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# Linear and Nonlinear Effects of Habitat Structure on Composition and Abundance in the Macroinvertebrate Community of a Large River

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**ABSTRACT.**—We used an experiment and regression analyses to quantify effects of spatial variation in habitat structure abundance on a riverine macroinvertebrate community under winter conditions. Concrete slabs (0.21 m<sup>2</sup>; n = 24) with different numbers of stones (mean individual stone surface area = 6.44 cm<sup>2</sup>) attached to upper faces were placed in the James River and retrieved after 28 d. Macroinvertebrate abundance and taxonomic richness on slabs were significantly positively related to stone abundance. Total macroinvertebrate abundance and abundance of oligochaetes (*Nais* spp.), Asiatic clams (*Corbicula fluminea*), caddisflies (Leptoceridae), riffle beetles (Elmidae) and stoneflies (*Strophopteryx* sp.) were linearly related to stone abundance. However, nonlinear relationships occurred between stone abundance and macroinvertebrate taxonomic richness and between stone abundance and abundance of dragonflies (*Erytrogomphus* sp.), caddisflies (Hydropsychidae), chironomids (*Eukiefferiella* spp.), mayflies (Ephemerelellidae) and stoneflies (*Taeniopteryx* sp.). Nonlinear relationships were usually characterized by dramatic increases in macroinvertebrate abundance and taxonomic richness across a gradient of increasing stone abundance when abundance was low (0–43 stones/0.08 m<sup>2</sup> slab face; 0–40% of slab face covered by stones), but weak responses to additional stones at higher stone abundance (84–160 stones/0.08 m<sup>2</sup>; 89–96% cover). These nonlinear relationships reflected similar nonlinear relationships between abundance of stones and particulate matter. We conclude that small quantities of habitat structure have significant positive effects on macroinvertebrate abundance and diversity in the James River during winter. At a local scale, habitat structure promotes macroinvertebrate colonization and retention by increasing habitat diversity. Stones and similar physical objects also indirectly benefit macroinvertebrates by trapping particulate matter that provides animals with food and additional habitat.

## INTRODUCTION

The abundance and type of habitat structure available in an ecosystem is an important determinant of biological community structure (Downes *et al.*, 2000; Ellner *et al.*, 2001). Habitat structure, defined here as physical objects in an environment that provide habitat (*e.g.*, rocks, trees, shells of sessile animals), promotes greater biomass, abundance and diversity of organisms by enhancing the abundance and variety of resources. For example, increased colonizable surface area and microhabitat diversity created by habitat structure reduces intensity of competition for living space (Downes *et al.*, 2000; Ellner *et al.*, 2001). Habitat structure also reduces the frequency of localized species extinctions by providing refuges from predation and physical disturbance (Bertness and Leonard, 1997; Lipcius *et al.*, 1998). Additionally, habitat structure indirectly benefits organisms by increasing the abundance and diversity of food resources (Fournier and Loreau, 1999; Siler *et al.*, 2001).

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Investigations conducted in a variety of ecosystems have demonstrated the beneficial effects of habitat structure. In studies of terrestrial communities, insect abundance and species richness were positively correlated with vegetation height and patch size (Fournier and Loreau, 1999; Collinge, 2000). Similarly, species richness of birds generally increases with forest patch size, and both clearcuts and second growth forests usually support fewer mammal species than mature forests with more diverse habitat structure (Trzcinski *et al.*, 1999; Lomolino and Perault, 2000). In aquatic ecosystems, habitat structure provided by stones, woody debris, plants, corals and mollusk shells stimulates increased abundance, production and diversity of organisms by creating multiple substratum types and variable hydrodynamic regimes (Bertness and Leonard, 1997; Lenihan, 1999; Downes *et al.*, 2000; Syms and Jones, 2000). Habitat structure also provides small aquatic organisms with refuges from predators and shear forces associated with wave action and strong currents (Stewart *et al.*, 1999; Lake, 2000). Furthermore, stones, woody debris and other physical objects indirectly increase food and habitat resources to macroinvertebrates by retaining particulate matter and providing substrata for algal colonization and growth (Downes *et al.*, 2000; Voelz and McArthur, 2000).

Although it is well established that habitat structure generally has positive effects on biological communities, a more complete understanding of relationships between habitat structure and community variables is needed to identify ecological patterns and devise improved strategies for maximizing diversity, abundance and production of commercially and ecologically important species (Lipcius *et al.*, 1998; Lenihan, 1999). Identification and consistent use of biologically meaningful measures of habitat structure are considered critical in attaining these goals (Commito and Rusignuolo, 2000; Downes *et al.*, 2000). Appropriate spatial and temporal scales of measurement are also required for elucidating cause-and-effect relationships between habitat structure and community variables (Downes *et al.*, 1998; Attrill *et al.*, 2000). Finally, improved descriptions of functional relationships between habitat structure abundance and community attributes are needed (Bender *et al.*, 1998; Lipcius *et al.*, 1998). For example, nonlinear regression analysis techniques can produce more precise descriptions of relationships between habitat and community variables than the most commonly used statistical procedures that assume linear relationships between these variables (McClendon, 1994; Baldi and Kisbenedek, 1999).

