

## MACROINVERTEBRATE COMMUNITY RESPONSE TO A SPATE DISTURBANCE IN A THIRD ORDER OHIO STREAM

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**ABSTRACT.** A spate, or sudden flood, is a common disturbance in streams and can be an important factor in structuring macroinvertebrate communities. However, the effects of spates are likely mediated by other factors, such as habitat. This study tested whether a spate (22.5 times higher than base flow) influenced macroinvertebrate community composition and abundance in riffles and pools within the Kokosing River in Knox County, Ohio. Five pools and five riffles were sampled before and after a spate for macroinvertebrates and physical parameters during fall 2011. Macroinvertebrate communities and physical parameters differed between riffles and pools. Riffles had higher flow rates, a higher % EPT (Ephemeroptera, Plecoptera and Trichoptera) index and increased Shannon diversity compared to pools. We found that habitat was more influential on macroinvertebrate communities than the occurrence of a single spate. However, this single spate disturbance altered water depth and current velocity, increased diversity in riffles and pools, and homogenized community composition across habitat types. Changes in community structure resulted from decreased abundance for some of the dominant riffle taxa (e.g., Hydropsychidae, Baetidae) and an increased abundance of some taxa in pools after the spate (e.g., Chironomidae). We also found more similarity between riffle and pool communities following the spate. These results suggest that the macroinvertebrate community is relatively resistant and resilient to a spate of this magnitude, but flooding can alter community composition in both riffles and pools in this river.

**Keywords:** flood, flow refugia, Kokosing River, pools, riffles

### INTRODUCTION

Natural flow disturbance is central in shaping lotic community structure (Power et al. 1988; Resh et al. 1988). During droughts, drastic declines in flow usually result in a reduction of available habitat for stream biota (Hynes 1958; Smock et al. 1994; Erman & Erman 1995). Alternatively, during sudden floods, or spates, greater discharge can increase the availability of habitat by inundating previously dry areas or scouring streambeds, resulting in a mosaic of patches that can be recolonized (Mackay 1992; Brooks 1998; Lake 2000). Spates, though, also increase current velocity and turbulence (Hose et al. 2007). Higher volumes of fast-moving water can suspend sediments; redistribute organic and

inorganic benthic materials (e.g., detritus and debris); uproot plants; and displace, injure, or kill aquatic animals (Lake 2000).

The impacts of spates on macroinvertebrate communities are usually negative. Macroinvertebrate abundance (Bond & Downes 2003; Melo et al. 2003; Mundahl & Hunt 2011) and species richness (Bond & Downes 2003; Death & Winterbourn 1995; Death 2002) may be significantly lower immediately after spates or experimental flow disturbance events. Angradi (1997) found that most macroinvertebrate taxa decreased in abundance by 70–95% following one spate. Alternatively, some spates had no significant effects on macroinvertebrate abundance (Palmer et al. 1992; Dole-Olivier et al. 1997) or Shannon diversity (Reice 1984) and, in some cases, evenness (Death & Winterbourn 1995; Mesa 2010) or Simpson's diversity increased (Death & Winterbourn 1995).

Stream habitats can potentially mitigate the response of macroinvertebrate communities to spates. For example, current velocity can increase substantially in riffles while maintaining relatively slower speeds in other areas

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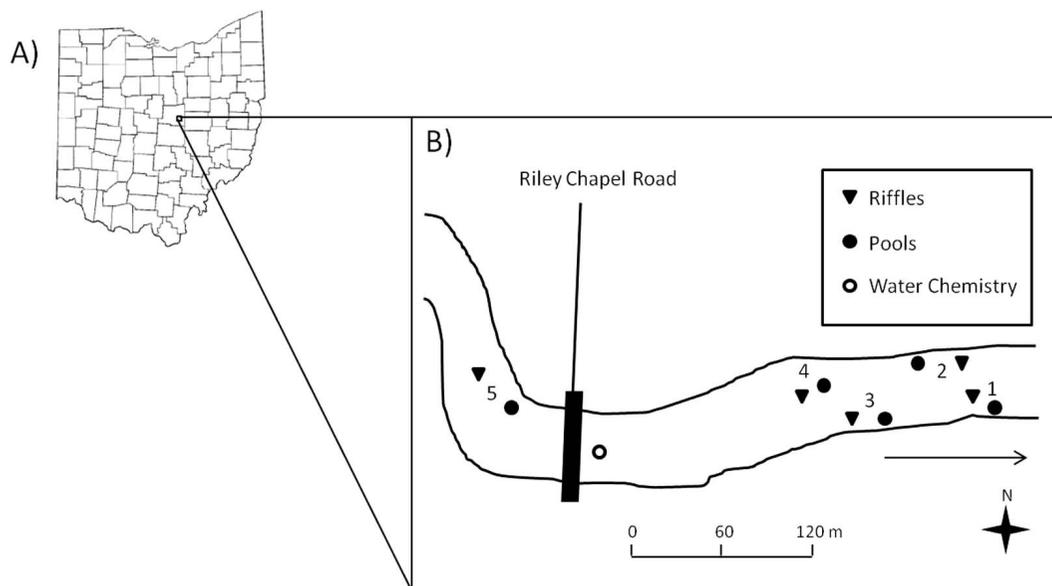


