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Linking disturbance and stream invertebrate communities: how best to measure bed stability

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Abstract. Substrate stability is a key determinant of stream invertebrate community composition, but its measurement can be problematic. Stream ecologists often use different approaches and techniques to quantify bed stability, and this variability makes comparison among studies difficult. We examined the link between 6 reach-scale measures of substrate stability and invertebrate community metrics in 12 New Zealand mountain streams. The strength of the link varied with the method used to define substrate stability. We used morphological budgeting to measure spatial patterns and volumes of scour and fill. We found that as erosion of sediments increased, invertebrate diversity declined exponentially. In particular, increases in the volume of scour reduced taxonomic richness, whereas deposition of coarse sediments was less relevant for invertebrate communities. Overall, the distance travelled by in-situ-marked tracer stones was most strongly linked with all invertebrate community metrics, whereas the bottom component of the Pfankuch Index related very well to diversity. Both metrics showed near-linear declines in diversity with decreasing stability. In contrast, the link between invertebrate communities and the proportion of bed area affected by entrainment was weak. Therefore, we propose tracer-based indices and the Pfankuch bottom component as the most suitable measures for research involving invertebrate–substrate-stability relationships. Measures derived from in-situ-marked tracer stones reflected only entrainment and transport of particles. In contrast, the bottom component of the Pfankuch Index encompassed the widest range of bed-stability characteristics but is prone to observer bias. An objective method that combines the efficiency of the Pfankuch Index with the characteristics measured using tracer stones could serve as a powerful explanatory tool in stream ecology.

Key words: community composition, diversity, flow competence, morphological budgeting, New Zealand, stream ecology, substrate stability, tracer-stone movement.

Lotic ecosystems can be strongly influenced by floods (Resh et al. 1988, Reice et al. 1990, Lake 2000, Death 2008). High discharges can result in coarse-substrate movement, which is a potential source of physical disturbance for periphyton (Biggs et al. 1999), invertebrate (Cobb et al. 1992, Death and Winterbourn 1995, Holomuzki and Biggs 2000), and bryophyte communities (Suren and Duncan 1999). Many diversity–disturbance models predict low diversity at severely disturbed sites. At intermediate levels of disturbance, diversity might peak (Grime 1973, Connell 1978), but most studies of lotic ecosystems do not support this hypothesis (Vinson and Hawkins 1998, Death 2008). Inclusion of habitat productivity, e.g., shifting the intermediate-disturbance peak relative to productivity, might improve the fit of physical disturbance–diversity models for

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lotic environments (Huston 1979, Hildrew and Townsend 1987, Death 2002). Substrate movement causes habitat alteration and can lead to displacement and death of stream invertebrates and to changes in their food sources. Thus, bed stability has a significant effect on the composition of benthic invertebrate communities (e.g., Townsend et al. 1997b, Matthaei and Townsend 2000, Effenberger et al. 2006, Death 2008). We started from the premise that streambed stability affects invertebrate community composition, and we investigated how best to measure the relevant aspects of bed stability.

Bed stability can be characterized by entrainment, transport, and deposition of particles at different scales (Schwendel et al. 2010a). However, most techniques assess only a limited subset of these aspects. Entrainment of coarse particles is difficult to assess because particles might be imbricated, sheltered by other particles, or have varying properties (e.g., shape or density) (Richards 1990, Gomez 1991). Furthermore, the hydraulic conditions that determine entrainment, such as relative depth or the available flow energy, are highly variable within a reach. Substrate entrainment usually is calculated with various modifications of the Shields equation (e.g., Komar 1989). Direct measurements of the force necessary to move particles with a spring balance (Downes et al. 1997) can account for substrate assemblage and particle properties but are very labor-intensive for reach-wide application.

Areas of the stream bed where erosion and deposition occur have been identified by stream ecologists using scour chains (Palmer et al. 1992, Matthaei et al. 1999b, 2003, Effenberger et al. 2006). However, tacheometric or global positioning system (GPS)-based channel surveys combined with morphological budgeting can provide high-resolution surveys of an entire reach and allow calculation of volumetric budgets (Lane et al. 1994, Brasington et al. 2000). Real-Time Kinematic differential GPS systems permit surveying of up to 4000 points/d (Schwendel et al. 2010b). When satellite coverage is low because of overhanging vegetation or valley topography, theodolite-electronic distance measurement (EDM) systems provide an alternative. However, maintaining a direct line of sight between the theodolite and the reflector can be laborious, and nonrobotic total stations require 2 operators. Surveys ideally should be done in association with individual floods to account for scour–fill compensation (Lindsay and Ashmore 2002), i.e., patches that are scoured during a first flood might be refilled in the following event, resulting in no observed change when assessed over a multievent scale.

Substrate transport often is assessed with tracer particles of various kinds (Laronne and Duncan 1992, Sear et al. 2000), bedload samplers (Bunte and Abt 2003), or acoustic devices (Bogen and Moen 2003). If benthic communities are to be sampled concomitantly, these techniques ideally should not interfere with the substrate. This restriction probably is why most stream ecologists have preferred the less-invasive tracer methods. An alternative is subjective visual evaluations of streambed stability like the Pfankuch Index (Death and Winterbourn 1994, Townsend et al. 1997b, McIntosh 2000), which theoretically should encompass all aspects of bed stability. These methods are popular because of their cost-effective, straightforward, and quick application but can suffer from observer bias.

This large range of potential measures of substrate stability combined with the variety of community characteristics (diversity, abundance, or community composition) that could be assessed makes it difficult for ecologists to identify an appropriate technique readily. We investigated the relationship between 6 bed-stability measures derived from 4 assessment techniques and invertebrate community metrics in 12 mountain streams. These methods each characterized a distinctive set of bed-stability aspects. They included morphological budgeting, flow competence at bankfull discharge, transport of initially embedded tracer stones, and the bottom component of the Pfankuch Index. Our aim was to identify the most useful and applicable reach-scale measure of bed stability for research on benthic invertebrate communities.