We used a field experiment and both linear and nonlinear regression analysis to quantify response of a benthic macroinvertebrate community to spatial variation in habitat structure abundance. Primary goals were to determine if: (1) local differences in habitat structure abundance affected abundance and taxonomic richness of macroinvertebrates inhabiting a large river under winter conditions and (2) functional relationships between habitat structure abundance and several community variables were linear or nonlinear. Results from this study were used to generate hypotheses of specific biological causes for relationships between habitat structure abundance and community attributes.

#### METHODS

*Study site.*—The experiment was conducted in the Piedmont region of the upper James River, near Wingina, Nelson County, Virginia (37°38'N; 78°42'W). The James River has a drainage area of 9576 km<sup>2</sup>, and discharge at the study site averaged 51.0 ± 5.2 m<sup>3</sup>/s during the 28 d study period (mean ± 1 SE; R. White, USGS, Richmond, VA, pers. comm.). Riverbanks at the study site were lined with deciduous trees (*e.g.*, American sycamore and red maple) that buffered the river from the surrounding agricultural landscape. Benthic substrata at the site consisted of a mixture of boulders, cobble, gravel and sand. The pH at the study site was 7.0 on 14 November 1999 (n = 3 measurements).

*The experiment.*—The experiment consisted of 5 treatments with 5 replicates, in which habitat structure was manipulated by attaching patio stones to concrete slabs ( $40 \times 20 \times 4$  cm;  $0.21 \text{ m}^2$  total surface area) that simulated bare rock. No stones were attached to slabs constituting the no cover treatment, with “cover” referring to the relative surface area of slab face covered by stones. Aquarium sealant was used to attach stones to upper faces of slabs ( $0.08 \text{ m}^2$  surface area) in remaining treatments. Stones were attached to slabs at randomly determined locations in low and intermediate cover treatments until approximately 13% and 40% of slab faces were covered, respectively (Table 1). Slab faces in high and very high cover treatments were almost completely covered with one and two layers of stones, respectively (Table 1). One slab of the no cover treatment overturned during the study, and this replicate was excluded from statistical analysis.

The experiment began on 14 November 1999 when slabs with attached stones (hereafter experimental substrata) were randomly placed on the riverbed within a  $2 \text{ m} \times 2 \text{ m}$  grid constituting the study site. Experimental substrata were separated by 0.5 m, and analysis of physicochemical measurements taken above or adjacent to substrata on 14 November 1999 indicated no differences in depth ( $67.3 \pm 0.7$  cm; overall mean  $\pm$  (ISE) SE;  $n = 24$ ), dissolved oxygen ( $10.7 \pm 0$  mg/L) and temperature ( $13.3 \pm 0$  C) among treatments (one way ANOVAs;  $P > 0.05$ ).

Experimental substrata were collected after 28 d on 12 December 1999. Each substratum was collected by quickly transferring it from the riverbed to a plastic tub located at the water surface. Stones were removed from the slab by hand, and both stone and slab surfaces were lightly scrubbed with a brush and rinsed to remove invertebrates and particulate matter. The slab and stones were then removed from the tub and stones were transferred to polyethylene bags so that stone abundance, stone volume, stone surface area and total substratum surface area could be quantified in the laboratory. Remaining tub contents were sieved through a  $40 \mu\text{m}$  mesh, and retained organisms and particulate matter were transferred to a jar and fixed in 5% buffered formalin.

*Habitat structure measurement.*—Several measures of habitat structure were recorded because more than one of these could have affected the macroinvertebrate community. Stone abundance was expressed as numbers of stones attached to the slab (Table 1). Stone volume (ml) was determined by placing stones in a graduated cylinder partially filled with

TABLE 1.—Mean (1 SE) number of stones, volume of stones, percent cover by stones and total substratum surface area in each treatment. NC, LC, IC, HC and VHC = no cover, low cover, intermediate cover, high cover and very high cover treatments, respectively. All stones were attached to upper faces (face surface area =  $0.08 \text{ m}^2$ ) of concrete slabs (total slab surface area =  $0.21 \text{ m}^2$ ). With exception of the NC treatment ( $n = 4$ ), all treatments consisted of 5 replicates

