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Annual and spatial variation for macroinvertebrates in the Upper Mississippi River near Cape Girardeau, Missouri

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With 5 figures, 5 tables and 1 appendix

Abstract: We sampled macroinvertebrates at four sites in the Open River section of the Upper Mississippi River near Cape Girardeau, Missouri (Rkm 106–114). In 1999, 2000, and 2002–2004, macroinvertebrates were sampled in the fine sediments downstream of four wing dikes with a Ponar dredge. In 1999 and 2001, macroinvertebrates on rocks were sampled on the upstream face of those same wing dikes with rock baskets. We identified 68 taxa in the fine sediments and 50 taxa on the rocks, with only 27 taxa being found in both. In both habitats, annual variability in population densities and community structure exceeded spatial variability. Macroinvertebrate densities in the fine sediments ranged from approximately 3700 to 11,700 individuals/m^2 with oligochaetes comprising 77–95 % of total density. Non-metric Multidimensional Scaling ordination suggests that annual differences in the fine sediment assemblage reflect variation in hydrological conditions (high spring flow and low annual flow). Macroinvertebrate density on the rocks ranged from approximately 57,800 to 163,000 individuals/m^2 with hydropsychid caddisflies (*Hydropsyche bidens/orris* and *Potamyia flava*) comprising 82–97 % of total density. This dominance of oligochaetes in fine bottom substrates and caddisflies on hard substrates is consistent with many other studies on big rivers in the Mississippi River Basin (e. g., Upper and Lower Mississippi, Ohio, Illinois, and Missouri Rivers), and may be the current "reference condition" for these big rivers. This makes traditional water quality monitoring and assessment efforts using macroinvertebrates more difficult because increased dominance by more pollution tolerant taxa is perceived as evidence of water or habitat degradation. However, macroinvertebrate assemblages in our study reach seem less stressed than other big rivers known to be impaired. Specifically, densities of the pollution-sensitive mayfly *Hexagenia* indicate that conditions in our study reach have improved markedly since the 1960's.

Key words: Upper Mississippi River, macroinvertebrates, bioassessment, large rivers, *Hexagenia*, functional feeding group.

Introduction

Knowledge of ecological structure and function of big rivers (i. e., ≥ 7th order) is limited relative to streams and small rivers (Hynes 1989, Benke & Cushing 2005). The issue is not that the faunas and floras are unknown because most species of aquatic insects, mussels, crayfish, fish, and plants in big rivers of North America and Europe have been described. Rather, big rivers are difficult and dangerous to study because of their greater depth and current velocity, and their spatial and temporal complexity. In addition, most big rivers could be considered unique (Allan & Benke 2005) because: (1) large rivers are not common on the landscape [Leopold et al. (1964) estimated that there are only 50 8th–10th order rivers in the entire USA, but > 2 million 1st–3rd order streams]; (2) the relative few that exist tend to be bio-

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geographically distinct from each other (e. g., Benke & Cushing 2005); and most have a spatially and temporally distinct suite of modifications in their mainstems, floodplains, and/or headwaters (e. g., drinking water diversion dams in the headwaters of the Delaware River versus hydroelectric dams in the lower Susquehanna River, Jackson et al. 2005). This uniqueness can confound generalizations across big-river studies. While much has been learned in the 16 years since Hynes (1989) observed that studies of big rivers represented only a small fraction of the lotic ecology literature (i. e., about 400 of 10,000 scientific articles), our understanding of big rivers still relies largely on spatial and temporal extrapolations. For example, we have limited knowledge of spatial or interannual variability for macroinvertebrates on the Mississippi River because, with the exception of monitoring efforts using the mayfly *Hexagenia,* most macroinvertebrate studies are from one location and span ≤ 1 year.