Study Sites

The study was carried out from October 2007 to September 2008 in 12 reaches of mountain rivers and streams in the southern part of the North Island of New Zealand (Fig. 1). The reaches were on the eastern and western slopes of the northeast–southwest trending Ruahine (5 sites) and Tararua Ranges (4), and the Central Volcanic Plateau around Mt. Ruapehu (3). The geology of the Central Volcanic Plateau is dominated by Quaternary andesitic volcanic deposits, whereas the Ruahine and Tararua ranges consist of Mesozoic greywacke and argillites of varying decomposition. The reaches were chosen to represent a wide range of anticipated bed stability. The composition of the substrate ranged between gravels and cobbles, although some sites contained a considerable proportion of boulders. Some of the study reaches were laterally confined by vegetated banks, whereas others migrated within a wide active-channel zone. None

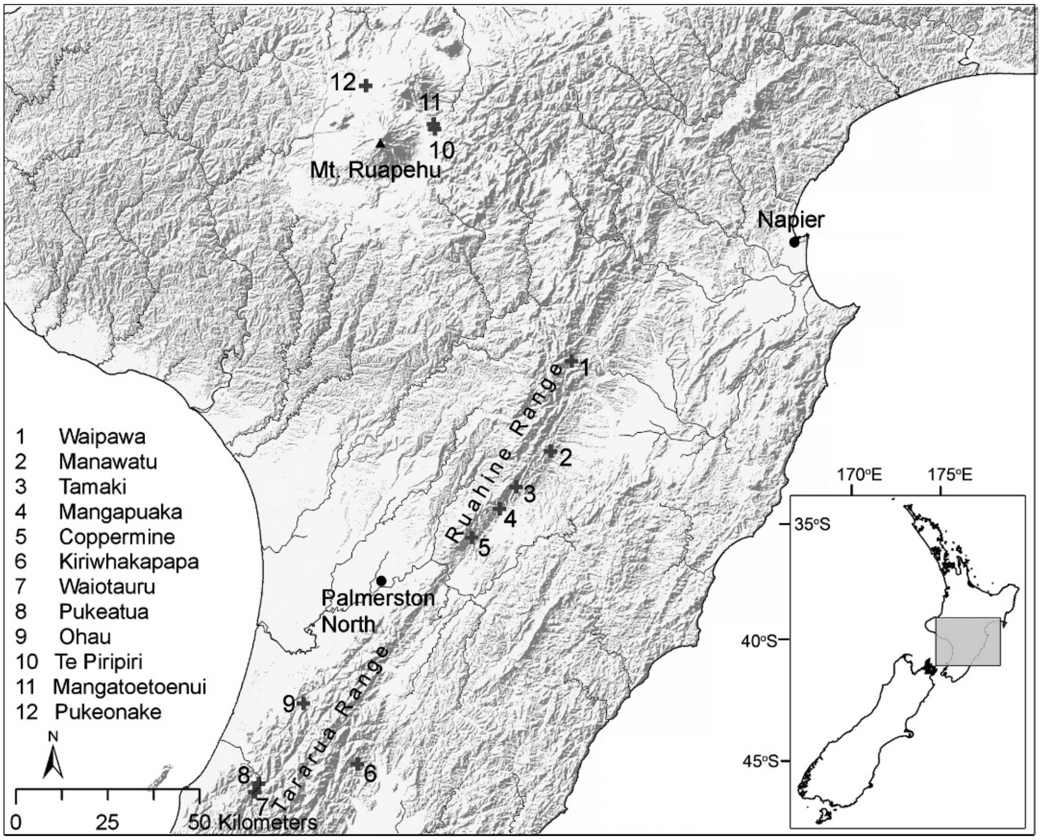


FIG. 1. Study sites investigated between October 2007 and September 2008 in the southern North Island of New Zealand.

had a closed forest canopy, but shading from riparian vegetation did occur occasionally. The streams varied considerably in terms of slope, width, conductivity, and sediment supply. Anthropogenic influence is relatively low in the mountainous catchments where the vegetation is dominated by native broadleaf–podocarp forests in the Tararua and Ruahine Ranges and tussock grassland and scrub on the Central Volcanic Plateau.

Methods

Invertebrates

Five Surber samples (500-µm mesh, 0.1 m^2) were collected from riffles at 3 times throughout a year (austral spring, late summer, and winter). Samples were stored in 4% formalin or >60% isopropyl alcohol. Abundant groups of taxa/families (>300 individuals/sample; e.g. Chironomidae, Leptophlebiidae, or Conosucidae) were subsampled using the process described in Vinson and Hawkins (1996). Individuals were identified to the lowest possible taxonomic level (usually species level) with the keys in McFarlane (1951), Winterbourn (1973), Towns and Peters (1996), and Winterbourn et al. (2006). Invertebrate abundance was significantly correlated between sampling dates ($r_S = 0.34$–0.99, df = 17–54, $p < 0.05$) at each site. Constancy of taxa abundances among seasons was significant (Kendall's coefficient of concordance, $W = 0.28$–0.72, df = 26–59, $p < 0.05$), and seasonal variability is generally low in New Zealand stream invertebrate communities (Towns 1981, Winterbourn 2004). Thus, 3 sampling occasions through the year were deemed sufficient to represent community composition between flood events.

Periphyton and physicochemical characteristics

Wetted stream width and depth were measured at each invertebrate sampling point (Table 1). Flow velocity (averaged over 60 s) was recorded with an electromagnetic flow meter (model 801; Valeport Ltd., Devon, UK) 0.05 m above the stream bottom. At each sampling site pH, conductivity (temperature-corrected), and temperature were measured using Eutech pHtestr2 and ECScan Low+ (Eutech Instruments, Singapore). Degree of substrate embeddedness was assessed subjectively by dislodging stones. Embeddedness was classified into 4 categories ranging from tight to loose (Death and Joy 2004). Composition of

TABLE 1. Abiotic characteristics of the study sites. Depth, width, velocity, conductivity, temperature, and pH measurements are mean values of measurements made during each of 3 seasonal sampling events between October 2007 and September 2008. Depth, width, and velocity were measured at each of the 5 invertebrate sampling points/site.