Habitat structure measurement	NC	LC	IC	HC	VHC
Number of stones	0	20.0 (0)	42.8 (0.9)	83.6 (4.3)	160.2 (4.0)
Volume of stones (ml)	0	214 (22)	414 (24)	887 (34)	1374 (30)
Percent cover (of slab upper face)	0	12.8 (1.0)	39.6 (1.6)	89.0 (2.5)	95.6 (0.9)
Percent cover (of entire slab surface)	0	4.9 (0.4)	15.2 (0.6)	34.2 (1.0)	36.8 (0.4)
Total substratum surface area ( $\text{cm}^2$ )	2080.0 (0)	2183.0 (0)	2300.5 (4.7)	2510.6 (22.1)	2905.2 (20.8)

water and recording change in water level (Table 1). Percent of slab face and total slab surface area covered by stones were visually estimated from photographs taken before and after the experiment (Table 1). Comparisons of photographs indicated no stones were lost during the experiment. Surface area of individual stones (mean  $\pm$  SE =  $6.44 \pm 0.14$  cm<sup>2</sup>; hereafter mean stone surface area) was estimated by wrapping 50 stones (2–3 per slab) in aluminum foil, weighing the foil and converting foil weights to area measurements using an equation constructed from a foil weight-to-area curve ( $Y = 3.0956 + 15.762X$ ;  $r^2 = 0.99$ ;  $P < 0.001$ ). Mean stone surface area was used to estimate total substratum surface area (slab + stones) available to macroinvertebrates (Table 1). We determined total substratum surface area using the following equation:

$$\begin{aligned} &\text{Total substratum surface area} \\ &= [(\text{mean stone surface area} \times \text{number of stones}) + \text{slab surface area}] \\ &\quad - [0.20 \times (\text{mean stone surface area} \times \text{number of stones})], \end{aligned}$$

where mean stone surface area is 6.44 cm<sup>2</sup>, and the quantity  $[0.20 \times (\text{mean stone surface area} \times \text{number of stones})]$  adjusts for surface area of stone and slab that were attached to each other and unavailable to macroinvertebrates. We based this adjustment on our estimate that 10% of stone surface area was attached to the slab, and that an equivalent area of slab was also unavailable for colonization.

*Macroinvertebrates and particulate matter.*—Within 24 h of returning to the laboratory, preserved organisms and particulate matter were sieved through a 500  $\mu$ m mesh overlying a 40  $\mu$ m mesh to separate macroinvertebrates from smaller particles, and material retained by each mesh was transferred to a separate jar containing 70% ethanol. Macroinvertebrates retained in the 500  $\mu$ m mesh were separated from other material with the aid of a stereomicroscope (10 $\times$ ). Remaining material from 40 and 500  $\mu$ m meshes was then combined, dried at 60 C and ashed at 500 C to quantify particulate organic matter (g ash-free dry mass = g AFDM; hereafter POM) and particulate inorganic matter (g ash mass; hereafter PIM; APHA, 1989). Macroinvertebrate abundance and taxonomic richness were expressed as the number of individuals and taxa collected from each experimental substratum, respectively. Taxonomic specialists confirmed or corrected identifications of all organisms (*see* Acknowledgments).

*Statistical analysis.*—One way ANOVAs and Tukey tests were used to identify treatment effects on the following response variables: macroinvertebrate abundance, taxonomic richness, POM and PIM. Before ANOVAs were conducted, response variable data were log ( $X + 1$ ) transformed to eliminate covariance between treatment means and variances, and scatterplots of transformed data points indicated this was achieved (Zar, 1999). If ANOVA indicated statistically significant treatment effects on a response variable ( $\alpha \leq 0.05$  except as described below), several least squares regression models were used to describe the functional relationship between habitat structure abundance and the response variable. Because 56 macroinvertebrate taxa were collected and there was a high likelihood of a type I error as a result of conducting multiple ANOVAs on the same data set, taxa were only included in regression analyses if ANOVA indicated a very highly significant effect on their abundance ( $\alpha \leq 0.001$ ; Bonferroni correction; Scheiner, 1993).

Stone abundance was used as the independent variable in all regression analyses. All habitat structure measures (Table 1) were highly correlated (Pearson correlation;  $r \geq 0.99$ ;  $P < 0.001$ ), and community attributes responded similarly if any habitat structure measure was used in regressions. Regression analysis consisted of comparing fits of four regression models to nontransformed data so that functional relationships between stone abundance

and response variables could be detected (Peake and Quinn, 1993; McClendon, 1994). Regression models tested were based on apparent relationships between stone abundance and response variables from scatterplots, and regression equations commonly found in the literature (Peake and Quinn, 1993; McClendon, 1994). First, simple linear regression ( $Y = a + bX$ ) was used to determine if there was a statistically significant linear relationship between stone abundance and the response variable of interest (McClendon, 1994). We then tested for nonlinearity by fitting a quadratic model ( $Y = a + bX + bX^2$ ) to the data and using an F test to determine if the  $R^2$  from the quadratic regression was significantly higher than the  $R^2$  from the linear regression (McClendon, 1994). This F test is recommended when comparing fits of polynomial and linear models because it accounts for increase in  $R^2$  due to chance and additional X variables in the polynomial regression (McClendon, 1994). Consequently, the relationship between stone abundance and the response variable was considered linear unless the F test revealed that the  $R^2$  produced by fitting the quadratic model to the data was significantly higher than the  $R^2$  from the linear regression (McClendon, 1994).

