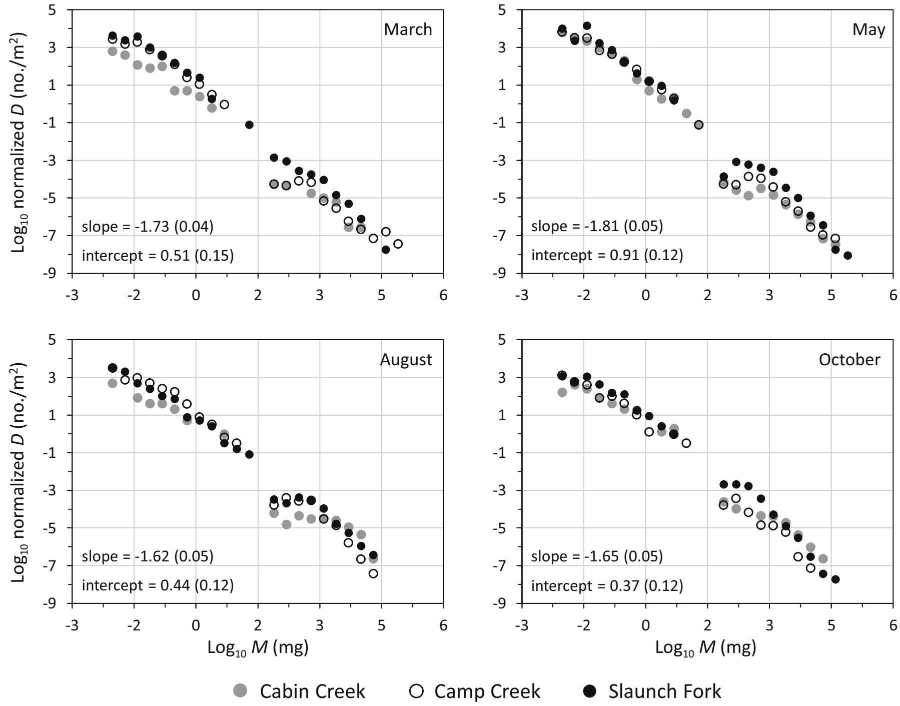

Fig. 1 Normalized density (D) size-spectra plots for macroinvertebrate and fish data collected in March, May, August, and October. Months are shown as separate plots and sample sites are indicated by symbols (see key at bottom). Size-spectra model coefficients ($\pm$ 1 S.E., shown in parentheses) from the most parsimonious model (*Month* $\times$ *Body Mass* + [1 | *Site*]; see Table 1) are shown in each plot. In each plot, points to the left of the $\mathrm{Log}_{10}\, M = 2$ mark are invertebrates and points to the right are fishes. To facilitate direct comparison, all plots are shown with identical axes and gridlines

Discussion

Accounting for seasonal variation in NSS model parameters

Decreasing NSS slopes necessarily imply one or both of two changes: relatively small organisms become more abundant, thereby increasing D within smaller M bins and elevating the left side of the NSS, and/or relatively large organisms become less abundant, thereby decreasing D within larger M bins and lowering the right side of the NSS. Following this logic, the May decrease in the NSS slope (relative to March; see Fig. 1) can be attributed to high densities of small macroinvertebrates. Invertebrate densities within the five smallest $\log_2 M$ bins (ranging from 0.013 to 0.410 mg dry mass) were particularly high in May, while densities of the much larger fishes were comparable between March and May. Thus, the left side of the May NSS was elevated and the overall NSS slope steepened. In August, densities of the smallest macroinvertebrates decreased slightly, relative to May, while densities of the largest fishes increased. Together, these changes produced an August NSS with a shallower slope that persisted through October (Fig. 1).