Site	Strahler (1952) stream order	Mean depth (m)	Mean width (m)	Mean flow velocity (m/s)	Mean conductivity (μS/cm)	Mean temperature (°C)	Mean pH	Slope (m/m)	Substrate D_{50} (mm)
Waipawa	3	0.20	5.4	1.000	103	8.8	8.2	0.032	59
Manawatu	3	0.20	4.3	0.603	66	9.4	7.8	0.047	65
Tamaki	2	0.17	3.3	0.811	64	10.8	7.6	0.021	35
Mangapuaka	2	0.09	2.3	0.584	69	8.6	6.7	0.029	28
Coppermine	3	0.13	4.4	0.592	90	13.5	7.4	0.042	51
Kiriwhakapapa	3	0.15	6.5	0.603	64	9.7	7.2	0.011	59
Waiotauru	5	0.26	17.4	0.716	68	11.3	7.7	0.012	84
Pukeatua	3	0.18	9.7	0.720	80	12.4	7.7	0.047	84
Ohau	4	0.24	14.0	0.694	72	12.7	7.6	0.012	64
Te Piripiri	3	0.19	2.0	0.742	69	8.5	7.7	0.014	35
Mangatoetoenui	4	0.26	8.6	0.597	139	7.1	8.0	0.025	97
Pukeonake	4	0.17	6.8	0.398	23	8.2	7.0	0.034	158

the riparian environment (% aerial cover of native riparian vegetation [NRV] or active channel [DAC]) also was estimated.

Periphyton biomass was measured concurrently to examine the interacting effects of bed stability and periphyton on benthic invertebrate communities. Five gravel-size stones were collected from a spot next to each invertebrate Surber sample. They were transported to the laboratory in the dark in cooled stream water before being stored at −18°C. Pigments were extracted in 90% acetone for 18 h at 5°C in the dark before chlorophyll *a* absorption was measured using a Cary 50 Conc UV-Visible spectrometer (Varian, Mulgrave, Australia). Chlorophyll *a* pigment concentration was calculated (Steinman and Lamberti 1996, APHA 1998) and corrected for stone surface area, which was estimated based on measurement of the *a*-, *b*- and *c*-axes of the gravels with a sliding caliper (Graham et al. 1988).

Morphological budgeting

Topographic surveys of the river beds and the adjacent floodplain were undertaken in Austral spring, summer, and autumn with a Trimble R8 differential GPS system (Trimble Navigation Limited, Sunnyvale, California) in real-time kinematic (RTK) mode (Brasington et al. 2000). Where satellite reception was limited, topographic data were retrieved with a Topcon electronic total station GTS 701 (Topcon Corporation, Tokyo, Japan). The GPS base station was installed some distance from the reach to prevent the occurrence of multipath errors (Kennedy 2002). The survey was designed to be terrain sensitive, i.e., point density was highest at breaks in slopes and highly structured surfaces (Fuller et al. 2005). Reach length was defined as ~5 to 7× active channel width and included, where present, at least 1 riffle–pool sequence (Leopold et al. 1964, Keller and Melhorn 1978). Thus, the area of the surveys varied between 132 m^2 and 2942 m^2, whereas the average point density was between 0.6 and 11.7 points/m^2.

The data sets consisting of 3-dimensional coordinates were triangulated and linearly interpolated on a regular quadratic grid with a width of 0.01 m using Surfer 8.01 (Golden Software, Golden, Colorado) (Schwendel et al., in review). For the larger reaches (Waipawa and Waiotauru) a larger grid width of 0.02 m was preferred. The resulting digital elevation models (DEMs) of 2 consecutive surveys were subtracted from each other to produce a DEM of topographic change. Errors in representation of the real surface, precision of measurement, and accuracy of the DEMs can propagate. Therefore, a level of minimal detection of genuine change was identified and applied to the DEMs when the area and volume of scour (VOS) and fill (VOF) relative to the survey area were calculated (Schwendel et al. 2010b).

Flow competence

The percentage of substrate that would move at bankfull discharge (flow competence bankfull [FCB]) was calculated by the method of Duncan et al. (1999). This approach uses a modified Shields and the DuBoys equation to relate mean boundary shear stress to entrainment of particles. The method assumes that all clasts on the river bed smaller than the critical grain size move under these conditions. The composition of the substrate (Table 1) was assessed with the Wolman pebble-count method (Wolman 1954), in which the *b*-axis of >100 randomly selected substrate particles is measured. Pebbles were classified according to a modified Wentworth scale. The necessary measurements of cross-sections and water-surface slope were attained with RTK-differential GPS or a tacheometric EDM-system. At each site, the density of ~20 random particles was measured. Fluid density was assumed to be 1000 kg/m^3. These densities were used to calculate specific masses in the Shields equation.

Tracer stones

Five randomly selected stones in each of 3 size classes (50^{th}-percentile particle diameter [D_{50}], D_{70}, and D_{90}) were marked with electronic radio-frequency identification (RFID) tags (23-mm glass tags; Texas Instruments, Dallas, Texas) and were used to assess the stability of the surface layer. Tags were attached in situ to randomly selected stones with underwater curing epoxy-concrete (K273; Nuplex Construction Products, Hamilton, New Zealand). Where underwater application was impossible because of swift current, stones were removed from the river bed. After the tag was attached, stones were carefully reembedded. This method appeared to have relatively little effect on substrate-stability assessment because the percentage of entrained re-embedded and in-situ-marked tracer stones were correlated ($r_S = 0.77$, df = 11, $p = 0.005$). Marked stones were relocated and identified without interference by their unique coded tags with a portable antenna and datalogger (Oregon RFID, Portland, Oregon). The number of marked stones in our study was low compared to the number of tracer stones used for assessment of reach-scale bed movement in other studies (e.g., 400 in Matthaei et al. 1999a), and might have been insufficient to account for the full spatial variability in bedload transport. However, experience from previous studies (Death and Zimmermann 2005) suggests that 15 stones are sufficient to provide a meaningful estimate of ecologically relevant bed stability.