Following quadratic regression, we conducted another regression analysis using a cubic model ( $Y = a + bX + bX^2 + bX^3$ ), followed by F tests to determine if the cubic model fit the data better than linear or quadratic models (McClendon, 1994). Last, a power regression model ( $Y = a + X^b$ ) was fit to the data if scatterplot examination suggested this model might best describe the relationship (Peake and Quinn, 1993). The power model was considered best if the  $R^2$  from this regression was higher than that from the linear regression, and if  $R^2$ s from polynomial regressions were not significantly higher than the power regression  $R^2$  (Peake and Quinn, 1993). All statistical analyses were conducted using SYSTAT 9.0 (SPSS Inc., 1999, Chicago).

## RESULTS

Total macroinvertebrate abundance, macroinvertebrate taxonomic richness, POM and PIM clearly differed across experimental treatments (ANOVAs;  $P \leq 0.006$ ), and habitat structure had positive effects on each of these response variables (Figs. 1, 2). The linear regression model best described the relationship between stone abundance and total macroinvertebrate abundance, suggesting that increases in total macroinvertebrate abundance were generally proportional to increases in numbers of stones (Fig. 1A). In contrast, taxonomic richness increased dramatically between no cover and low cover treatments, but only small additional increases occurred between low and very high cover treatments (Fig. 1B). Similarly, responses of POM and PIM to increasing stone abundance were greatest when stone abundance was low (Fig. 2). The power model best described the nonlinear relationship between stone abundance and taxonomic richness (Fig. 1B), and the quadratic model best described POM and PIM responses to changing stone abundance (Fig. 2).

A total of 56 macroinvertebrate taxa were collected from experimental substrata, and a complete list of these taxa and their abundance in each treatment is available from the corresponding author. Ten taxa differed in abundance among treatments, and each was more abundant in one or more treatments with stones than in the no cover treatment (ANOVAs;  $P \geq 0.001$ ; Table 2). Regression analysis results indicated a mixture of linear and nonlinear responses of taxa to changing stone abundance. Significant positive linear relationships between stone abundance and numbers of *Nais* spp. (oligochaete), *Corbicula fluminea* (Asiatic clam), Leptoceridae (caddisflies) and Elmidae (riffle beetles) suggest abundance of these taxa increased in a similar manner across all levels of habitat structure

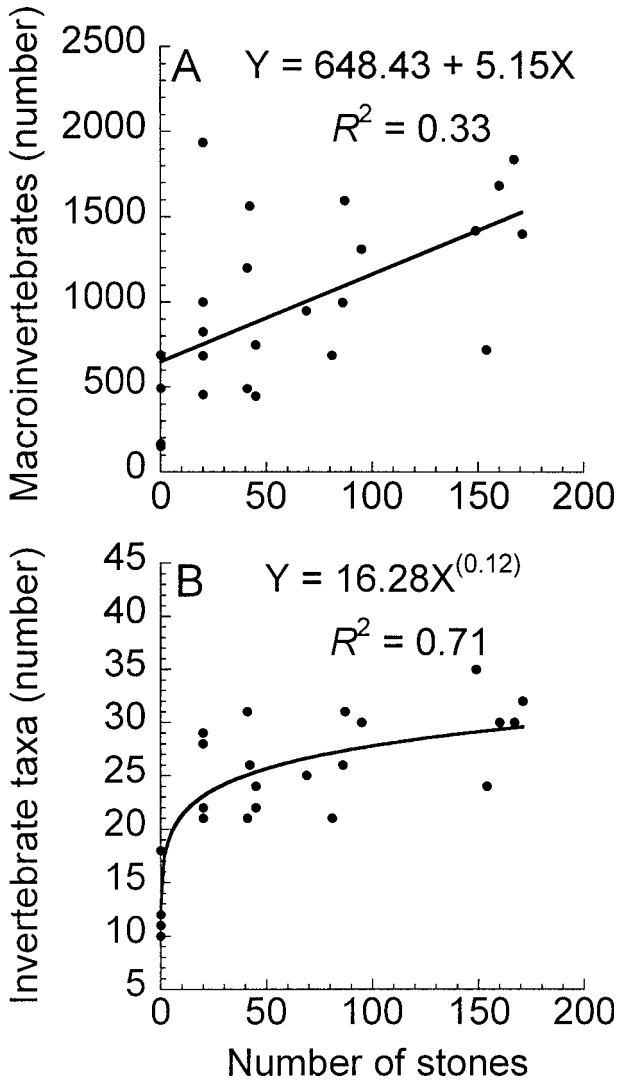


FIG. 1.—Scatter plots and regression curves describing relationships between number of stones on concrete slabs and total number of macroinvertebrates (A) and macroinvertebrate taxonomic richness (B). Exclusive of surface area provided by stones, total slab surface area was  $0.21 \text{ m}^2$ , and the surface area of the face where stones were attached was  $0.08 \text{ m}^2$ .

