Hydrobiologia (2006) 568:309–316
DOI 10.1007/s10750-006-0208-y
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Primary Research Paper

Effects of stream size on taxa richness and other commonly used benthic bioassessment metrics

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Received 27 April 2005; in revised form 10 March 2006; accepted 24 March 2006; published online 29 May 2006

Key words: macroinvertebrates, stream size, river continuum concept, bioassessment, species richness, EPT

Abstract

Benthic macroinvertebrate samples were collected from natural substrates in disturbed and undisturbed South Carolina upper coastal plain streams to determine if taxa richness and other bioassessment metrics were significantly related to stream size as predicted by the River Continuum Concept (RCC). Linear, quadratic, and lognormal regression models indicated that stream width was positively related to total number of taxa; number of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa; and total number of organisms. Linear regression showed that the expected number of taxa at undisturbed sites ranged from 35 in 2.0 m wide streams to 64 in 16.0 m streams. Comparable values were 8–20 for EPT and 109–261 for number of organisms. Stream width was inversely related to biotic index values indicating a decrease in average organism tolerance with increasing stream size. ANCOVA showed that the effects of stream size were similar for disturbed and undisturbed sites. Rank correlations and multidimensional scaling (MDS) showed that Lepidoptera and Trichoptera were more abundant in larger streams and Annelida in smaller streams. Stream size related changes in benthic macroinvertebrate community composition are often ignored in bioassessment protocols; however, failure to adjust metrics for stream size can lead to erroneous conclusions. Adjustments are possible by analyzing regression residuals stripped of stream size related variance, dividing the area beneath the maximum taxa richness line into equal size units for metric scoring, or scaling metrics based on predicted reference values.

Introduction

The River Continuum Concept (RCC) is an important conceptual framework for understanding changes in biotic communities with progression from headwater to higher order stream reaches (Vannote et al., 1980). This progression results in a gradient of abiotic and biotic conditions including flow regime, temperature, insolation, food quality and quantity, and substrate composition that result in predictable changes in benthic macroinvertebrate assemblages. In addition to changes in macroinvertebrate functional group composition, the RCC predicts that the taxonomic richness of benthic communities changes with stream size, reaching a maximum in mid-order streams where environmental heterogeneity is greater than in headwaters or large rivers (Minshall et al., 1985). This prediction is empirically supported by data from temperate zone streams (e.g., Minshall et al., 1985; Grubaugh et al., 1996; Céréghino et al., 2003), especially those with relatively steep gradients in headwater reaches (Brussock & Brown, 1991). However, local changes in hydraulic and geomor-

phic factors can cause departures from expectations (Brussock & Brown, 1991; Wright & Li, 2002) as can localized environmental conditions such as ice formation and availability of food (Andrews & Minshall, 1979). In Brazilian streams, Melo & Froehlich (2001) found that taxonomic richness peaked in lower order stream reaches than predicted by the RCC suggesting that species richness patterns in tropical streams may differ somewhat from temperate streams.

The longitudinal changes in benthic macroinvertebrate community composition predicted by the RCC have significant implications for the application of macroinvertebrate bioassessment techniques to streams because such changes could be confounded with disturbance related changes. Many bioassessment protocols show little or no provision for changes in community structure associated with stream size, although Royer et al. (2001) demonstrated that macroinvertebrate bioassessment methods used on small streams must be modified for application in larger rivers. If important and commonly used bioassessment metrics like taxa richness naturally change with downstream progression as predicted by the RCC, failure to consider these changes will result in inaccurate comparisons between streams or stream reaches of different size.

This study tested the hypothesis that taxa richness and other commonly used bioassessment metrics were not significantly affected by stream size. The hypothesis was tested on disturbed and undisturbed first through fourth order streams on the upper coastal plain of South Carolina (USA). The RCC has not been tested in these streams, which may function differently than temperate zone streams with steeper gradients (Benke & Meyer, 1988) where the RCC may be more applicable.