Differential trends in D for small invertebrates and large fishes can potentially be explained by water temperature (see Morin et al., 1995) and the annual accumulation of degree days. Because mean daily water temperatures remained $< 10°\mathrm{C}$ through March 2014, growth of benthic macroinvertebrates and fishes would have remained low. As temperatures warmed through the spring and summer months, macroinvertebrate and fish production would have increased (e.g., Hynes, 1970; Vannote & Sweeney, 1980; Brittain, 1982; Jenkins and Burkhead, 1994; Stauffer et al., 1995; Stewart & Stark, 2002), but at different initial rates because minimum thermal thresholds for growth are generally lower for macroinvertebrates than for fishes (Corkum, 1992; Chezik et al., 2013). Using 10 and 14°C thresholds for invertebrates and fishes, respectively (see Methods and Materials), we expect that the growing season would have begun for invertebrates about 1 month sooner than for fishes (April vs. May; see Fig. 2A). This difference can explain why D increased for the smallest size classes in May, while D remained relatively constant for larger size classes. Production of early invertebrate instars would start in April when mean daily temperatures consistently exceeded 10°C, but fish production would not begin until May.

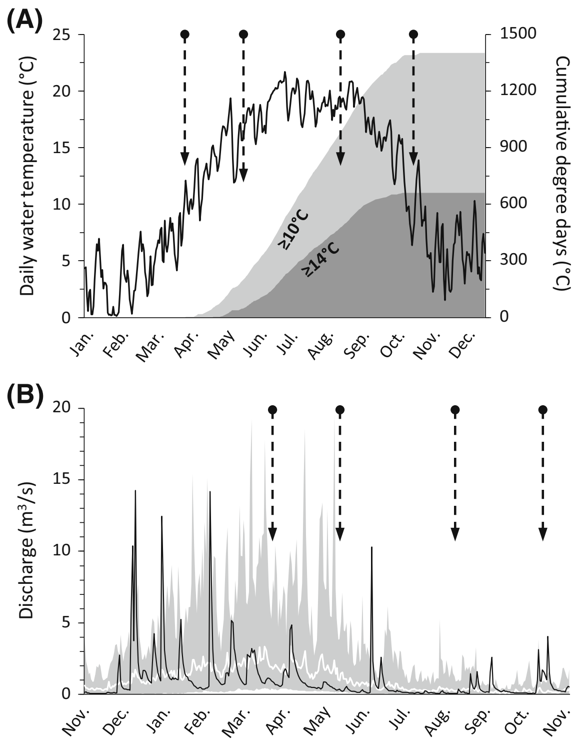

Fig. 2 Plots illustrating the timing of the four seasonal samples in Slaunch Fork, relative to intra-annual patterns of water temperature (**A**) and discharge (**B**). In panel A, mean daily water temperature is shown as a solid black line (primary *y*-axis) for the complete 2014 calendar year. Cumulative degree days are shown by gray shaded areas (secondary *y*-axis). Light gray corresponds to a $\geq$ 10°C minimum growth threshold. Dark gray corresponds to a $\geq$ 14°C growth threshold (see main text). The four seasonal sampling dates are shown as dashed vertical arrows. Water temperature readings were collected at 15-min intervals. In **B**, mean daily discharge records from November 1, 2013 to November 1, 2014 are shown as a solid black line. Long-term discharge records (1946–2014) are shown by the white solid line (daily means over the entire period of record) and gray shaded area (5th to 95th percentiles of daily discharge over the period of record). Sampling dates are again shown as dashed arrows. Records prior to January 1, 2014 are included in panel B to illustrate the potential effect of winter flooding on subsequent spring (March) samples

A similar explanation may account for the observed increase in August and October NSS slopes, relative to May (see Fig. 1). By August, fishes in each of the study streams experienced a substantial window for growth, as indicated by a rapid increase in cumulative degree days (Fig. 2A). This fish growth, combined with recruitment of new adults, would have elevated the right side of the NSS, thereby increasing the NSS slope (i.e., making it less steep). A similar increase in the NSS slope, driven by rapid summer growth of relatively large organisms, was reported by Dossena et al. (2012) in a mesocosm study of warming effects on aquatic biota. Additionally, invertebrate *D* in August and October samples may have been diminished by summer emergence events (Hynes, 1970; Merritt et al., 2008), thereby lowering the left side of the NSS and increasing the slope. This could have a significant impact on NSS slopes, as emergence rates from high-elevation streams peak in July for numerous insect taxa (e.g., Füreder et al., 2005; Harper & Peckarsky, 2006).