(Figs. 3A, B, D, E). Abundance of stones and the stonefly *Strophopteryx* sp. also were positively linearly related, but this relationship was relatively weak ( $Y = 5.96 + 0.06X$ ;  $R^2 = 0.18$ ;  $P = 0.042$ ; Table 2).

The quadratic model best described the relationship between abundance of stones and the chironomid *Eukiefferiella* spp. (Fig. 3F). *Eukiefferiella* abundance increased from no cover to high cover treatments, then declined when additional stones were present (Table 2; Fig. 3F). The cubic model best described the relationship between stone abundance and



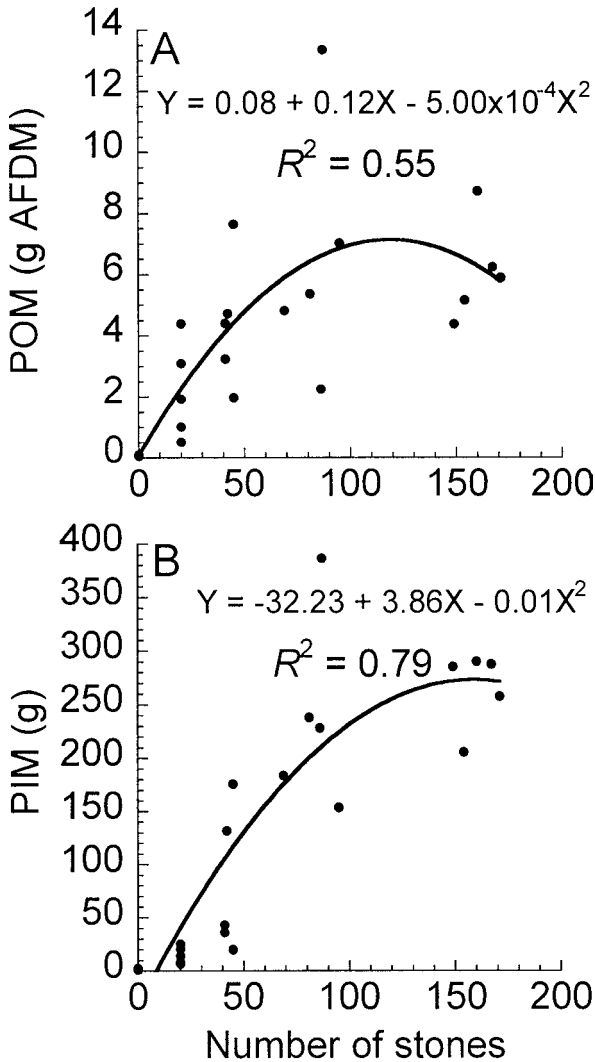


FIG. 2.—Scatter plots and regression curves describing relationships between number of stones on concrete slabs and particulate organic matter mass (POM; A) and particulate inorganic matter mass (PIM; B). Exclusive of surface area provided by stones, total slab surface area was  $0.21 \text{ m}^2$ , and the surface area of the face where stones were attached was  $0.08 \text{ m}^2$

abundance of Hydropsychidae (Fig. 3C) and nymphs of the dragonfly *Erpetogomphus* sp. ( $Y = 0.16 - 0.04X + 0.001X^2 - 5 \times 10^{-6}X^3$ ;  $R^2 = 0.69$ ;  $P < 0.05$ ). Response of Hydropsychidae were characterized by significant increases in abundance of these net spinning caddisflies in the low cover treatment relative to the no cover treatment, followed by declines in abundance until an increase occurred again from high to very high cover treatments (Table 2; Fig. 3C). A similar sigmoidal response of *Erpetogomphus* was caused by the near absence of this taxon in all but high and very high cover treatments where its abundance did not differ

TABLE 2.—Mean (1 SE) number of individuals for macroinvertebrate taxa exhibiting differences in abundance among treatments ( $P \leq 0.001$ ). NC, LC, IC, HC and VHC = no cover, low cover, intermediate cover, high cover and very high cover treatments, respectively. Superscripts indicate locations of significant differences in abundance of a taxon, and these differences occur among treatments without the same letter