This study examines spatial and annual variation in macroinvertebrate assemblages sampled at four sites (i. e., near wing dikes) along an 8-km reach of the Mississippi River. Macroinvertebrate sampling focused on two common habitats adjacent to the main channel at each site: fine silt sediments that accumulate immediately behind or downstream from the dikes and the rocks on the upstream faces of wing dikes. These habitats were chosen because they can be consistently identified at various river stages, and they support markedly different assemblages of macroinvertebrate species. Five years of data from the fine sediments and two years of data from rocks provide unique insight into the annual variation for each habitat. For additional perspective, we compare our results to data from the Upper and Lower Mississippi, Ohio, Illinois, and Missouri Rivers. Our main goals are to describe the structure and abundance of macroinvertebrate assemblages in the Mississippi River and to relate information regarding the temporal variability and dominance of taxa in the assemblages to water quality monitoring of big rivers.

Study site

The Mississippi River is the largest river in North America and, in its natural state, had a river corridor that was physically complex (e. g., main and side channels, open and isolated channels, islands and deep pools, erosional and depositional areas, and backwaters and floodplains; Fremling 1989, Patrick 1998, Delong 2005). Across this natural template, the two most common benthic substrates supporting aquatic macroinvertebrates were fine substrates such as gravel, sand, silt, or clay and plant material such as tree trunks, branches, roots, and aquatic macrophytes (e. g., Jahn & Anderson 1986). Anthropogenic activities modified the physical structure of the channel throughout most of the Mississippi River. Numerous dams create lakes and widen the channel in some locations while flood-control levees and dredging narrow the channel and isolate the floodplain in other locations. Sediments are redistributed by dams and dredging, and by lateral wing dikes (a.k.a., wing dams) that redirect flow toward the navigation channel and increase lateral sediment deposition. Riverbanks that were formerly clay, silt and snags are now covered with erosion protection materials such as limestone rocks or articulated concrete mattresses. Woody debris is now scarce or absent in the main channel.

Our study reach (37° 19′ 49″ N, 89° 29′ 39″ W) was on the Open River section of the Upper Mississippi River (UMR) near Cape Girardeau, Missouri. The Open River section (also referred to as the beginning of the UMR) is 312 km long, beginning at the confluence of the Mississippi and Missouri Rivers at St. Louis, MO and ending at the confluence with the Mississippi and Ohio Rivers at Cairo, IL (Delong 2005). The Missouri River increases the discharge of the Mississippi by one-third and with the addition of the Ohio River the UMR becomes 10th order. The Open River section is unimpounded and relatively free flowing even though it is downstream of the lock and dam system that forms Pools 1–26 in the UMR and six mainstem dams on the Missouri. Much of the Mississippi near our study reach is constrained by naturally high banks west of the channel and by flood levees east of the channel. The river at this location is approximately 0.8-km wide. Mean discharge of UMR is 5794 m^3s^{-1} at Thebes, IL (35 km downstream of our site; USGS gage 07022000; Delong 2005), with peak high flow in April and May, and low flow from August through February (Fig. 1). At the stage recorder closest to our sampling site (24 km downstream; USGS 07020850 Mississippi River at Cape Girardeau, MO, discharge not calculated), average monthly river stage ranges from 4.3 m in October to 9.0 m in May. Flow typically exceeds the flood stage (9.8 m) at least several days each year. Water released from dams in the Upper Missouri and UMR maintain low flow levels for river barge traffic; however, stages < 1.5 m can occur (e. g., Oct 2003). Average water