Unlike the slopes, changes in NSS intercepts are thought to indicate system-level processes that have simultaneous, proportional influences on all size classes (Trebilco et al., 2013; Sprules & Barth, 2016). Accordingly, NSS intercepts are often interpreted as indices of ecosystem productivity or ‘height’ (Kerr & Dickie, 2001; Daan et al., 2005). This interpretation could explain the substantial increase in NSS intercepts between March and May (Fig. 1). As noted above for NSS slopes, the growing season began between April and May for invertebrates and fishes (see cumulative degree days in Fig. 2A). Growth of current residents and recruitment of new individuals would therefore tend to occur in all size classes, raising the overall NSS intercept. However, instream growth through the summer months cannot explain the large decrease in the August and October NSS intercepts. This decrease was counterintuitive because degree days continued to accumulate for invertebrates and fishes through September, creating an opportunity for the NSS intercepts to increase again in August. Instead, we suggest that the lower NSS intercepts in August and October may reflect a large early-June flood event (Fig. 2B). This flood was the highest June discharge event on record (dating to 1946) and may have greatly reduced both invertebrate and fish *D* (Stock & Schlosser, 1991; Miller & Golladay, 1996). Thus, we propose that seasonal variation in the NSS intercept was likely driven by a combination of seasonal shifts in water temperature and hydrologic disturbance.

A broader context for our stream size-spectra results

Direct comparison with size-spectra results from other lotic systems is difficult because the standardized method of Kerr and Dickie (2001) has not been widely adopted in stream and river research. Lotic size-spectra studies have used a variety of taxic and ataxic datasets, combinations of taxonomic groups (periphyton, meiofauna, macroinvertebrates, fish), normalized and non-normalized *D* (and biomass) estimates, and *M* bin sizes ($\log_2$, $\log_5$, $\log_{10}$). Recognizing this variation, Morin (1997) encouraged authors to publish their raw data, thereby allowing others to recalculate size-spectra results for use in direct comparisons.

For now, we note that some evidence of generality does exist when comparing our size-spectra results with previous lotic studies. For instance, Cattaneo (1993) used identical methods (ataxic, normalized data within $\log_2$ *M* bins) with combined periphyton and invertebrate data to model size-spectra in three eastern Canada streams. While she reported on biomass (*B*), rather than *D*, her results are directly comparable with ours because the slope of the normalized *B* size-spectrum is equivalent to the slope of the NSS for $D + 1$ (see Peters, 1983; Sprules & Barth 2016; this $D = B + 1$ slope conversion factor was also confirmed for our own NSS results; data not shown). When converted to normalized *D*, the NSS slopes of Cattaneo (1993) range from − 1.97 to − 1.81, indicating lower densities of large individuals, relative to smaller organisms, in their study streams. In a separate study of 12 streams in eastern Canada, Morin & Nadon (1991) used a combination of original samples and literature data on the abundances of microscopic organisms (bacteria and ciliates), periphyton and invertebrates to model the community-level size-spectrum, reporting a NSS slope of ca. − 2 (after converting normalized *B* to *D*; see above). Huryn & Benke (2007) combined data on macroinvertebrate and fish *D* in two New Zealand streams and found NSS slopes ranging from − 1.91 to − 1.59 (after applying a − 1 conversion factor to obtain normalized *D* slopes from their reported non-normalized values; see Eqs. 14 and 15 in Marquet et al., 2005). And Poff et al. (1993) observed a community-level NSS slope of − 1.82 (after converting non-normalized to normalized slopes as above) when they combined meiofauna, macroinvertebrate, and fish samples from a fourth-order Virginia (USA) Piedmont stream. Similarity between the slope of this latter study and our southern West Virginia results (Fig. 1) is particularly interesting, given the geographic proximity between study sites. If the slopes of NSS, as reported herein and by Morin & Nadon (1991), Cattaneo (1993), and Poff et al. (1993) are broadly representative of their respective regions, these results would provide preliminary evidence of a latitudinal size-spectra gradient, with NSS slopes becoming flatter (i.e., relatively high densities of larger individuals) at lower latitudes.