Materials and methods

Study area and field methods

The study was conducted on 27 sites in 12 first through fourth order streams on the Savannah River Site (SRS), a 780 km^2 Department of Energy (DOE) reservation on the upper coastal plain of South Carolina. Sand was the predominant substrate in most streams, and woody debris (e.g., snags, logs, twigs, and leaves) constituted most of the instream structure along with overhanging shoreline vegetation, undercut banks, root masses and aquatic plants (in larger streams). The streams were about 2–16 m wide, 0.6–2.5 m/km in average gradient, mildly acidic (pH 4.5–6.9), and had relatively low conductivity (11–104 μS/cm). Mesohabitats generally consisted of pools and runs; riffles were scare. All sample sites had substantial flow and none were associated with extensive floodplain swamps that remained flooded for extensive periods as is typical of higher order coastal plain rivers (Benke & Meyer, 1988). Some of the streams were largely undisturbed with little or no agriculture, urbanization, or industrialization in their watersheds. Others receive or received discharges from industrial facilities or seepage basins (where radioactive or other toxic materials were deposited) or were altered by changes in flow regime, construction activities, or prior discharge of heated nuclear reactor cooling water. Conditions were improving in most disturbed SRS streams during this study because of environmental remediation programs and the shutdown of the SRS nuclear reactors in the 1980s.

Sixteen sites were sampled in 1997, 18 in 2000, and 22 in 2003; 12 were sampled in all 3 years. Sampling was conducted in the fall when most insect larvae were comparatively large prior to emergence. The multiple habitat sampling protocol (SCDHEC, 1998) used in this study was similar to other methods used to collect macroinvertebrates for bioassessment and regulatory purposes (Barbour et al., 1999). In 1997 and 2000, sampling was conducted for two man-hours at each site by sweeping with a D-frame dip net (800×900 μm mesh) along shoreline areas, sorting fine substrates with a hand sieve, and by hand collecting from the different natural substrates found at each site. Generally similar methods were used in 2003 except that sampling was conducted for three man-hours rather than two, with the last 1.5 h directed mainly towards collection of additional species rather than collecting more individuals of species already represented in the collections. All macroinvertebrate samples were taken to the laboratory, identified to the lowest practical taxonomic level (generally genus or species), assigned to functional groups using appropriate references (e.g., Merritt & Cummins, 1996), and assigned a pollution tol-

erance rating (NCDEHNR, 1997) for Biotic Index (BI) calculations. The BI value for a site was calculated by averaging the tolerances of the individual taxa weighted by taxon abundance.

The sampling protocol used in this study emphasized the survey of all representative stream habitats with the objective of collecting as many taxa as possible rather than collecting all individuals observed. Thus, numbers of organisms collected with this protocol may be less than with other methods. Variables generated by this (and similar) protocols can be considered more accurate when related to taxa richness and community composition and less accurate when related to numbers of organisms.

Stream width at the water surface was measured at each sample site before or after macroinvertebrate sampling at 7–12 evenly spaced transects across the stream perpendicular to the direction of water flow.

Data analysis

Total number of taxa; number of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa; and BI values were tested against stream size using a linear model, although lognormal (Minshall et al., 1985) and quadratic models (i.e., second degree polynomial model, Melo & Froehlich, 2001) were also examined. The simplest model (i.e., with fewest parameters) is usually preferred when more than one model is theoretically appropriate, unless the improved fit of more complex models is significant relative to the increase in number of parameters in these models (Motulsky & Christopoulus, 2003). In this case, the linear model was considered the basic model and the improvement in fit provide by the other models was tested relative to it. An *F*-test of the squared polynomial term was used to determine if the quadratic model provided a significantly better fit than the linear model. Akaike's Information Criterion (AIC with correction for small sample size, Motulsky & Christopoulus, 2003) was used as a measure of the increase in goodness of fit provided by the lognormal model relative to the linear model because the linear model was not nested within the lognormal model as it was within the quadratic model. Models with lower AIC scores are more likely to be correct. Analysis of Covariance (ANCOVA) with disturbance (i.e., disturbed vs. undisturbed) as a categorical factor and stream width as a covariate was used to test if relationships between stream size and the benthic metrics differed between disturbed and undisturbed streams.