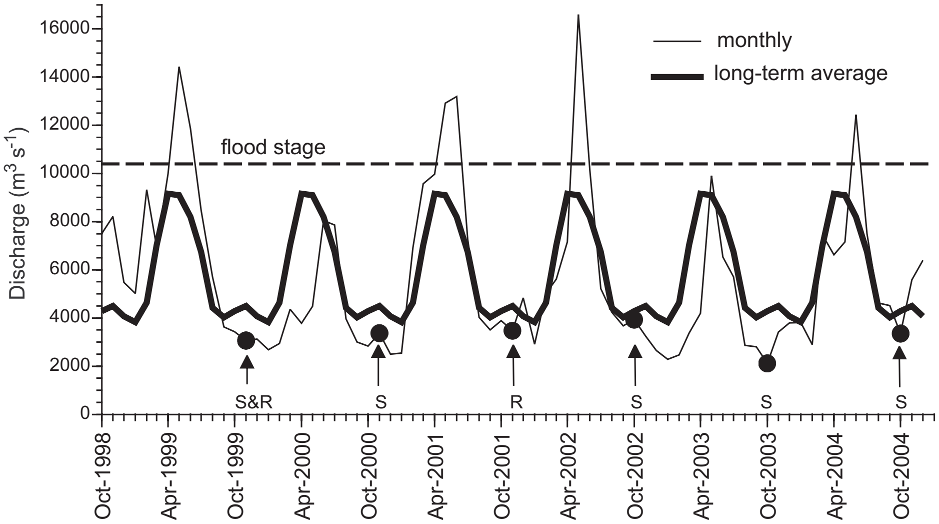

Fig. 1. Monthly and long-term average (1933–2004) discharge (m^{3}s^{-1}) on the Mississippi River near Thebes, IL at Rkm 70 (USGS Gage 07022000; USGS 2005). S and R indicate when sampling occurred in the fine sediments (S) and on the rocks (R).

temperature is 16.6 °C at Thebes, IL (range = 0 to 31.5 °C; USGS gage 07022000).

We focused our sampling around wing dikes because they are common throughout the Open River reach – there are 656 charted wing dikes in the 312 km between St. Louis, MO and Cairo, IL (range = 0–10 wing dikes/km). Wing dikes are constructed of limestone rocks and timbers. Most wing dikes in the UMR were first constructed between 1878–1907 as part of efforts to deepen the navigation channel (Delong 2005; Fremling 2005). The height and length of the dikes vary, presumably in response to hydrologic conditions, navigational needs, and recent efforts to improve fish habitat diversity. Our study dikes were roughly 50 m long, perpendicular to the bank, ranged from 2.5–6 m high, and appeared to have comparable habitats.

Macroinvertebrates were collected near four wing dikes upstream of Cape Girardeau at 106.30,111.85, 112.49 and 113.7 River km (Rkm) upstream of Cairo, IL and are referred to hereafter as dikes U1, U2, N1, and N2, respectively. Dike labels refer to un-notched (U) and notched (N); a notch (≈ 5 m wide) in the middle of a dike allows flow through during moderate to high flow. This modification was done on our study dikes prior to 1999 and is part of modern fisheries management efforts to diversify habitat around dikes. Despite a history of repair and modification for these dikes, there was no evidence of recent modifications or manipulations that may have affected our sampling.

Methods

Fine sediments

Aquatic macroinvertebrates were sampled from fine sediments in the slow depositional areas located immediately downstream of each wing dike using a Petite Ponar dredge (250-cm^2 sample area) deployed from a boat. Samples were collected on the 18 Nov 1999, 15–16 Nov 2000, 5 Oct 2002, 8–9 Oct 2003, and 6–7 Oct 2004 (Fig. 1). At each of the four dikes, five to ten samples were collected in 1999, nine samples in 2000, and 18 samples in 2002–2004. Water depth at the sample locations varied spatially and annually depending on bottom topography and river stage, respectively; average water depth across all samples was 5 m. Sediments collected were consistently dark-colored silt and clay that had little or no sand or gravel. Samples were processed using a 0.355-mm mesh-size sieve and preserved with 5 % buffered formalin. In the laboratory, entire samples were processed (no subsampling) and macroinvertebrates were identified to genus/species (aquatic insects) or order/family (most non-insects) and enumerated.

Rocks

The upstream face of dikes has rocky substrates and fast currents. Aquatic macroinvertebrates were sampled with artificial substrate samplers (i. e., rock basket samplers) that simulated the rock/rubble habitat found on the wing dikes and along the shoreline. The baskets were constructed with plastic aquaculture netting (3.2 × 3.2 cm mesh, Memphis Net and Twine, Memphis, Tennessee) folded to form a 25 × 25 cm envelope and bound together with plastic ties. Each basket was filled with limestone rocks from a 2739-cm^2 container (mean = 18 rocks/basket; range = 12–28 rocks/basket) from a nearby

Table 1. Macroinvertebrate density (individuals/m^2 ± 1 SE) in fine sediments of the Upper Mississippi River during the fall of 1999, 2000, 2002, 2003, and 2004. Relative abundance (RA) is based on the 5-yr average. A 2-way ANOVA (dike, year, dike * year interaction) was done on taxa that comprised ≥0.2 % of the total. Year means followed by similar letters did not significantly differ from each other based on a Tukey's test.