Resolving differences between community-level datasets and samples of individual taxonomic groups would be particularly helpful in building a more robust understanding of size-spectra patterns. We detected no significant differences in NSS slopes or intercepts when the identities of the two major taxonomic groups, benthic macroinvertebrates and fishes, were included in our NSS models (Table 1). This continuous, community-level NSS relationship was consistent with theoretical predictions and is thought to reflect the transfer of energy between predators and their prey (Kerr & Dickie, 2001; Marquet et al., 2005; Trebilco et al., 2013; Andersen et al., 2016). Our community-level results were also comparable to empirical lake and marine studies that reported a continuous size-spectrum among trophic levels (e.g., Schwinghamer, 1981; Jennings & Mackinson, 2003; Yurista et al., 2014). However, the prevalence of constant size-spectra relationships within and among trophic levels is questionable in lotic systems. For example, the NSS slope of Poff et al. (1993) was driven entirely by differences in the average densities of the three taxonomic groups in their study; no evidence of negative *D* versus *M* relationships was observed within taxonomic groups (see Fig. 2 of Poff et al., 1993).

Nevertheless, it is increasingly clear that the NSS has the potential to serve as a simple, integrative tool for understanding among- and potentially within-trophic level linkages in lotic ecosystems. This is relevant for basic and applied research because a strong scaling relationship among size-structured assemblages of invertebrates and fishes implies that abundance and size-structure within one group (i.e., trophic level) can be predicted, with at least a moderate degree of accuracy, from information on the other group (see Cyr & Peters, 1996). Indeed, efforts to predict fish abundance or productivity within size-structured fisheries are foundational to the history of size-spectra research (Morin, 1997; Kerr & Dickie, 2001) and our results indicate that this approach may be applicable in at least some lotic systems.

One major caveat when interpreting or comparing our NSS models is the fact that our samples were collected in an unusual water year. A high frequency of large flood events occurred through the winter months, prior to collection of March samples, and a major summer storm occurred between the May and August samples (Fig. 2B). These floods matched or exceed the 95th percentiles of corresponding daily discharge over the past 70 years and likely had a strong, negative impact on local invertebrate and fish densities (Stock & Schlosser, 1991; Miller & Golladay, 1996). If so, the March 2014 samples may have underestimated typical fish and invertebrate densities in each of the study streams, with potential carryover effects on the August and October samples. (We assumed that the Slaunch Fork discharge data were representative of discharge in the other two ungauged study streams as heavy precipitation and flooding were widespread throughout southern West Virginia in late 2013 and 2014.) This would clearly undermine the assumption that our results may be representative of 'normal' conditions in the study region.