Sample sizes were 16 for 1997, 18 for 2000, and 22 for 2003. Combining data across years produced a comprehensive data set with a larger sample size of 27 (i.e., 27 unique sites). Data from sites sampled in more than 1 year were averaged to produce the comprehensive data set since repeated samples from the same site were not independent. Before combining data, the possible effects of differences in sampling effort (Li et al., 2001) between 1997, 2000, and 2003 were investigated using repeated measures ANOVAs with data from the five undisturbed sites sampled all 3 years. Data from only undisturbed sites were used to avoid confounding temporal changes in disturbance with temporal changes in sampling effort at disturbed sites.

Data were analyzed by individual years and all years combined (i.e., the comprehensive data described above) for both the identification of best fitting model type (linear, quadratic, and lognormal) and the ANCOVAs. Only the results of the comprehensive data analysis are presented because results for the comprehensive data and individual years were similar. Data were not transformed for the preceding analyses because all variables passed tests for normality (Kolmogorov–Smirnov) and constant variance (Spearman rank correlations between the absolute value of residuals and dependent variables).

Stream size related changes in assemblage structure were investigated by (1) calculating Spearman rank correlations between the percent abundance of individual taxa and stream width at undisturbed sites and (2) comparing a taxonomically based nonmetric multidimensional scaling (MDS) ordination (Clarke & Warwick, 2001) of the undisturbed sample sites with stream width. Similar analyses were conducted to evaluate the effects of stream size on functional group composition. Only undisturbed sites were used to avoid confounding disturbance related differences with stream size related differences. Combined data (with averages for sites sampled more than once) were used in the rank correlation analysis to maintain the assumption of independence required for statistical testing. However, individual yearly samples were used in the

MDS which was only descriptive. The MDS was based on a Bray–Curtis taxa by sample site by year matrix calculated from abundance data that were $\log_{10} + 1$ transformed to more equitably represent common and rare taxa (Clarke & Warwick, 2001). Both the MDS and the Spearman rank correlations were calculated with high resolution (mostly genus and species) and low resolution (mostly order) taxonomic data in case patterns differed with taxonomic level.

Statistical analyses were conducted with PRIMER (Clarke & Warwick, 2001) and SYSTAT 10.2 (SYSTAT Software Inc., 2002).

Results

Three hundred and fifty taxa comprising over 225 genera were collected from all sites combined; most were in the orders Diptera (mainly Chironomini, Orthocladiinae, Tanypodinae, and Tanytarsini), Trichoptera, Ephemeroptera, Odonata, Crustacea, Coleoptera, and Mollusca.[1] In contrast, the number of taxa at each site (or average number at sites sampled more than once) ranged from 9 to 76, the number of EPT taxa ranged from 0 to 20, and BI values ranged from 4.72 to 8.35. The number of organisms collected at each site ranged from 18 to 379.

Taxa richness, EPT, and total number of organisms collected per site were sometimes slightly greater in 2003 than in 1997 and 2000, but these differences were not significant ($p \leq 0.05$, Table 1). Similarity in taxa richness metrics among years despite changes in sampling effort suggests that the lower effort used in 1997 and 2000 was sufficient to accumulate most taxa likely to be collected with the sampling methods in use. Similarity in total number of organisms among years is likely due to the reduced effort to collect additional organisms during the latter portion of the longer 3 h sampling protocol used during 2003. This absence of sampling effort effect supported the use of combined data in the following analyses.

R^2 values for linear, quadratic, and lognormal regressions of taxa number on width differed little. The linear model ($R^2 = 0.44$) was significant at $p < 0.001$. The slight increase in goodness of fit associated with the quadratic model ($R^2 = 0.45$) was not significant ($p = 0.453$, F-test of a second degree polynomial term added to the linear model). Similarly, the minor improvement in fit associated with the lognormal model ($R^2 = 0.47$) was less than expected based on the increase in number of model parameters (AIC value of 138.1 compared with 136.9 for the linear model). These analyses indicated that the more parsimonious linear model adequately described the relationship between stream size and taxa number for the range of stream sizes in this study. Similar analyses showed that linear models were also best for describing the relationship between stream width and the other collective properties.