Figure 1.—Location of study site in Knox County, Ohio (A). Sampling sites (1–5) in the Kokosing River (B). Arrow indicates the direction of water flow.

(Negishi et al. 2002). As a result, some stream habitats might act as flow refugia where density-independent losses of macroinvertebrates are likely to be minimal (Lancaster & Hildrew 1993). Flow refugia have been documented in pools, backwaters, interstitial spaces, and hyporheic zones (Brooks 1998; Palmer et al. 1992; Dole-Olivier et al. 1997; Negishi et al. 2002). Because streams differ in the amount of flow refugia that are present, the resilience of macroinvertebrate communities to spates is also likely to differ. Systems with larger rocks, intact riffle and pool sequences, and potentially more refugia (Matthaei et al. 1996, 1997; Brooks 1998) should display faster recolonization of disturbed habitat patches, while streams with sandy substrates and few refugia are likely to demonstrate slower recolonization rates after spates (Fisher et al. 1982; Grimm & Fisher 1989).

While it is well-known that flow disturbances influence macroinvertebrate communities, the direction and magnitude of these effects are unresolved (Death & Winterbourn 1995). In this study, we examined how macroinvertebrate communities in two habitat types were affected by a spate in the Kokosing River (Knox Co., Ohio). The Kokosing River experiences a wide range of flow regimes and has a variety of habitat types that are well-represented. Our

specific objectives were to (1) characterize macroinvertebrate communities in pools and riffles within the Kokosing River, (2) document community changes within each habitat type after a spate, and (3) compare changes in community structure across habitat types after a spate.

## METHODS

**Study site and design.**—The Kokosing River (40° 22.352' N and 82° 12.029' W) is a third order stream in Knox County, Ohio located within the Muskingum (Ohio) River drainage basin (Fig. 1). The Kokosing River bears a Scenic River designation from the Ohio Department of Natural Resources, indicating a waterway that retains much of its natural character with limited human disturbance (Ohio EPA 2010). The substrate of the Kokosing River is primarily composed of bedrock, boulders, and large cobble derived from the Blackhand Sandstone formation (Slucher et al. 2006).

Our study site in the Kokosing River was designated as Exceptional Warmwater Habitat (EWH) and was in full attainment prior to this study (Ohio EPA 2010). A relatively high QHEI score (88) also indicated the presence of a diversity of stream habitats and a moderately intact riparian zone (Ohio EPA 2006).

The riparian zone was dominated by sycamore (*Platanus occidentalis* L.), eastern cottonwood (*Populus deltoides* Bartram ex Marshall), silver maple (*Acer saccharinum* L.), and box elder (*Acer negundo* L.).