However, the observation that invertebrates and fishes consistently adhered to common NSS slopes and intercepts in each of the four sample months, despite significant changes in the overall NSS parameters among months, also suggests a high level of synchrony in the regulation of invertebrate and fish size-structure. Had the NSS parameters differed among invertebrate and fish models, it might have implied a 2-stage dynamic where each taxonomic group (i) responded independently to an environmental shift or disturbance, then (ii) reacted to the other group (e.g., fish predators adjusting to invertebrate prey abundance) with a lagged time response. Instead, the fact that the seasonal NSS parameters were common among taxonomic groups, but shifted in synchrony as the overall NSS parameters changed among seasons, suggests that organisms within size-structured stream communities may track and respond to abundances of smaller and/or larger organisms in near real time. The temporal dynamics that underpin aquatic size-spectra are not yet well understood (see Silvert & Platt, 1978; Heath, 1995; Datta et al., 2010). But if our interpretation of flood effects on the seasonal size-spectra is correct, then collecting periodic, repeat samples after a known disturbance may be an effective way to enhance the understanding of the size- and time-dependent connections that link organisms within the size-spectrum.

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Online Resource 1

Seasonal comparison of community-level size-spectra in southern coalfield streams of West Virginia (USA)

HYDROBIOLOGIA

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LEGEND – This is a compilation of summary information on each of the three sample streams included in this study. For each stream, we include a map of the parent county with elevation indicated by the color ramp and the study site shown as a white circle. Total numbers of fish species and macroinvertebrate taxa (general or family level identification) collected throughout the year (i.e., summed among the four sampling events) are shown at top. Summary physical habitat characteristics, including sample site latitude and longitude, basin area (upstream of the study site), mean wetted channel width, survey reach length, total survey area (as mean width × length), and mean channel gradient are shown in the upper-left table for each site. Appalachian Stream Classification values were taken from Olivero Sheldon et al. (2015)[1]. Water chemistry variables, including temperature, pH, specific conductivity, and dissolved oxygen, were measured during each sampling event and are shown in the center table. Photos of each site are shown at bottom.

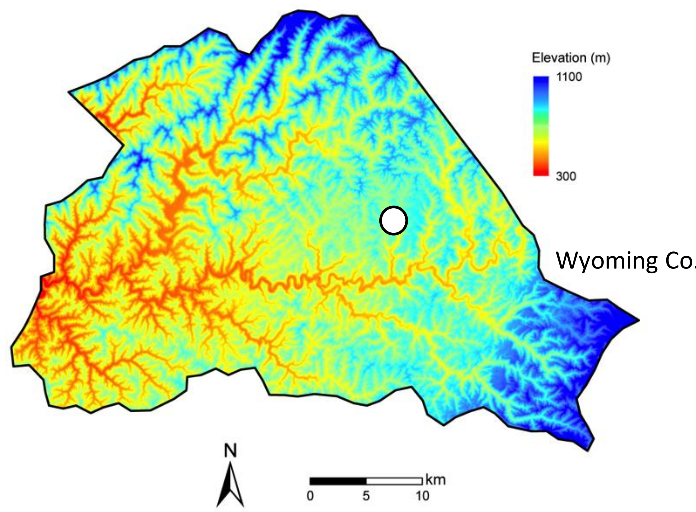
[1] – Olivero Sheldon, A., A. Barnett & M. G. Anderson, 2015. A stream classification for the Appalachian Region. The Nature Conservancy, Eastern Regional Office, Boston, MA.