Positions of the stones were measured with tacheometric ground survey or from marked locations on riparian vegetation and stable banks. Mean recovery rate was 71% (range: 41–100% across all sites). The distance travelled was recorded and converted to an index of bed stability, which was the weighted (by geometric mean of the size class) sum of distance travelled. Stones that were not recovered were assigned a travel distance between 50 m and 200 m depending on estimated stream power. Two surveys were done to find the stones within 6 mo after marking. Thus, 2 measures of tracer-stone movement were calculated: distance travelled by the 1^{st} survey (ITM; ~81 d) and the distance travelled over the entire period (TTM; ~161 d).

Pfankuch Stability Index

The Pfankuch Stability Index is a method for visual evaluation of streambed and bank stability and of the capacity for morphological adjustment to floods (Pfankuch 1975). The bottom component of this index (BCP) was used because it relates best to biological data (Death and Winterbourn 1995). The method involves assignment of an observer's subjective evaluation of 6 attributes (substrate brightness, angularity, consolidation, % stable materials, scouring, and amount of clinging aquatic vegetation) to predetermined categories (range: 1–4 for each attribute). Attribute scores are weighted according to their perceived importance. The sum of the scores results in a stability index, where high values represent low stability. The index was calculated twice at each site by the same observer within a few months, and the results were averaged.

Data analysis

Data were not normally distributed, so the nonparametric Spearman rank correlation (r_s; Statistix 9.0; Analytical Software, Tallahassee, Florida) was used to investigate the connection between measurements of bed stability and invertebrate community metrics. Invertebrate community metrics were total number of individuals, total number of taxa, evenness (Berger–Parker dominance index), taxonomic richness (Margalef's Index) (cf. Death and Winterbourn 1995), and rarefied taxonomic richness. Rarefied taxonomic richness allows comparison of taxonomic richness among samples with differing number of taxa and was calculated in PRIMER (version 6; Plymouth Marine Laboratory, Plymouth, UK) with the methods of Sanders (1968) and Hurlbert (1971). Significance from the multiple correlations was adjusted using false discovery rate correction (Benjamini and Hochberg 1995). The nature of the established relationships between measures of bed stability and community metrics was subsequently examined with regression analysis (Statistix). Our use of regression techniques was not entirely appropriate because of the nonnormal data distribution of some variables, so the derived results should be interpreted carefully when they indicate a nonmonotonic link. Diversity metrics describe only community structure, so the community composition at each site was characterized by nonmetric multidimensional scaling (NMDS) of standardized (by maximum) species abundance using Bray–Curtis similarity among sites (PRIMER). The links between bed-stability measurements, specific invertebrate taxa, and NMDS-axes was examined using Spearman rank correlation.

Results

Bed stability

Bed stability was generally highest at the sites on the Central Volcanic Plateau, and in particular, at Pukeonake Stream (Fig. 2A–F). In contrast, the Waipawa site was rated amongst the least stable sites by almost all measures except VOF (Fig. 2E). Some streams in the eastern Ruahine Ranges and Pukeatua Stream were characterized as unstable based on the BCP (Fig. 2A), FCB (Fig. 2B), ITM (Fig. 2C), and TTM (Fig. 2D), but ranking of the sites varied considerably among methods.

Measurement of topographic change with morphological budgeting techniques resulted in assessment of both relative volume and area of scour and fill. Area and volume were highly correlated for scour and fill ($r_S = 0.95$ and 0.98, df = 11, $p = 0.0001$), so only volumes are reported here. VOS was highest at Pukeatua (Fig. 2F), whereas VOF was highest at the Te Piripiri site (Fig. 2E). BCP was significantly correlated ($r_S > 0.73$, df = 11, $p < 0.01$) with all the other bed-stability measures except VOF and FCB. FCB was only weakly correlated with the other measures ($r_S < 0.66$, df = 11, $p > 0.02$). ITM and TTM were highly correlated ($r_S > 0.94$, df = 11, $p < 0.001$).

Invertebrate communities

Taxa number.—The composition of the invertebrate communities at each site was relatively constant over the 10-mo study period. The total number of taxa from all sites was 110, and each site contained between 27 and 60 taxa. The Tararua and Ruahine sites were dominated by Trichoptera, Plecoptera, and Ephemeroptera (85–94% of individuals and 43–69% of taxa), whereas the sites on the Central Volcanic Plateau had a smaller fraction of individuals in these orders (18–70%) and more Diptera. Total number of taxa was not significantly correlated with any measure of bed stability, but it was strongly correlated with % NRV (Table 2).

Total number of individuals.—The mean number of individuals of all samples at each site ranged from 21.2 at Mangatoetoenui Stream to 625.8 at Manawatu River. The strongest link with the measured environmental variables was with % NRV (Table 2). In contrast, no significant monotonic relationship with any bed-stability measure could be established.

Diversity indices.—Community evenness (Berger–Parker Index) had the highest significant positive correlation with TTM, followed by BCP and ITM (Table 2). Taxonomic richness was significantly correlated with the VOS, BCP, ITM, and TTM. Rarefied taxonomic richness was not significantly correlated with any bed-stability measure or abiotic variable. Regression analysis revealed that the relationship between diversity measures and VOS was best explained by logarithmic or power functions (Fig. 3A, B). Linear models were of similar quality to curvilinear models for the remaining measures of bed stability (Table 3).