On 18 October 2011, the river was at base flow, approximately  $1.22 \text{ m}^3/\text{s}$  (USGS 03136500 gauging station, [http://waterdata.usgs.gov/nwis/uv?site\\_no=03136500](http://waterdata.usgs.gov/nwis/uv?site_no=03136500)). We sampled ten areas before the spate – five riffles and five pools (Fig. 1). At each pool and riffle, we measured water depth with a meter stick and current velocity with a flow meter (General Oceanics Flow Meter Model 2030, Miami, FL). For riffles, water depth and current velocity were measured at 20%, 40%, 60%, and 80% of the width of the riffle. The average of each variable was used in later analyses. For pools, water depth and current velocity were measured in the center of each pool. At each location, macroinvertebrates were collected with a Surber sampler (area:  $900 \text{ cm}^2$ ;  $250 \mu\text{m}$  mesh) and preserved in 70% ethanol. In pools, we added a base extension to the Surber sampler to minimize collection of fine sediments outside of the target area. We used a YSI® 556 Multi-Parameter Water Quality Meter (Yellow Springs, Ohio) to measure basic water chemistry (e.g., water temperature, specific conductance, dissolved oxygen, pH) between sites 4 and 5 (Fig. 1). Water samples were also collected between sites 4 and 5 and placed on ice for transport back to the laboratory for further laboratory analyses of  $\text{SiO}_2$ ,  $\text{PO}_4$ ,  $\text{NO}_3\text{-N}$ ,  $\text{SO}_4$ , Cl, total hardness, turbidity and total alkalinity (see Lab Methods).

Over 5 cm of precipitation occurred on 19 and 20 October 2011, resulting in a peak discharge of  $22 \text{ m}^3/\text{s}$  on 20 October 2011. On 26 October 2011, the Kokosing River was revisited during its flood state, when discharge was  $6.03 \text{ m}^3/\text{s}$ . We sampled ten areas after the spate – five riffles and five pools (Fig. 1). Collection of macroinvertebrates and physico-chemical properties during the flood stage followed the protocol utilized during the first visit.

**Lab methods.**—Macroinvertebrates were examined using stereoscopes. Insects were identified to family level; other invertebrates were identified to class or order using Voshell (2002), Merritt et al. (2008), and Thorp & Covich (2010). Taxonomic resolution to family is sufficient for most bioassessment studies of

anthropogenic and natural disturbance using macroinvertebrates (Waite et al. 2004).

Water samples were analyzed for  $\text{SiO}_2$  (Method 8185),  $\text{PO}_4$  (Method 8048),  $\text{NO}_3\text{-N}$  (Method 8171), and  $\text{SO}_4$  (Method 8051) using a Hach DR/890TM colorimeter (Loveland, CO). Total hardness (Ca mg/L) and chlorine (mg/L) were measured with testing strips (Hach Company, Loveland, CO). Stream water turbidity was determined with a HACH 2100P™ turbidity meter (Loveland, CO) and total alkalinity was determined using titration (Hanna Instruments Method 4811).

**Statistical analyses.**—To analyze the effects of habitat type and spate condition, we used analyses of variance (ANOVAs) (Minitab 16 (Minitab Inc., 2010)). Response variables were water depth, current velocity, and macroinvertebrate community metrics (i.e., abundance (individuals/ $\text{m}^2$ ), taxa richness, Shannon diversity ( $H'$ ), and % EPT [the percentage of total organisms in the orders Ephemeroptera, Plecoptera and Trichoptera] (Resh & Jackson 1993; Magurran 2004). Normality of response variables was assessed with probability plots and Anderson-Darling tests. Square root transformations were used for abundance and current velocity and an arcsine transformation was used for % EPT.

To evaluate macroinvertebrate community composition, we used non-metric multidimensional scaling (NMDS) to create an ordination plot of samples based on a Bray-Curtis dissimilarity matrix (Kruskal 1964; Mather 1976). Rare taxa were defined as those occurring in only one sample and were removed from the data set prior to ordination analysis. A Monte Carlo test was used to compare 50 runs of our data to 50 runs of randomized data to determine whether an ordination solution with comparable stress could be obtained by chance alone. To test for significant differences between habitat types and spate condition, non-parametric multi-response permutation procedures (MRPP) were used. Finally, indicator species analyses were employed to determine which taxa were most influential for distinguishing among habitats before and after the spate. Indicator analysis combines information on the relative abundance and relative frequency of each taxon within each sample group (Dufrêne & Legendre 1997). A perfect indicator would be both exclusive to that group and always present in samples from that group

Table 1.—Water chemistry in the Kokosing River on 18 October 2011 (Pre-spate) and 26 October 2011 (Post-spate).