Taxon	NC	LC	IC	HC	VHC
<i>Nais</i> spp.	1.3 (0.5) <sup>a</sup>	58.6 (20.4) <sup>b</sup>	90.6 (42.8) <sup>b</sup>	105.4 (25.5) <sup>b</sup>	157.4 (26.0) <sup>b</sup>
<i>Corbicula fluminea</i>	0.3 (0.3) <sup>a</sup>	2.0 (0.5) <sup>b</sup>	8.8 (4.5) <sup>b,c</sup>	17.0 (1.6) <sup>c,d</sup>	27.2 (3.9) <sup>d</sup>
<i>Ephetogomphus</i> sp.	0 <sup>a</sup>	0.2 (0.2) <sup>a</sup>	0 <sup>a</sup>	2.2 (0.3) <sup>b</sup>	2.0 (0.8) <sup>b</sup>
EphemereUidae	4.0 (1.6) <sup>a</sup>	100.8 (53.0) <sup>b</sup>	82.2 (31.8) <sup>b</sup>	68.2 (20.0) <sup>b</sup>	74.4 (11.2) <sup>b</sup>
<i>Strophopteryx</i> sp.	0.5 (0.5) <sup>a</sup>	10.0 (3.7) <sup>b</sup>	8.8 (2.2) <sup>b</sup>	13.6 (3.0) <sup>b</sup>	12.8 (5.0) <sup>b</sup>
<i>Taeniopteryx</i> sp.	0.5 (0.3) <sup>a</sup>	23.0 (11.3) <sup>b</sup>	26.4 (9.9) <sup>b</sup>	12.0 (5.5) <sup>b</sup>	17.2 (2.4) <sup>b</sup>
Hydropsychidae	0.3 (0.3) <sup>a</sup>	3.8 (1.5) <sup>b</sup>	5.8 (1.7) <sup>b</sup>	4.4 (1.6) <sup>b</sup>	11.8 (2.4) <sup>b</sup>
Leptoceridae	1.2 (1.2) <sup>a</sup>	5.8 (1.8) <sup>a,b</sup>	18.3 (5.1) <sup>b,c</sup>	15.4 (5.4) <sup>b,c</sup>	28.8 (4.3) <sup>c</sup>
Elmidae	0.3 (0.3) <sup>a</sup>	2.2 (0.8) <sup>a,b</sup>	5.8 (2.7) <sup>b,c</sup>	8.8 (1.9) <sup>b,c</sup>	11.0 (2.6) <sup>c</sup>
<i>Eukiefferiella</i> spp.	9.5 (2.3) <sup>a</sup>	66.6 (14.7) <sup>b</sup>	96.2 (19.9) <sup>b,c</sup>	164.8 (18.2) <sup>c</sup>	109.0 (11.7) <sup>b,c</sup>

(Table 2). Finally, no regression model adequately described relationships between stone abundance and abundance of either Ephemerellidae (mayflies) or *Taeniopteryx* sp. (a stonefly;  $P > 0.05$ ). However, significantly greater numbers of these taxa in all treatments with stones relative to the no cover treatment suggest a positive nonlinear response occurred (Table 2).

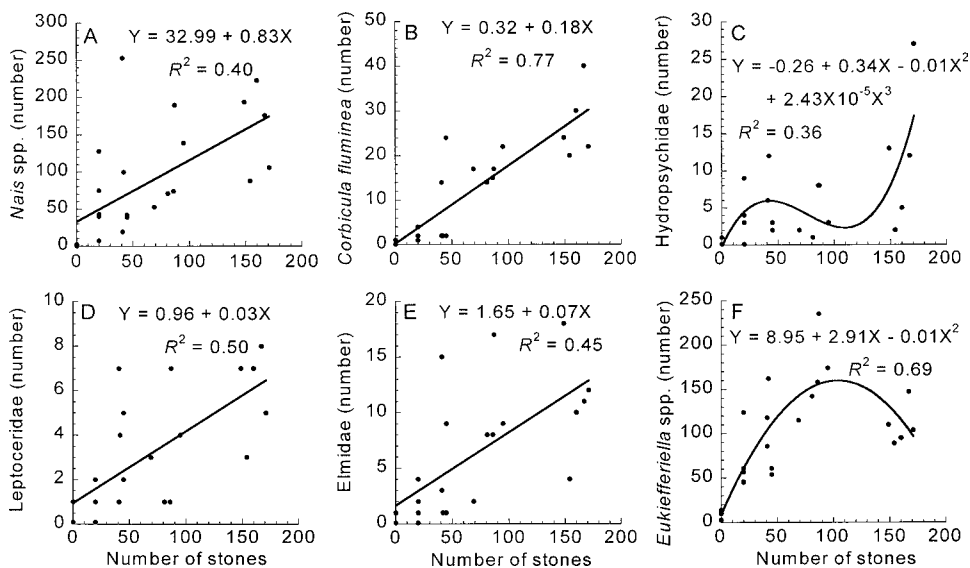


FIG. 3.—Scatter plots and regression curves describing relationships between number of stones on concrete slabs and number of *Nais* spp. (A), *Corbicula fluminea* (B), Hydropsychidae (C), Leptoceridae (D), Elmidae (E) and *Eukiefferiella* spp. (F). Exclusive of surface area provided by stones, total slab surface area was 0.21 m<sup>2</sup>, and the surface area of the face where stones were attached was 0.08 m<sup>2</sup>