Taxa	1999	2000	2002	2003	2004	5-year Average	RA	Dike Effect	Year Effect	Inter. term
Total Macroinvertebrates	5426 ± 915^{b}	8706 ± 2174^{b}	3737 ± 635^{c}	6655 ± 1285^{b}	11675 ± 1996^{a}	7240±1373		***	***	***
Nematoda	7±3	37±34	11±2	13±3	19±3	18±5	0.2	ns	ns	*
Oligochaeta	4713 ± 949^{b}	7984 ± 2113^{b}	2887 ± 603^{c}	6036 ± 1265^{b}	11116 ± 2011^{a}	6548±1413	90.4	***	***	***
Bivalvia										
Corbicula	60 ± 34^{a}	8 ± 5^{a}	0 ± 0^{b}	1 ± 1^{b}	2 ± 1^{b}	14±12	0.2	ns	***	*
Ephemeroptera										
Ephemeridae										
Hexagenia	184 ± 18^{ab}	102 ± 15^{c}	427 ± 152^{a}	251 ± 68^{b}	287 ± 52^{a}	250±54	3.4	***	***	***
Trichoptera										
Hydropsychidae	19 ± 11^{c}	80 ± 18^{a}	39 ± 20^{b}	34 ± 10^{b}	20 ± 4^{bc}	39±11	0.5	**	***	***
Diptera	379 ± 83^{a}	466 ± 122^{a}	313 ± 49^{a}	294 ± 51^{a}	209 ± 39^{b}	332±43	4.5	***	***	**
Ceratopogonidae	77 ± 36^{a}	78 ± 22^{a}	60 ± 11^{a}	54 ± 6^{a}	21 ± 8^{b}	58±10	0.8	**	***	ns
Probezzia	34 ± 10^{ab}	20 ± 9^{bc}	51 ± 11^{a}	23 ± 4^{bc}	11 ± 4^{c}	28±7	0.3	ns	***	*
Chironomidae	299 ± 55^{ab}	384 ± 103^{a}	250 ± 44^{ab}	237 ± 57^{ab}	186 ± 31^{b}	271±34	3.7	***	*	**
Ablabesmyia	24 ± 12^{d}	64 ± 10^{b}	134 ± 28^{a}	95 ± 13^{ac}	54 ± 9^{bc}	74±19	1.0	**	***	**
Chironomus	43 ± 16^{b}	144 ± 52^{a}	19 ± 10^{b}	69 ± 58^{b}	29 ± 19^{b}	61±22	0.8	***	***	**
Coelotanypus	28 ± 20^{ab}	41 ± 15^{a}	19 ± 5^{ab}	21 ± 6^{ab}	11 ± 4^{b}	24±5	0.3	***	**	ns
Cryptochironomus	60 ± 8^{a}	47 ± 15^{ac}	24 ± 6^{bc}	12 ± 4^{b}	23 ± 6^{bc}	33±9	0.4	*	***	ns
Polypedilum	50 ± 16^{a}	11 ± 4^{b}	2 ± 1^{b}	4 ± 2^{b}	4 ± 2^{b}	15±9	0.2	*	***	ns
Procladius	25 ± 22^{ac}	36 ± 31^{a}	6 ± 3^{bc}	6 ± 1^{bc}	3 ± 2^{b}	15±6	0.2	***	***	***

ns Not statistically significant
* $0.01 < p < 0.05$
** $0.001 < p < 0.01$
*** $p < 0.001$

quarry. Baskets were placed in the river along the upstream edge in strong current near the end of the dikes, secured with nylon rope tied to an iron stake, and allowed to colonize for 28–29 d. In 1999, 30 rock baskets (range 5–10 baskets/site) were deployed on 22 Oct and recovered 18–19 Nov. (Fig. 1). In 2001, 42 rock baskets (range 8–14 baskets/site) were deployed 6 Oct. and recovered 3 Nov. Stones were scrubbed in a water-filled basin, and the contents of basin were rinsed through a 0.355-mm mesh sieve and preserved with 5 % buffered formalin.