|                                     | Pre-spate | Post-spate |
|-------------------------------------|-----------|------------|
| Conductivity (mS/cm)                | 0.52      | 0.45       |
| Total Dissolved Solids (g/L)        | 0.34      | 0.29       |
| Salinity (mg/L)                     | 0.25      | 0.22       |
| Dissolved Oxygen (mg/L)             | 11.30     | 12.07      |
| pH                                  | 8.90      | 8.43       |
| Alkalinity (CaCO <sub>3</sub> mg/L) | 300       | 260        |
| NO <sub>3</sub> (mg/L)              | 1.20      | 3.60       |
| PO <sub>4</sub> (mg/L)              | 0.12      | 0.22       |
| SiO <sub>2</sub> (mg/L)             | 5.60      | 8.00       |
| SO <sub>4</sub> (mg/L)              | 30        | 32         |
| Turbidity (NTUs)                    | 2         | 4          |
| Water Temperature (°C)              | 12.5      | 11.0       |

(McCune & Grace 2002). Two Monte Carlo tests with 5000 randomizations were used to test the significance of indicator values for habitat type before and after the spate. MRPP and indicator analyses were all conducted in PC-ORD version 6.08 (McCune & Mefford 2011).

RESULTS

Water chemistry in the Kokosing River was similar on both sampling days and was not included in further analyses (Table 1). Physical parameters changed during the study: water depth (Table 2, Fig. 2A) and current velocity

(Table 2, Fig. 2B) both significantly increased after the spate. Current velocity was also faster in riffles compared to pools throughout the course of the study (Table 2, Fig. 2A).

Some macroinvertebrate community metrics were different between habitats and changed after the spate. Riffles had a significantly higher % EPT index than pools (Table 2, Fig. 3A). Percent EPT decreased in riffles after the spate, but increased in pools, as indicated by a significant habitat × spate interaction term (Table 2, Fig. 3A). Shannon diversity (*H'*) was significantly higher in riffles (Table 2, Fig. 3B) and there was a trend towards increased Shannon diversity after the spate in both habitat types, although this result was not significant (*p* = 0.057, Table 2, Fig. 3B). Variance in % EPT index and Shannon diversity (*H'*) was also greater in pools after the spate (Fig. 3A & 3B). Taxa richness and total macroinvertebrate abundance were not significantly affected by habitat or spate condition (Table 2, Figs. 3C & 3D).

The NMDS ordination showed that macroinvertebrate community composition was distinctly different between riffles and pools before the spate, but overlapped after the spate (Fig. 4) (3-dimensional solution stress = 7.06, *p* = 0.04). MRPP analysis confirmed the visual patterns evident with NMDS. Riffle communities differed significantly from pool communities

Table 2.—ANOVA summary of the effects of habitat type and spate condition on physical parameters and macroinvertebrate community metrics in the Kokosing River.

| Response                 | N  | Source          | F     | <i>p</i> |
|--------------------------|----|-----------------|-------|----------|
| <b>Water Depth</b>       | 20 | Habitat Type    | 0.75  | 0.400    |
|                          |    | Spate Condition | 6.73  | 0.020    |
|                          |    | Habitat × Spate | 0.07  | 0.790    |
| <b>Current Velocity</b>  | 20 | Habitat Type    | 91.73 | <0.001   |
|                          |    | Spate Condition | 5.72  | 0.029    |
|                          |    | Habitat × Spate | 1.15  | 0.298    |
| <b>% EPT</b>             | 20 | Habitat Type    | 25.19 | <0.001   |
|                          |    | Spate Condition | 0.01  | 0.933    |
|                          |    | Habitat × Spate | 6.00  | 0.026    |
| <b>Shannon Diversity</b> | 20 | Habitat Type    | 10.31 | 0.005    |
|                          |    | Spate Condition | 4.22  | 0.057    |
|                          |    | Habitat × Spate | 1.82  | 0.196    |
| <b>Taxa Richness</b>     | 20 | Habitat Type    | 0.37  | 0.553    |
|                          |    | Spate Condition | 0.11  | 0.741    |
|                          |    | Habitat × Spate | 0.00  | 0.947    |
| <b>Abundance</b>         | 20 | Habitat Type    | 0.00  | 0.955    |
|                          |    | Spate Condition | 1.04  | 0.323    |
|                          |    | Habitat × Spate | 0.23  | 0.634    |