Community composition.—The 2nd NMDS axis (stress 0.06; Fig. 4A, C) was correlated with the BCP, ITM, TTM, VOS, and periphyton biomass, whereas the 3rd axis was strongly connected with % NRV (Fig. 4B, Table 2). The 1st and 3rd axes were not significantly correlated with any bed-stability measure. Larvae of the mayfly *Austroclima sepia*, the caddisfly *Pycnocentria gunni*, and Diptera of the family Empididae and Platyhelminthes were found only at sites that were identified as being relatively stable (low values on 2nd NMDS axis). The first 2 taxa are often associated with moss (Winterbourn et al. 2006) on stable substrates. Diamesinae, Orthocladiinae, *Chironomus zealandicus*, the caddisfly *Neurochorema* sp., and Simuliidae also were much more abundant at these sites than at less stable reaches. In contrast, Hydrophilidae beetles were collected exclusively at more unstable sites, a result that agrees with data from other New Zealand studies (Sagar 1986, Townsend et al. 1997a).

Periphyton.—Periphyton biomass was negatively correlated with the 2nd NMDS axis. Periphyton biomass was not correlated with any measure of bed stability, but high biomass usually was found at stable sites with high and intermediate invertebrate diversity.

Discussion

The assumption that bed stability is one of the principal abiotic factors influencing stream invertebrate community composition is supported by our findings. However, the strength and form of the correlation between invertebrate community structure and bed stability varied with the particular measure of bed stability used. Distance travelled by in-situ-marked tracer stones was consistently the best predictor for the influence of bed stability on the composition and diversity of invertebrate communities. ITM and TTM longitudinally integrate bedload

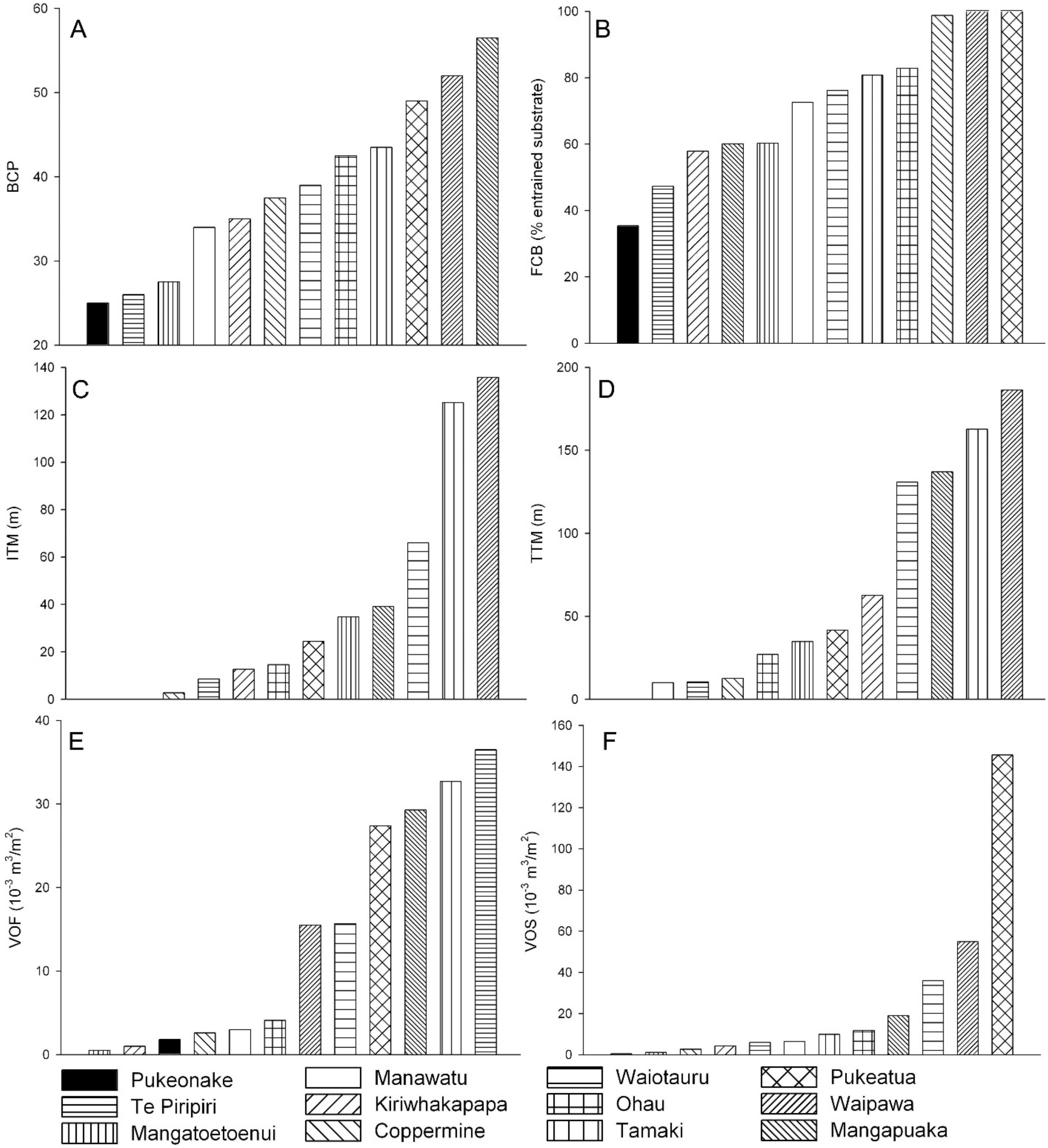


FIG. 2. Bed stability assessed at 12 study sites based on the bottom component of the Pfankuch Index (BCP) (A), flow competence at bankfull discharge (FCB) (B), initial tracer-stone movement (ITM) (C), total tracer-stone movement (TTM) (D), volume of fill (VOF) (E), and volume of scour (VOS) (F). The sites are ranked from high stability (left) to low stability in each panel.