Because each rock basket sample contained thousands of individual macroinvertebrates and many of these belonged to one taxonomic group (i. e., hydropsychid caddisflies), a two-step process was used to describe the content of each sample. First, in the laboratory each sample was poured into a white enamel pan and examined to remove the large, rare non-hydropsychid taxa (e. g., mayflies, stoneflies, midges). Then, each sample was split into several subsamples and processed by separating the aquatic macroinvertebrates from the detritus under a dissecting microscope. The data from the subsamples were converted to full samples and combined with the data from the initial survey of the full sample. In 2001, some samples were combined to reduce sample variance and processing time, which resulted in 10, 6, 6, and 5 samples/site. Counts/sampler were converted to individuals/m^2 by estimating the rocks in the sampler covered 0.0625 m^2 of the dike's surface.

Data analysis

For both the fine sediment and the rock samples, two-way ANOVA (dike, year, dike × year) were performed using ln transformed (Elliott 1977) densities of the dominant taxa or groups of taxa, followed by a Tukey's test on significant variables. When specimens were too small or damaged to identify to genus they were labeled as 'unidentified' at the family level. Non-metric Multidimensional Scaling (NMS) ordination technique was used to examine how taxa differed among dikes and years for the fine sediment data (McCune & Mefford 1999). Analysis was done using log (x + 1) transformed densities for 55 common taxa (taxa present > 1 sample × year). The following options were used in the NMS: Sorenson (Bray-Curtis) distance, 102 iterations, cut-off r^2 set at 0.29, and step length set at 0.2. Three axes were used based on results of a Monte Carlo test (50 runs, $p = 0.0196$). The plot of stress versus iteration number was used to determine solution was stable (final stress = 10.9, instability = 0.00001). To improve interpretation of ordination a second matrix with hydrological variables were included. Hydrological records from USGS gage 7022000 at Thebes, IL were summarized as: mean annual discharge, high spring flow (highest average monthly discharge 12 prior to sampling; occurred in May or June), low annual flow (lowest average monthly discharge 12 months prior to sampling; occurred from October to February), and low sum-