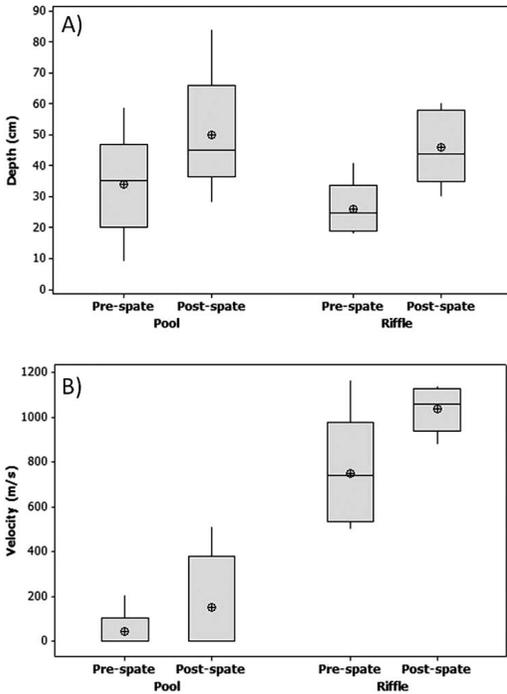


Figure 2.—Depth (A) and current velocity (B) in five pools and five riffles in the Kokosing River before (18 October 2011) and after (26 October 2011) a spate event ( $N=20$ ). For each response, circles represent the mean, horizontal lines show the median, gray boxes represent the interquartile range (IQR) and whiskers indicate values occurring within the upper ( $3^{\text{rd}}$  quartile +  $1.5 \times \text{IQR}$ ) and lower ( $1^{\text{st}}$  quartile -  $1.5 \times \text{IQR}$ ) limit.

before the spate ( $T = -2.20$ ,  $A = 0.16$ ,  $p = 0.038$ ) while post-spate communities in the two habitats were not significantly different from one another ( $T = -1.09$ ,  $A = 0.05$ ,  $p = 0.127$ ). Pre-spate macroinvertebrate communities demonstrated stronger separation between habitats (more negative  $T$  values) as well as greater within-habitat homogeneity (higher  $A$  values) compared to post-spate communities. However, MRPP analyses within each habitat type indicated macroinvertebrate assemblages were not significantly different before and after the spate (Riffles:  $T = 1.09$ ,  $A = -0.05$ ,  $p = 0.883$ ; Pools:  $T = -0.11$ ,  $A = 0.01$ ,  $p = 0.364$ ).

Indicator species analysis prior to the spate showed that Baetidae (IndVal = 43.9,  $p = 0.007$ ) and Hydropsychidae (IndVal = 47.5,  $p = 0.007$ ) were indicative of riffle habitat due to high abundance and high frequency in riffle

samples (Table 3). Heptageniidae (IndVal = 42.6,  $p = 0.086$ ) were somewhat indicative of riffle habitat, but had lower abundance than the two aforementioned families (Table 3). After the spate, only Heptageniidae (IndVal = 37.7,  $p = 0.046$ ) were indicative of riffle habitat.

In general, the average abundance of dominant macroinvertebrate taxa declined after the spate. In riffles, the three most abundant macroinvertebrate groups decreased 51.6% - 83.8% after the spate (Baetidae: 83.8%, Hydropsychidae: 80.3%, Heptageniidae: 51.6%) (Table 3). In pools, the most abundant group decreased by 94.6% after the spate (Pleuroceridae), but the second most abundant group actually increased by 43.0% (Chironomidae) (Table 3).

## DISCUSSION

Water depth and current velocity both increased significantly after the spate, but macroinvertebrate riffle and pool communities were relatively resistant and resilient to a spate of this magnitude. For example, total macroinvertebrate abundance was not reduced by the spate. This finding is in contrast to many previous studies examining the effects of spates in streams (Lamberti et al. 1991; Angradi 1997; Bond & Downes 2003; Melo et al. 2003). There are at least three possible reasons for this finding. First, a large amount of variation was present in macroinvertebrate densities prior to the spate and thus, even with a decline in abundance after the spate, the result was not statistically significant. When examining individual groups of invertebrates, the average of many abundant groups declined after the spate (Table 3; Angradi 1997). One exception to this pattern was the increase in Chironomidae in pools after the spate. A second likely explanation is that the community was relatively resistant to this spate. Some organisms in the Kokosing River, such as the heptageniid mayflies, are well-adapted to high flow conditions and have adaptations for clinging to substrates, such as dorsoventrally flattened bodies and holdfast organs (Hora 1930). Heptageniids declined, but were still a large percentage of the riffle community after the spate. It is also likely that the spate was not strong enough to completely dislodge organisms. This spate was 22–23 times the average base flow for October, but at the highest discharge ( $22 \text{ m}^3/\text{s}$ ), was equal to the average