TABLE 2. Correlation coefficients for stream macroinvertebrate community characteristics (evenness = Berger–Parker Index, taxonomic richness = Margalef's Index) and periphyton biomass with 6 measures of bed stability (BCP = bottom component Pfankuch Index, FCB = flow competence at bankfull discharge, ITM = initial tracer-stone movement, TTM = total tracer-stone movement, VOS = volume of scour, VOF = volume of fill) and biotic and abiotic variables (NRV = % native riparian vegetation area, DAC = dry active channel area) from 12 New Zealand rivers. Samples and measurements were collected between October 2007 and September 2008. Significance from multiple correlations was adjusted using False Discovery Rate and is indicated by * for $\alpha = 0.1$ and ** for $\alpha = 0.05$. NMDS = nonmetric multidimensional scaling.

	Number of taxa	No. of individuals	Evenness	Taxonomic richness	Rarefied taxa richness	NMDS axis 1	NMDS axis 2	NMDS axis 3	Periphyton biomass
Bed stability									
BCP	−0.19	−0.16	0.59*	−0.64*	−0.63	0.15	0.80**	0.00	−0.42
FCB	−0.08	−0.11	0.08	−0.22	−0.18	0.26	0.33	−0.09	−0.08
ITM	−0.54	−0.46	0.58*	−0.56*	−0.43	0.05	0.59*	0.36	−0.54
TTM	−0.38	−0.30	0.65*	−0.59*	−0.46	0.00	0.68*	0.20	−0.66
VOS	−0.08	−0.04	0.42	−0.71*	−0.57	0.22	0.62*	0.08	−0.11
VOF	0.05	−0.01	0.33	−0.36	−0.32	0.35	0.26	0.10	0.16
Periphyton	0.52	0.34	−0.53	0.50	0.42	0.01	−0.64*	−0.08	
Abiotic variables									
Depth	−0.38	−0.25	−0.23	−0.15	0.04	−0.10	−0.13	0.34	0.12
Velocity	−0.13	−0.12	0.06	−0.35	−0.08	0.19	0.13	0.18	−0.13
Conductivity	−0.21	−0.30	−0.24	0.14	0.29	−0.34	−0.09	0.34	0.16
pH	−0.19	−0.17	−0.36	0.02	0.19	−0.27	−0.27	0.30	0.22
NRV	−0.69*	−0.64*	0.09	−0.22	−0.01	0.18	0.18	0.69*	−0.27
DAC	−0.51	−0.38	0.64	−0.54	−0.54	0.01	0.55	0.40	−0.34

transport over the entire reach, and in-situ tagging incorporates entrainment of particles. The BCP allows, to a certain degree, incorporation of other aspects of bed stability, such as sedimentation, and was correlated with measures of diversity and community composition. However, entrainment and particle transport appear to be more relevant for communities than simple deposition of coarse sediments. Diversity of invertebrate communities and number of individuals declined linearly with decreasing bed stability measured by both techniques. Periphyton biomass opposed bed stability on the 2nd NMDS-axis, a result that is typical for open-canopy streams where the effects of substrate stability on invertebrates and their food source are difficult to distinguish (Suren 1993, Death and Zimmermann 2005). Other aspects contributing to the growth of periphyton communities, such as partial shading and valley orientation, were not factored out separately, but no evidence was found for a strong overriding effect of amount of periphyton biomass on the relationship between bed stability and composition of invertebrate communities.

Morphological budgeting

VOS and VOF derived from the subtraction of DEMs were not linearly related to the abundance of individuals or the number of taxa. In contrast, a strong link existed between taxonomic richness and VOS, which was best described by curvilinear functions. However, when the Pukeatua site, where the highest volumes of scour were found, was removed from the analyses, the linear relationship improved and had a much steeper slope (Fig. 3B). Exclusion of this site was reasonable because excessive scour was mainly a consequence of lateral erosion of a fan from a steep tributary stream at the margin of the site and, thus, was not representative of the entire stream bed of the reach. The strong link between VOS and the 2nd NMDS axis points to a more important influence of entrainment than sedimentation on community composition. Morphological budgeting permits identification of such spatial patterns of scour and fill and is a well-established method for assessing changes in morphology in gravel-bed rivers (Fuller et al. 2002). Coarseness of the substrate (e.g., at Pukeonake reach) can impede the survey, which is designed to measure topography at a bedform scale. Boulders and large cobbles require a grain-size resolution that is impractical for large reaches. The survey can be designed to exclude sections of the river bed with many boulders, but this practice can result in errors in cases of occasional movement of large-sized substrate. Application of a rigorous level-of-change detection minimizes the influence of errors associated with substrate size, measurement, and interpolation. However, a spatially uniform (reach-

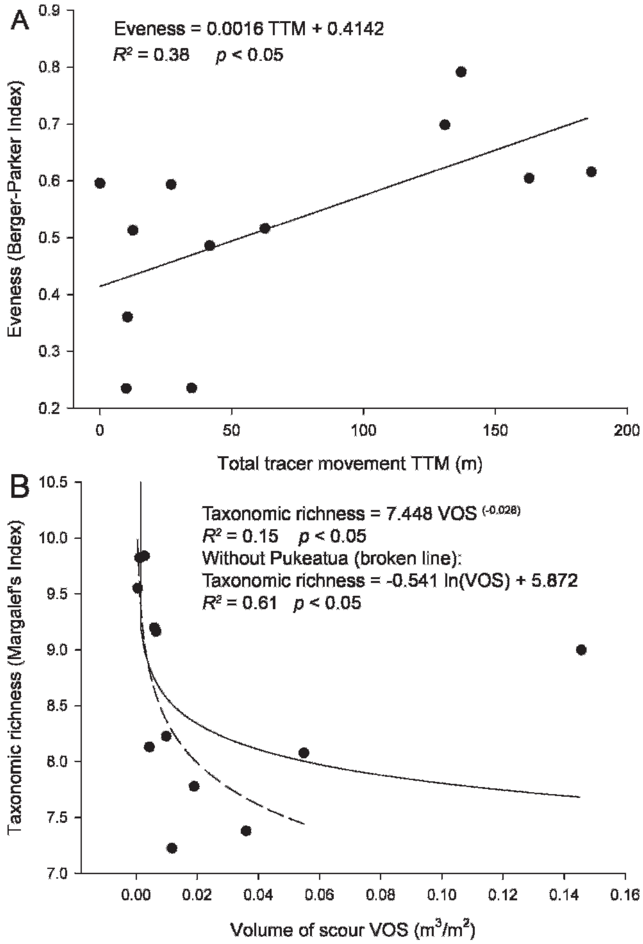


FIG. 3. Evenness as a function of total tracer-stone movement (TTM) (A) and taxonomic richness as a function of volume of scour (VOS) (B). These relationships were for the highest correlated measures and best regression models of stream macroinvertebrate community structure and bed stability. The taxonomic richness relationship improved when the Pukeatua site (high local sediment supply from a tributary) was omitted (broken line).