ANCOVA models including a linear stream width term and a categorical term for disturbance indicated that taxa number and EPT increased significantly with stream width ($p < 0.001$ for both models), and that these relationships were similar for disturbed and undisturbed sites (i.e., homogeneity of slopes, Fig. 1). Both variables were strongly correlated with the number of organisms collected ($r = 0.92$ and 0.80) which, in turn, was also significantly related to stream width ($p = 0.003$, Fig. 1). ANCOVA further showed that taxa number and EPT but not number of organisms differed significantly ($p < 0.001$) between disturbed and undisturbed sites. The expected number of taxa at undisturbed sites ranged from 35 in 2.0 m wide streams to 64 in 16.0 m streams. Comparable values were 8–20 for EPT and 109–261 for number of

Table 1. Differences in macroinvertebrate metrics among years at undisturbed macroinvertebrate sample sites

Year	Taxa number	EPT	Number of organisms
All undisturbed sites (13 sites)			
1997	40.2 (9.7)	13.1 (5.1)	125.0 (62.9)
2000	41.1 (15.5)	11.7 (7.4)	195.8 (102.9)
2003	45.7 (15.9)	11.1 (5.8)	199.4 (76.5)
Undisturbed sites sampled all 3 years (five sites)[a]			
1997	41.6 (11.2)	12.4 (5.7)	135.0 (73.1)
2000	38.6 (15.4)	11 (8.0)	195.2 (114.9)
2003	43.8 (6.6)	10 (4.9)	177.0 (16.8)

[a]Differences among years were analyzed for these sites and found not significant ($p \leq 0.05$, repeated measures ANOVA).

[1] Electronic supplementary material is available for this article at http://dx.doi.org/ 10.1007/s10750-006-0208-y and accessible for authorised users.