Cabin Creek

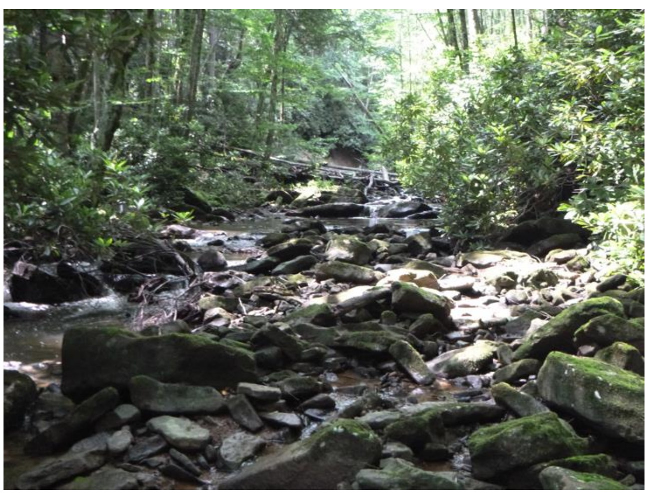
Wyoming County, West Virginia

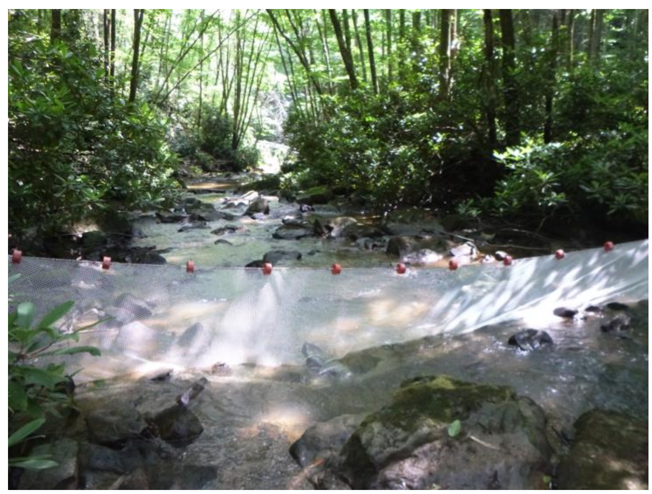
Fish species: 11   Macroinvertebrate taxa: 38

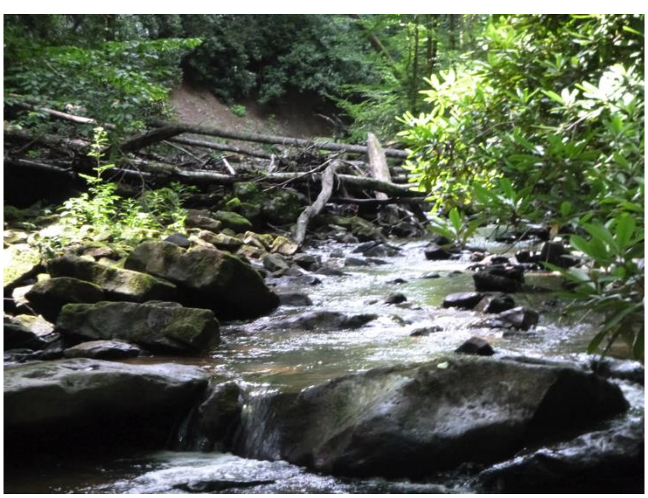
Latitude (dd)	37.617
Longitude (dd)	-81.454
Basin area (km^2)	18.46
Channel width (m)	10.9
Reach length (m)	100
Survey area (m^2)	1097
Mean gradient (%)	5.2
Appalachian Stream Classification	Perennial runoff, transitional cool, medium gradient



Environmental variable	March	May	August	October
Water temperature (°C)	4.4	14.4	17.5	11.3
pH	5.0	6.0	6.4	5.0
Specific conductivity (μS/cm)	77.9	83.1	116.2	99.9
Dissolved oxygen (mg/L)	11.83	8.95	8.60	9.65