## DISCUSSION

Habitat structure created by stones attached to concrete slabs increased macroinvertebrate abundance and taxonomic richness at a local scale under winter conditions in the James River. These findings are consistent with habitat structure effects in a variety of ecosystems, including rivers and streams where macroinvertebrate abundance and taxonomic richness are generally highest in environments where stones, woody debris, plants and other forms of habitat structure are abundant (Downes *et al.*, 2000; Matthaei *et al.*, 2000; Voelz and McArthur, 2000). Identifying underlying causes for habitat structure effects on macroinvertebrates is difficult because several mechanisms operate independently and interactively (Downes *et al.*, 2000; Lake, 2000). For example, habitat structure increases available surface area for colonization and foraging and reduces the frequency of localized extinctions due to chance (Downes *et al.*, 1998). Habitat structure also provides abundant microhabitats that support species with diverse requirements (Lake, 2000; Rempel *et al.*, 2000). Similarly, stones and similar objects increase macroinvertebrate abundance and diversity by providing refuges from predation and high shear forces experienced during floods (Stewart *et al.*, 1999; Lake, 2000; Voelz and McArthur, 2000). Invertebrates actively crawl or swim to these refuges, or reach refuges by passive drift (Hart and Finelli, 1999; Lake, 2000). Additionally, habitat structure indirectly affects food and habitat resources for macroinvertebrates by increasing particulate matter abundance (Downes *et al.*, 2000; Rempel *et al.*, 2000; Siler *et al.*, 2001). Drifting particulate matter is trapped in spaces between stones, and rough surfaces provide stable substrata for algal growth (Downes *et al.*, 2000; Matthaei *et al.*, 2000; Rempel *et al.*, 2000; Siler *et al.*, 2001).

In our study, statistical comparisons of regression models revealed a mixture of linear and nonlinear responses of macroinvertebrate community variables to changing abundance of habitat structure. In other words, increases in taxonomic richness and abundance of several macroinvertebrate taxa were not constant across all levels of increasing stone abundance. Additional experiments are needed to identify biological mechanisms for observed functional responses. However, hypotheses for responses can be constructed from a basic understanding of macroinvertebrate ecological requirements and relationships we quantified between stone abundance, particulate matter and macroinvertebrate community variables. Because this study was conducted during the winter, responses of macroinvertebrate abundance and taxonomic richness are assumed to result from habitat structure effects on organism colonization and retention, and not reproduction.

The linear relationship between habitat structure and total macroinvertebrate abundance in our study was influenced by linear responses of several macroinvertebrate taxa to changing habitat structure abundance. We hypothesize that positive linear responses of *Nais* spp., Leptoceridae and Elmidae to increased habitat structure abundance primarily resulted from stones increasing surface area for clinging (Brinkhurst and Gelder, 1991; White and Brigham, 1996; Wiggins, 1996). However, these taxa also graze on microorganisms and other particulate matter, and Leptoceridae use particulate matter for constructing protective cases (Brinkhurst and Gelder, 1991; White and Brigham, 1996; Wiggins, 1996). Therefore, increased particulate matter on substrata with stones was another potential cause for increase abundance of these taxa when stones were present. Additionally, we attribute the positive linear relationship between abundance of stones and *Corbicula fluminea* to combined effects of fine particulate matter (primarily sand) that accumulated between stones and provided habitat for burrowing, and the stones themselves that increased overall substratum stability (Hakenkamp *et al.*, 2001).

In addition to stones directly increasing substratum surface area and physical complexity, stones indirectly affected macroinvertebrates by increasing particulate matter abundance. Particulate matter causes increased macroinvertebrate abundance and diversity in streams and rivers by providing food and additional habitat (Rempel *et al.*, 2000; Siler *et al.*, 2001). Drifting leaves and macroalgae also transport macroinvertebrates to physically complex substrata, which macroinvertebrates colonize when the debris they inhabit is trapped by structural projections and between crevices (Siler *et al.*, 2001). Nonlinear responses of particulate matter to changing stone abundance in our study were caused by particulate matter accumulating in spaces between stones, but only in spaces within the bottom layer of stones (T. Stewart, pers. obs.). Particulate organic matter on experimental substrata primarily consisted of allochthonous leaves and filamentous algae drifting from upstream sources, and PIM primarily consisted of sand.

Although POM and PIM increased along with increasing stone abundance, the relative effects of stones declined as stones became more abundant. Nonlinear effects of stones on particulate matter are suspected causes for similar nonlinear relationships between abundance of stones and several macroinvertebrate taxa. For example, dramatic increases in *Eukiefferiella* spp. in the low cover treatment relative to the no cover treatment reflect increased availability of particulate matter these chironomids use for food, case construction and dispersal (Coffman and Ferrington, 1996; Siler *et al.*, 2001). Similar responses of Ephemerellidae and *Taeniopteryx* sp. to increasing stone abundance were also likely caused by particulate matter these taxa use for refuges and food (Stewart and Harper, 1996; Lee and Hershey, 2000).