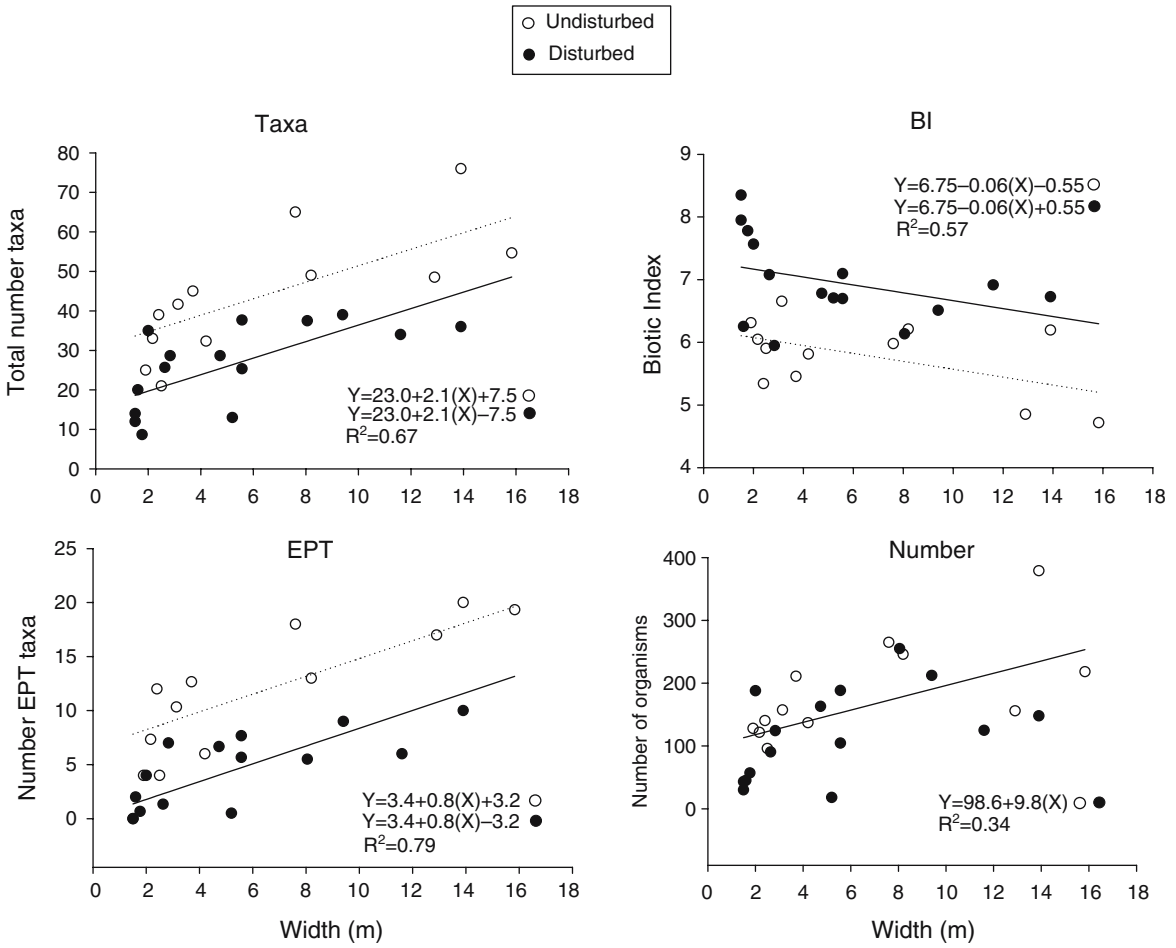

Figure 1. Relationship between macroinvertebrate metrics and stream size in upper coastal plain streams of South Carolina.

organisms. Including disturbance as a factor increased ANCOVA model R^2 values to 0.67 for taxa richness, 0.79 for EPT, and 0.40 for number of organisms.

ANCOVA showed that BI values were significantly related to stream width ($p = 0.026$), and that the relationship was inverse rather than direct (Fig. 1). This indicated that average organism tolerance increased as stream size decreased (because BI increases with organism tolerance). Like taxa number and EPT, average BI differed significantly between disturbed and undisturbed streams ($p < 0.001$, $R^2 = 0.57$).

Taxonomic composition was also affected by stream size, but not as strongly as the previous metrics. Spearman rank correlations with stream width were significant ($p \leq 0.05$) for Lepidoptera and Trichoptera, although the percent abundance of most taxonomic groups was unrelated to stream size (Table 2). Axis 1 in the MDS of undisturbed sites reflected a stream size gradient, with larger sites generally clustering on the right and smaller sites on the left (Fig. 2). The abundances as opposed to percent abundances in the Spearman correlation analysis of Tanytarsini, Trichoptera, Orthocladiinae, Lepidoptera, Ephemeroptera were directly correlated with axis 1, generally agreeing with the ANCOVA which showed increasing number of organisms with stream size (Fig. 1). Comparable analyses with lower level taxonomic data (mostly genus) produced similar findings so are not presented.

MDS of functional group data from the undisturbed sites did not reveal stream size related patterns in functional group composition. Similarly, there were no significant Spearman rank

Table 2. Spearman rank correlation coefficients (and probabilities of significance) between stream width and percent abundance of higher taxonomic groups of macroinvertebrates

Taxa	*R*s	*p*
Annelida	−0.34	0.27
Mollusca	−0.07	0.82
Crustacea	0.18	0.57
Ephemeroptera	0.14	0.64
Odonata	0.07	0.82
Heteroptera	−0.05	0.85
Megaloptera	−0.13	0.67
Plecoptera	0.13	0.68
Trichoptera	0.60	0.04
Lepidoptera	0.70	0.01
Coleoptera	0.13	0.67
Chironomini	−0.46	0.12
Orthocladiinae	0.03	0.92
Tanypodinae	0.20	0.51
Tanytarsini	−0.34	0.27

correlations between functional group percent composition and stream width.

A residual plot of taxa number indicated the importance of controlling for stream size when using stream size related metrics for bioassessment (Fig. 3). The large stream site "uc" had a slightly negative residual indicating the presence of fewer species than expected. However, this site possessed the third greatest number of species when uncorrected for stream size and, on this basis, would be considered excellent since high taxa richness indicates high biotic integrity. Conversely, the small stream site "pc" had a positive residual indicating the presence of substantially more species than expected for a stream of this size. However, uncorrected for stream size, this site had less than the average number of species suggesting low biotic integrity.