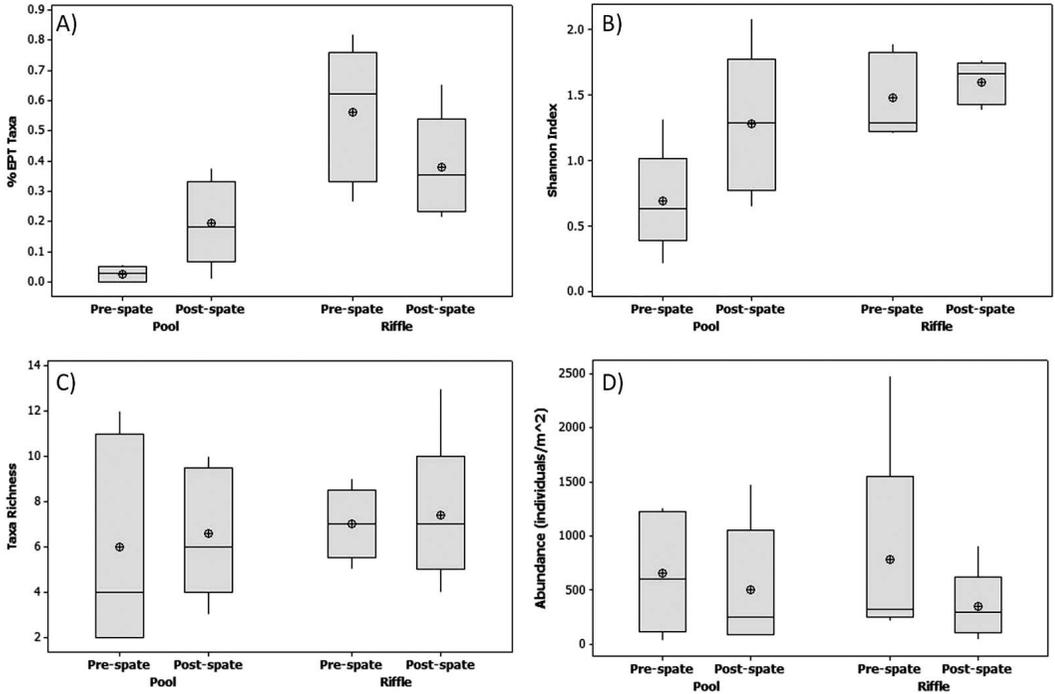


Figure 3.—% EPT taxa (A), diversity (B), taxa richness (C) and abundance (D) in five pools and five riffles in the Kokosing River before (18 October 2011) and after (26 October 2011) a spate event (N=20). For each response, circles represent the mean, horizontal lines show the median, gray boxes represent the interquartile range (IQR) and whiskers indicate values occurring within the upper (3<sup>rd</sup> quartile + 1.5\*IQR) and lower (1<sup>st</sup> quartile + 1.5\*IQR) limit.

base flow in some spring months and remained within the bankfull height of the Kokosing River (USGS 2011). A third explanation is that the community was relatively resilient to this spate and recovered quickly. Recolonization of disturbed habitat patches happened rapidly following this disturbance and was facilitated by habitat refugia and morphological, behavioral, and physiological traits of the organisms (Wallace & Anderson 1996; Lytle & Poff 2004). Angradi (1997) found that full recovery of macroinvertebrate density in Appalachian streams can take 4–6 months to occur and some invertebrate groups may not recover to pre-flood densities 22 months after the event (Mundahl & Hunt 2011). However, invertebrates in desert streams in the western United States recovered in 2–4 weeks (Fisher et al. 1982; Grimm & Fisher 1989), similar to Australian tropical rainforest streams (Rosser & Pearson 1995). Given that this post-spate sampling date was 5 days after peak flood discharge, the community did not have time to completely recover; however, some recovery had already started. This spate caused