Particulate matter is also an important resource for Hydropsychidae and *Erpetogomphus* sp., but the relative abundance of stones and particulate matter likely determined the sigmoidal response of these taxa across the range of stone abundance in our study (Poepperl, 2000; Siler *et al.*, 2001). We hypothesize that high particulate matter abundance in the high cover treatment caused slight reductions in hydropsychid abundance between intermediate and high cover treatments by interfering with net construction. However, an additional layer of stones in combination with minimal differences in particulate matter abundance caused increased hydropsychid abundance in the very high cover treatment relative to the high cover treatment. We attribute this to increased availability of clean, hard substrata in the very high cover treatment that provide favorable sites for net construction and accessing food particles in the water column (Poepperl, 2000; Rempel *et al.*, 2000). In contrast to hydropsychids, *Erpetogomphus* sp. nymphs were equally abundant in high and very high cover treatments, but were virtually absent in no cover, low cover, and intermediate cover treatments. Soft substratum is critical habitat for this burrowing taxon, and suitable quantities of particulate matter were apparently not present until stones covered almost the entire slab face and provided interstices where particulate matter accumulated (Suhling, 1999).

Finally, competitive and predator-prey interactions might also have affected macroinvertebrate responses to changing habitat structure abundance in our study, as experiments have revealed these interactions to at least occasionally be important macroinvertebrate community structuring agents in rivers and streams (Peckarsky and Dodson, 1980; Cooper *et al.*, 1990). For example, slightly reduced abundance of *Eukiefferiella* spp. in the very high cover treatment relative to the high cover treatment could result from competition with other invertebrates that responded positively to stones. Additionally, reduced abundance of these chironomids could have been caused by macroinvertebrate predators (*e.g.*, the oligochaete *Chaetogaster diastrophus*; Brinkhurst and Gelder, 1991) that exhibited statistically nonsignificant increases as habitat structure abundance increased.

The power model describing the relationship between stone abundance and macroinvertebrate taxonomic richness in our study reflects a dramatic increase in taxonomic richness between no cover and low cover treatments, followed by only minor increases when stone abundance and percent cover exceeded 20 stones/0.08 m<sup>2</sup> slab face and 13% cover of slab face, respectively. Stones increased substratum surface area and the mathematical relationship between habitat area and taxonomic richness that we observed is consistent with "species-area" relationships in a variety of ecosystems (Inouye, 1998; Baldi and Kisbenedek, 1999; Mac Nally and Lake, 1999). Various mechanisms may be responsible for the typically positive, yet gradually declining rate of increase in number of taxa as a function of area sampled. According to one hypothesis, taxa are distributed randomly across the landscape, and the power curve describing this "species"-area relationship is based on the probability of finding a new taxon as total area sampled increases (Downes *et al.*, 1998; Baldi and Kisbenedek, 1999). An alternative hypothesis states that the taxonomic richness increases with area sampled because larger areas usually contain a greater variety of habitats (Downes *et al.*, 1998; Baldi and Kisbenedek, 1999). In studies conducted in stony bottomed streams during summer months, Downes *et al.* (1998) and Douglas and Lake (1994) found that macroinvertebrate taxonomic richness was significantly higher on bricks with small quantities of habitat structure (*e.g.*, crevices, rough surfaces) than on smooth substrata of comparable surface areas. Similarly, in a study conducted in a river during winter and spring, Robson and Barmuta (1998) reported that ceramic tiles with modest amounts of habitat structure had greater macroinvertebrate taxonomic richness than tiles with smooth surfaces. In our study, mean taxonomic richness was 2× greater in the low cover treatment (mean ± SE = 24.2 ± 1.8 taxa per experimental substratum) than in the no cover treatment (mean ± SE = 12.8 ± 1.8 taxa per experimental substratum), although total substratum surface area was only 1% greater in the low cover treatment (Table 1). These results suggest that small quantities of habitat structure dramatically increase habitat diversity and associated resources that enhance colonization and retention of macroinvertebrate taxa. Additionally, similar community responses to habitat structure can be expected during multiple seasons in a variety of rivers and streams.

In conclusion, even small quantities of physically complex habitat cause significant localized increases in macroinvertebrate abundance and taxonomic richness in the James River during winter. For some taxa, abundance at a local scale should be proportional to the abundance of stones or similar substratum particles on the surrounding riverbed. However, our results suggest that spatial differences in taxonomic richness and abundance of several other taxa are especially dramatic when habitats with no structure and small quantities of structure are compared. The presence of stones and similar types of habitat structure stimulate local increases in James River macroinvertebrates in at least two important ways. First, these objects themselves increase colonizable surface area and diversity of habitat. Additionally, this habitat structure increases particulate matter abundance. Benthic particulate matter provides food and habitat to macroinvertebrates, and drifting particulate matter that is trapped by physical objects delivers macroinvertebrate colonists to physically complex substrata.

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