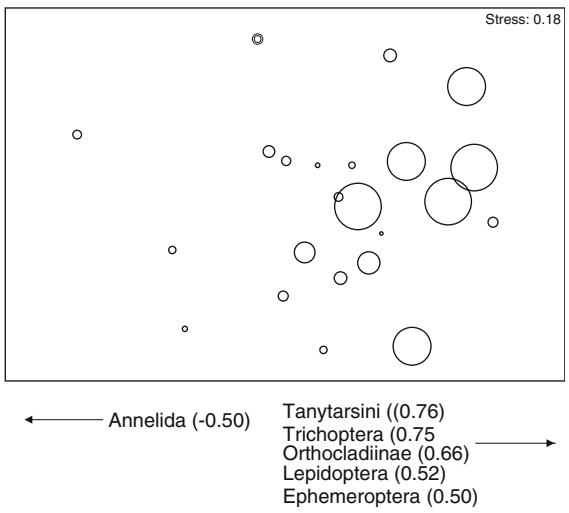

Figure 2. Ordination (nonmetric multidimensional scaling) of undisturbed stream sites based on macroinvertebrate assemblage structure. Bubble size is proportional to stream width. Also shown are Spearman correlations between the abundances of individual taxa and the ordination scores on the horizontal axis. Directions of increasing abundance are shown by arrows.

Discussion

The River Continuum Concept predicts that macroinvertebrate species richness peaks in medium size (third to fifth order) streams (Vannote et al., 1980). This relationship between species richness and stream size (often expressed as catchment area or stream order) appears graphically as a "hump" and can be described by a lognormal or quadratic model (Minshall et al., 1985; Melo & Froehlich, 2001). Strong positive relationships were observed between stream size and both total taxa richness and EPT taxa richness in our study. While our study was not designed to test the RCC, the observed linear increase in taxa richness with stream size was not incompatible with RCC predictions since the comparatively narrow range of stream sizes (first through fourth order) in the study may have represented only the ascending slope of the hump resulting in a linear rather than lognormal or quadratic fit.

Like stream size and taxa richness, a positive relationship was observed between stream size and number of organisms per sample. Sampling effort was similar among streams of different size suggesting that, on this basis alone, number of organisms collected should have been independent of stream size (or higher in smaller, shallower streams where benthic habitats were more accessible). In Appalachian streams, abundance increased with stream size in bedrock but not depositional habitats, while abundance in cobble increased only at higher stream orders (5–7) (Grubaugh et al., 1996). Further sampling with different protocols will be needed to verify relationships between stream size and macroinvertebrate abundance in South Carolina coastal plain streams because the