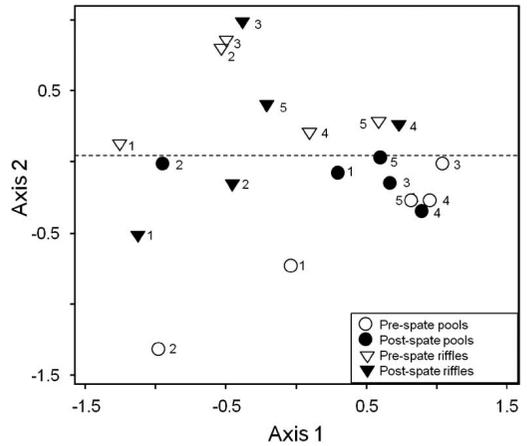


Figure 4.—NMDS ordination plot for relative abundance of macroinvertebrate taxa in riffles and pools before (18 October 2011) and after (26 October 2011) a spate event (N=20). Triangles represent riffles; circles represent pools. Open symbols indicate pre-spate conditions; closed symbols indicate post-spate conditions. Numbers correspond to sites in Fig. 1. Dotted line bisecting axis 2 separates riffle sites from pool sites before the spate, but not after the spate.

Table 3.—Mean abundance of macroinvertebrate taxa per m<sup>2</sup> ( $\pm$  1 SE) of macroinvertebrate taxa before and after the spate in riffles and pools.

| Taxa            |                           | Riffles   |            | Pools     |            |
|-----------------|---------------------------|-----------|------------|-----------|------------|
|                 |                           | Pre-Spate | Post-Spate | Pre-Spate | Post-Spate |
| Ephemeroptera   | Baetidae                  | 124 (61)  | 20 (17)    | —         | —          |
|                 | Caenidae                  | —         | 4 (4)      | —         | —          |
|                 | Ephemerellidae            | 4 (4)     | 2 (2)      | 9 (9)     | —          |
|                 | Ephemeridae               | —         | 7 (7)      | —         | 22 (15)    |
|                 | Heptageniidae             | 64 (36)   | 31 (15)    | 7 (7)     | —          |
|                 | Leptophlebiidae           | —         | 2 (2)      | —         | —          |
|                 | Oligoneuriidae            | —         | 7 (7)      | —         | —          |
| Odonata         | Gomphidae                 | —         | —          | 2 (2)     | —          |
|                 | Libellulidae              | —         | —          | 2 (2)     | —          |
|                 | Unknown Anisoptera        | —         | —          | —         | 2 (2)      |
| Plecoptera      | Chloroperlidae            | —         | —          | —         | 4 (4)      |
|                 | Perlidae                  | —         | —          | —         | 7 (3)      |
|                 | Perlodidae                | 9 (6)     | —          | 4 (4)     | —          |
|                 | Unknown Plecoptera        | 2 (2)     | —          | —         | —          |
| Megaloptera     | Corydalidae               | —         | —          | —         | 2 (2)      |
| Trichoptera     | Hydropsychidae            | 324 (240) | 64 (35)    | 2 (2)     | 4 (3)      |
|                 | Hydroptilidae             | —         | 2 (2)      | —         | —          |
|                 | Limnephilidae             | —         | —          | 2 (2)     | —          |
| Lepidoptera     | Pyrilidae                 | 2 (2)     | —          | —         | —          |
| Coleoptera      | Elmidae                   | 7 (3)     | 24 (19)    | 7 (3)     | 4 (4)      |
|                 | Psephenidae               | —         | 2 (2)      | —         | —          |
|                 | Athericidae               | —         | 4 (4)      | —         | —          |
| Diptera         | Chironomidae              | 78 (24)   | 40 (15)    | 244 (107) | 349 (240)  |
|                 | Culicidae                 | —         | 2 (2)      | —         | —          |
|                 | Simuliidae                | —         | —          | 2 (2)     | —          |
|                 | Tabanidae                 | —         | —          | —         | 2 (2)      |
|                 | Tipulidae                 | —         | 2 (2)      | —         | —          |
|                 | Crustacea                 | Amphipoda | 2 (2)      | —         | 7 (7)      |
|                 | Copepoda                  | —         | —          | —         | 4 (4)      |
|                 | Ostracoda                 | —         | —          | 2 (2)     | 2 (2)      |
| Chelicerata     | Acari                     | 7 (7)     | —          | 4 (4)     | 4 (3)      |
| Gastropoda      | Ancylidae                 | —         | —          | —         | 7 (7)      |
|                 | Lymnaeidae                | —         | —          | 2 (2)     | 2 (2)      |
|                 | Physidae                  | —         | 4 (3)      | 4 (3)     | 13 (13)    |
|                 | Pleuroceridae             | 142 (137) | 96 (87)    | 331 (207) | 18 (9)     |
| Bivalvia        | <i>Corbicula fluminea</i> | —         | —          | 9 (6)     | 2 (2)      |
| Annelida        | Oligochaeta               | 11 (6)    | 22 (9)     | 16 (10)   | 42 (17)    |
| Platyhelminthes | Turbellaria               | 4 (4)     | 4 (4)      | —         | 2 (2)      |
| Cnidaria        | <i>Hydra</i>              | —         | —          | —         | 7 (7)      |
| TOTAL           |                           | 782 (430) | 342 (148)  | 658 (250) | 502 (263)  |