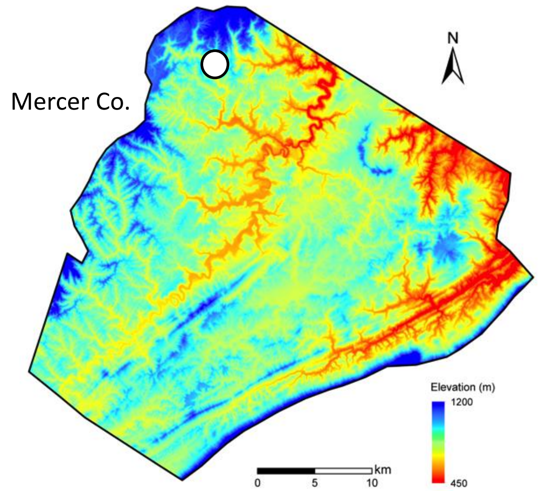


Camp Creek

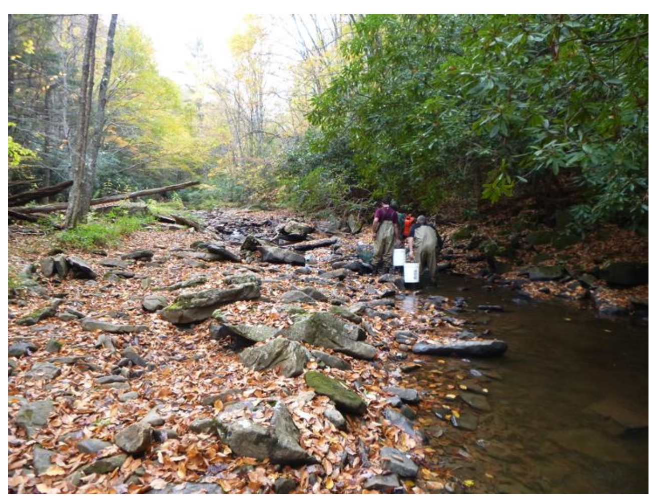
Mercer County, West Virginia

Fish species: 10 Macroinvertebrate taxa: 54

Latitude (dd)	37.550
Longitude (dd)	- 81.131
Basin area (km^2)	26.05
Channel width (m)	13.1
Reach length (m)	153
Survey area (m^2)	2012
Mean gradient (%)	3.2
Appalachian Stream Classification	Perennial runoff, transitional cool, medium gradient



Environmental variable	March	May	August	October
Water temperature (°C)	5.4	15.6	16.5	12.4
pH	4.5	5.0	5.5	5.0
Specific conductivity (µS/cm)	141.4	92.6	206.2	71.3
Dissolved oxygen (mg/L)	11.60	9.05	7.20	9.37

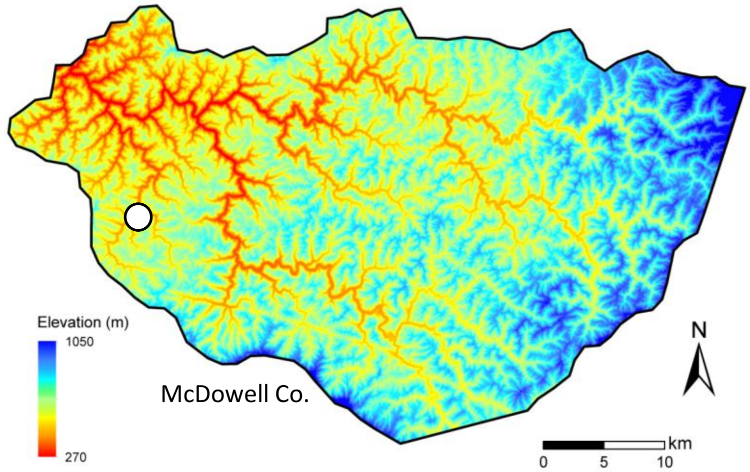


Slaunch Fork

McDowell County, West Virginia

Fish species: 19 Macroinvertebrate taxa: 60

Latitude (dd)	37.396
Longitude (dd)	-81.889
Basin area (km^2)	35.4
Channel width (m)	11.3
Reach length (m)	185
Survey area (m^2)	2093
Mean gradient (%)	2.3
Appalachian Stream Classification	Perennial flashy, transitional cool, medium gradient



Environmental variable	March	May	August	October
Water temperature (°C)	5.3	15.4	18.6	12.8
pH	5.5	6.4	6.4	--
Specific conductivity (µS/cm)	77.6	203.1	171.5	131.7
Dissolved oxygen (mg/L)	11.40	8.62	7.66	9.30