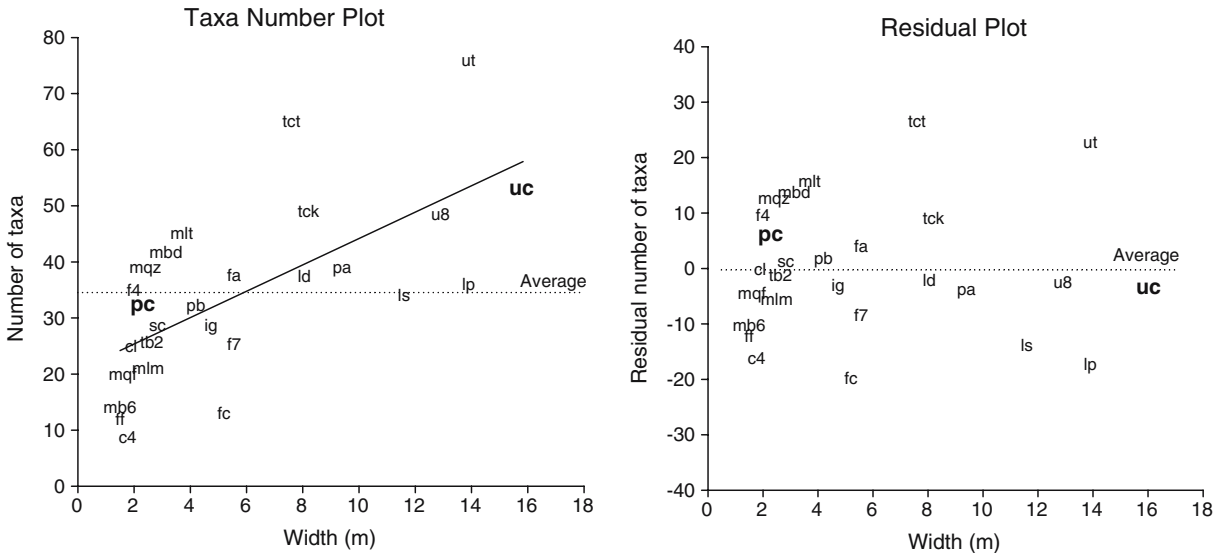

Figure 3. Relationship between taxa number, residual taxa number (i.e., taxa number with stream size related variance removed by regression analysis) and stream size. Two or three letter symbols designate individual stream sites.

sampling methods employed in this study were not designed to precisely assess abundance.

Trichoptera and Lepidoptera constituted a significantly greater proportion of the macroinvertebrate assemblages in larger streams. Lepidoptera consisted solely of *Parapoynx obscuralis*, which were associated with the aquatic vegetation found in higher order streams. More aquatic vegetation in larger streams may have also contributed to increases in Trichoptera with stream size because many Trichoptera larvae consume products of plant decomposition (Merritt & Cummins, 1996). Increases in these comparatively sensitive taxa contributed to the decrease in BI values that occurred with stream size (Fig. 1). Stream size related changes in taxonomic composition were also indicated by ordination, possibly because of stream size related differences in substrate composition, although methodological biases (such as failure to adequately sample deeper pools in larger streams) may have also played a role. In contrast, functional group composition was unrelated to stream size, perhaps because the functional group analysis was based on number rather than biomass. RCC related predictions concerning longitudinal changes in functional group composition may be better supported by biomass than numbers (Grubaugh et al., 1996).

Relationships between macroinvertebrate species richness and stream size may not always be apparent because the relationship between stream size and taxa richness will likely depend upon the region of the taxa richness "hump" under study. Thus, sampling small to medium size streams (i.e., the ascending leg of the hump) can result in an apparent linear relationship between taxa richness and stream size, sampling only middle size streams (i.e., the top of the hump) can result in weak relationships between taxa richness and stream size likely obscured by sampling variability, and sampling only medium to large streams (i.e., the descending leg) can result in a decreasing relationship between these variables. Also, there are situations where taxa richness may not vary predictably over even a wide range of stream sizes because of ecological factors that cause departures from the RCC, which seems to fit best in forested, temperate zone streams with appreciable headwater slopes (Ward, 1986; Brussock & Brown, 1991).

The results of this study indicate that taxa richness and other commonly used bioassessment metrics are significantly affected by stream size in first through fourth order streams on the upper coastal plain of South Carolina. Failure to understand the influence of stream size on these metrics can lead to erroneous conclusions con-

cerning stream health. It is likely that explicit tests of the relationship between bioassessment metrics and stream size contribute more to this understanding than general multivariate analyses of taxonomic data because the latter may be dominated by disturbance or other gradients. Where significant relationships exist, it will be necessary to adjust metric expectations for the effects of stream size by analyzing regression residuals stripped of stream size related variance (Fig. 3), dividing the area beneath the maximum taxa richness line into equal size units for metric scoring (Fausch et al., 1984), or scaling metrics based on predicted reference values (Yuan & Norton, 2003).

Acknowledgements

We wish to thank Dr R. Kelley of ETT Environmental, Greenville, SC for taxonomic identifications and help with field collections. We also thank an anonymous reviewer for suggestions that improved this paper. This report was developed during U.S. Department of Energy Contract No. DE-AC09-96SR18500.

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