declines of some macroinvertebrate groups, but total abundance was not affected by a spate of this magnitude.

Even though macroinvertebrate abundance was not significantly affected, Shannon diversity slightly increased in both riffles and pools after the spate. Intermediate levels of disturbance are thought to create situations that yield maximum levels of diversity by reducing the abundance of strong competitors

and creating space for pioneer species to reestablish (Connell 1978). In riffle habitat of the Kokosing River, this spate reduced the abundance of the dominant macroinvertebrates (i.e., Hydropsychidae and Baetidae; Table 3), potentially opening patches for less abundant taxa (e.g., Elmidae and Ephemeridae; Table 3). In pools the pattern was slightly different, with one of the two most dominant groups decreasing in abundance (i.e., Pleuroceridae),

and the other dominant group increasing in abundance (i.e., Chironomidae). Regardless, many of the less abundant taxa increased, resulting in a more even distribution of taxa (Death & Winterbourn 1995). In contrast, other studies indicate that floods drastically reduced the richness (Bond & Downes 2003; Effenberger et al. 2008) or Simpson's diversity of macroinvertebrate communities (Death 2002). These conflicting findings can likely be explained by different disturbance regimes with greater reduction in macroinvertebrate abundance, species richness, and species diversity occurring with floods of greater magnitude or frequency.

Across habitat types, macroinvertebrate communities became more homogeneous after the spate. Taxa that served as indicators for riffle communities before the spate, declined after the spate. This included steep decreases in the two most dominant pre-spate riffle taxa (i.e., Hydroptychidae and Baetidae); however, there was little evidence that pools in the Kokosing River served as refugia for these dominant riffle organisms. No baetid mayflies were recovered in pools after the spate and only a few hydroptychid caddisflies were observed in this habitat throughout the study. Conversely, chironomids decreased in riffles after the spate and increased in pool samples. Chironomids might have used pools as refugia, but it is also possible that disturbed sediments uncovered chironomids that were previously buried. Brooks (1998) found evidence for the passive movement of chironomids from riffles to pools during a large flood. Brooks (1998) also reported mayflies in pools following a large flood, but that was not the case in the current study.

Negishi et al. (2002) found that pool taxa were most negatively affected by a flood, with taxa richness significantly decreasing. In that study, backwaters and inundated areas, instead of pools, acted as refugia for the recolonization of riffle habitat. The hyporheic zone could serve as a flow refugium for benthic invertebrates during times of flooding in the Kokosing River (Williams & Hynes 1974). While the hyporheic zone was not sampled in this study, some studies have concluded that it serves a major refugium for some benthic taxa, including *Gammarus* and cladocerans (Dole-Olivier et al. 1997). However, Palmer et al. (1992) found little evidence that the hyporheic zone was important as a refugium for benthic invertebrates.

Macroinvertebrate assemblages were more influenced by habitat differences than by the occurrence of a single spate in the Kokosing River. Shannon diversity and % EPT were always greater in riffles when compared to pools, confirming previous studies. A single spate caused reductions in dominant riffle taxa, which caused diversity to increase within riffles after the spate and homogenized taxa composition and evenness across two habitats after the spate. Macroinvertebrate assemblage structure in the Kokosing River is driven by habitat variables, but disturbances of this magnitude are likely to be important for maintaining diversity within different habitat types in this system.

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