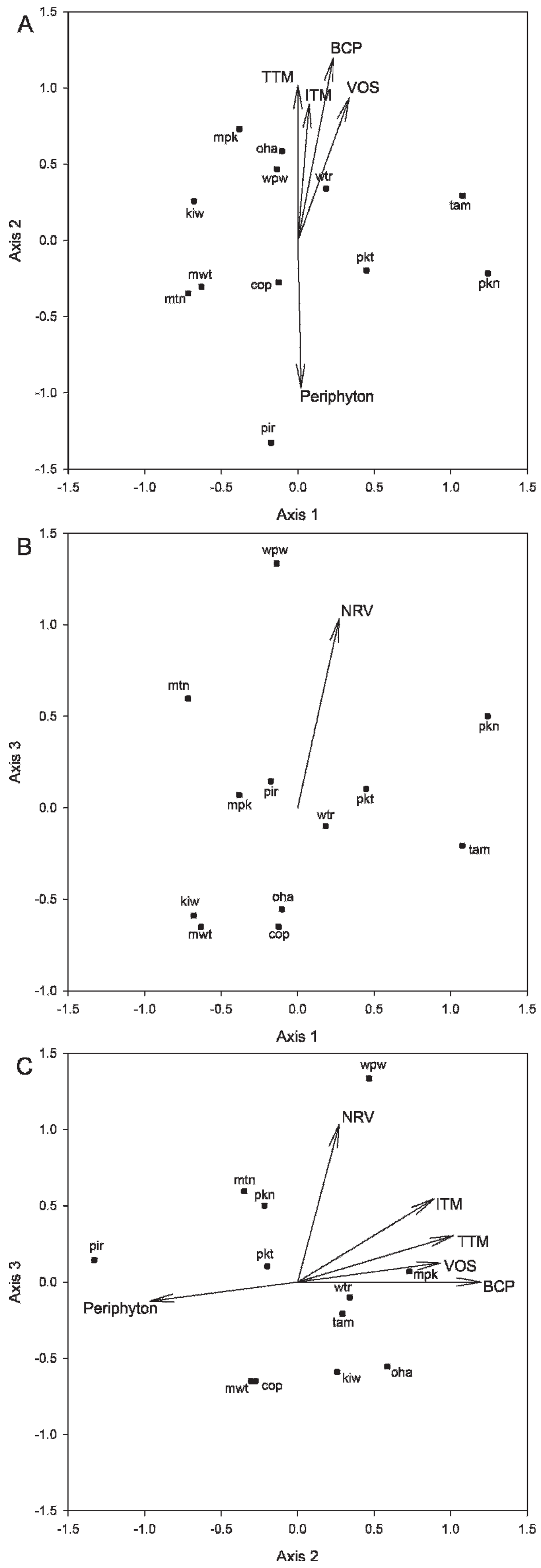
scale) level of detection could prevent registration of subtle erosion or deposition to which invertebrate communities might be sensitive. Thus, measurement of topographical change at the riffle scale or application of spatially variable error assessment might relate better to invertebrate community metrics. Morphological budgeting also cannot account for sediment that is completely transported through the reach or for scour–fill compensation during a single event (Fuller et al. 2003).

Flow competence calculation

FCB and calculation of the resulting % of bed surface in motion have been used successfully to show that periphyton biomass (Biggs et al. 1999) and bryophyte cover (Duncan et al. 1999) increase with bed stability. However, our study showed no link between FCB and invertebrate community composition or periphyton biomass. This result could have been a consequence of our definition of bankfull discharge. We estimated bankfull stage as the level below which no perennial vegetation occurred or on the basis of flood trash lines and indicative channel forms. However, these criteria bear some uncertainties depending on the magnitude of recent floods. We compared our estimated bankfull stage with mean annual flood (MAF) data (Pearson and McKerchar 1989) and found that for all sites, except Waipawa, the estimated bankfull stage was considerably lower than MAF stage. We did not use the MAF data to calculate FCB (cf. Duncan et al. 1999) because channel cross-sections were measured only to bankfull stage and extrapolation was likely to generate error. Furthermore, use of a higher stage would have increased FCB and resulted in an upper truncation.

TABLE 3. Comparison of regression models of invertebrate community metrics and measures of bed stability (BCP = bottom component Pfankuch Index, ITM = initial tracer-stone movement, TTM = total tracer-stone movement, VOS = volume of scour). Models are compared by their Akaike's Information Criterion for small samples (AICc) (Akaike 1974). The lowest value (bold) signifies the best model. Significance indicated by * for $\alpha = 0.1$ and ** for $\alpha = 0.05$.

Variables	Linear	Polynomial	Logarithmic	Exponential	Power
Evenness (Berger–Parker Index)					
BCP	−40.39**	−35.89	−39.91**	**−40.56****	−40.31
ITM	**−36.42**	−32.56	−34.59	−36.31	−34.63
TTM	**−40.11****	−35.64	−34.43	−39.91**	−34.43
Taxonomic richness (Margalef's Index)					
BCP	0.98**	4.69*	0.45**	0.83**	**0.35****
ITM	3.77	6.54	**3.44***	3.70*	3.52*
TTM	0.35**	2.75**	3.79*	**0.19****	3.87*
VOS	6.00	3.70**	1.42**	5.99	**1.14****



Tracer stones

Tracer particles can be used to quantify entrainment, transport length, and path of surface stones. The bed-stability measures derived from their transport distance were consistently correlated with diversity metrics and invertebrate community composition. ITM seems more relevant to predict the number of taxa and individuals present. ITM is more sensitive than TTM to fine gradations in bed stability at relatively unstable sites because initial transport of a large fraction of stones beyond the search distance (e.g., at Tamaki) might result in disproportionate importance of a few immobilized particles in subsequent measurement periods. This situation could lead to a disproportionately low TTM relative to more stable sites that have shorter transport distances over all periods. On the other hand, tracer monitoring over a longer period better characterizes the flood regime.

The strong link between tracer-stone measures and community composition emphasizes the importance of the transport and entrainment components of bed stability for benthic communities. Negative linear relationships between the number of taxa and measures of tracer-stone movement have been recorded in many studies (Robinson and Minshall 1986, Death and Winterbourn 1995, Death 2002, Death and Zimmermann 2005), but quadratic relationships had occasionally similar (Death 2002, Death and Zimmermann 2005) or higher explanatory power (Townsend et al. 1997b), or no relationship was observed (Reice 1985, Englund 1991). However, Townsend et al. (1997b) measured only entrainment of tracers rather than transported distance, whereas other studies focused on smaller scales (e.g., a single stone; Robinson and Minshall 1986). A connection between invertebrate density and tracer-stone movement was

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FIG. 4. Nonmetric multidimensional scaling (NMDS) plot showing site scores based on stream macroinvertebrate community similarity plotted on Axes 1 and 2 (A), 1 and 3 (B), and 2 and 3 (C). Length and direction of arrows show strength and correlation of bed-stability measures with the NMDS axes. Site codes are: wpw = Waipawa, mwt = Manawatu, tam = Tamaki, mpk = Mangapuaka, cop = Coppermine, kiw = Kiriwhakapapa, wtr = Waiotauru, pkt = Pukeatua, oha = Ohau, pir = Te Piripiri, mtn = Mangatoetoenui, pkn = Pukeatua). NRV = % native riparian vegetation, ITM = initial tracer-stone movement, TTM = total tracer-stone movement, VOS = volume of scour, BCP = bottom component of the Pfankuch Index. Periphyton = chlorophyll *a* concentration on stones on the stream bed.

found by Death and Winterbourn (1995) and Matthaei et al. (2000), but no correlation was found in other studies (Death 2002, Death and Zimmermann 2005). However, most studies agree that invertebrate abundance decreases with increasing physical disturbance (Vinson and Hawkins 1998, McCabe and Gotelli 2000). Strong links between diversity (number of taxa, evenness, rarefied taxonomic richness) and tracer-stone movement are supported by many studies (Boulton et al. 1988, Englund 1991, Death and Winterbourn 1995, Rosser and Pearson 1995, Death 2002, Death and Zimmermann 2005), although the nature of the tracers varied (e.g., unembedded stones).

Presence of in-situ-marked tracer stones after floods can provide information about the patchiness of disturbance (Matthaei et al. 1999a, Downes et al. 1998) and availability of refugia for invertebrates on stable surface stones (Matthaei et al. 2000). In-situ-marked stones reflect actual entrainment more realistically (Downes et al. 1998) than tracer stones placed on the river bed. Under conditions of strong imbrication (e.g., Pukeonake), low sediment supply (e.g., Manawatu), or the presence of a bed armor layer, differences in entrainment between in-situ-marked particles and stones placed on the channel bottom could be expected to be immense. However, the form of the connection between community characteristics and movement of in-situ-marked stones found in our study corresponds with the relationships observed using unembedded stones (Death and Winterbourn 1995, Death 2002, Death and Zimmermann 2005). A frequently observed weakness of this method is the decrease in transport rate with time because of immobilization (burial, storage on bars and floodplain) of tracers (Ferguson et al. 2002), especially when the number of tracers is small. Another complication caused by use of a relatively small number of tracer stones is that the spatial variability of bedload transport within the reach might not be accounted fully (Ferguson 2003, Vericat and Batalla 2007). Malfunction or loss of the RFID tags can be another, albeit rare, constraint of this method. Nevertheless, the low cost of RFID tags (2.61 USD/tag), high recovery rate, possibility of noninvasive relocation, and ability to find invisible tracer stones proved to be major advantages of this technique.

Pfankuch Index

The BCP is a bed-stability measure that incorporates entrainment, deposition, and transport of the substrate. It was linked with invertebrate community composition and diversity, especially taxonomic richness, but not the number of taxa and individuals. Death and Winterbourn (1995) and Death (2002) found a strong negative linear relationship between the number of taxa and the BCP, whereas Townsend et al. (1997b), who used the full Pfankuch Index recorded only a weak correlation. In contrast with our results, Death and Winterbourn (1995) found a strong negative linear connection between invertebrate density and the BCP, but weaker relationships with evenness and taxonomic richness. A potential cause for these differences could be that visual assessment of stream characteristics is prone to subjectivity. Large differences can occur between evaluations of the same reach by the same observer under varying conditions (e.g., weather; ACS, unpublished data). However, the approach is straightforward, quick, and cost-effective.

Conclusions

The Pfankuch Index and use of a limited number of tracer stones do not fully account for the spatial variability in substrate stability, but they are relevant bed-stability measures for invertebrate communities. Use of tracer stones requires frequent site visits and is more laborious than the potentially observer-biased Pfankuch Index. Therefore, we recommend that future research should be focused on development of a straight-forward surrogate for measurement of tracer-stone movement that is less affected by subjectivity than the Pfankuch Index. Such a method could facilitate assessment of ecologically relevant streambed-stability characteristics and would be an effective tool for research on abiotic effects on benthic communities.

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