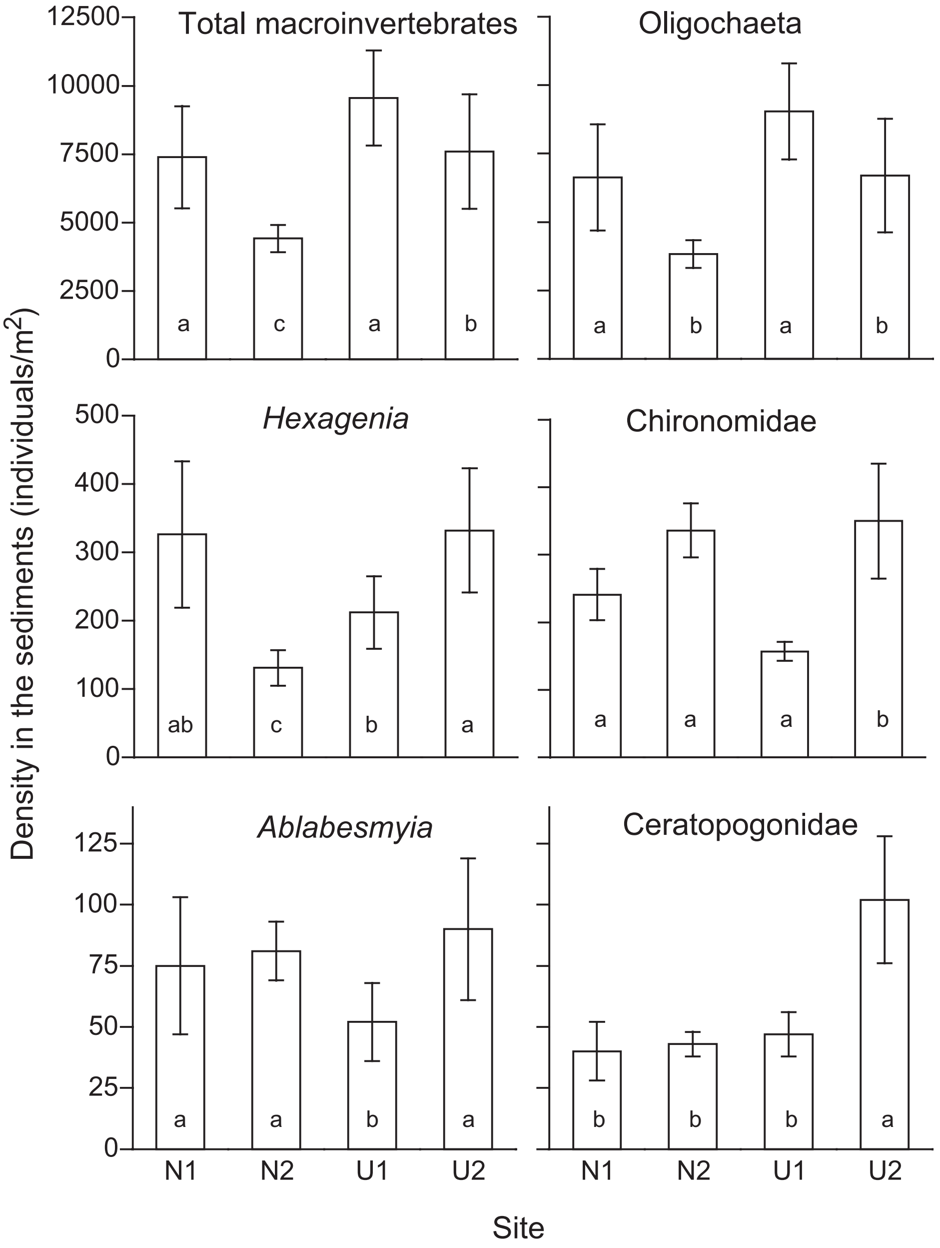

Fig. 2. Densities (mean ± 1 SE) of six common taxa in the fine sediments. Significant differences based on 2-way ANOVA (see Table 1, df = 19) and Tukey's test; columns with the same letter do not differ significantly from each other ($p > 0.05$).

mer flow (lowest average monthly discharge during July to September prior to sampling).

Results

Macroinvertebrate assemblages

Fine sediment substrates

A total of 68 taxa were found associated with the fine sediments in the UMR near Cape Girardeau, MO during the five sample years (Appendix). Most (55) of these were insects such as 15 EPT (Ephemeroptera, Plecoptera, Trichoptera) taxa and 37 Diptera taxa, which included 28 chironomid midges. Total macroinvertebrate density in the fine sediments averaged 7240 individuals/m^2, but varied spatially and temporally from ≈ 2300 individuals/m^2 at U1 in 2002 to ≈ 14,500 individuals/m^2 at N2 in 2004 (Table 1, Fig. 2). Oligochaete worms were always the dominant taxon, representing 77–95 % of the total macroinvertebrate density. Insect density was dominated by the mayfly *Hexagenia* (250 individuals/m^2) and several chironomid midge species (271 individuals/m^2). Most (> 93 %, primarily oligochaetes and *Hexagenia*) macroinvertebrates in the fine sediments were collector-gatherers (Table 2).

Densities for 13 of the 16 dominant taxa or groups of taxa differed significantly among dikes (Table 1). However, there was no consistent pattern across taxa of one dike having higher densities compared to another, and notched dikes (i.e., N1 and N2) did not dif-

Table 2. Mean density and relative abundance (RA) of each functional feeding group (FFG) in the fine sediments and on rocks in the Upper Mississippi River. Means for sediments are based on data collected in the fall of 1999, 2000, and 2002 – 2004 using a Petite Ponar dredge. Means for rocks are based on data collected in the fall of 1999 and 2001 using rock baskets. See Appendix for classification of feeding group for individual taxa.

FFG	Fine sediments		Rocks	
	Individuals/m^2	RA	Individuals/m^2	RA
Collector-filterers	57	0.9	105,360	95.5
Collector-gatherers	5754	93.9	1376	1.3
Scrapers	2	<0.1	288	0.3
Shredders	18	0.3	1648	1.5
Predators	237	3.9	176	0.2

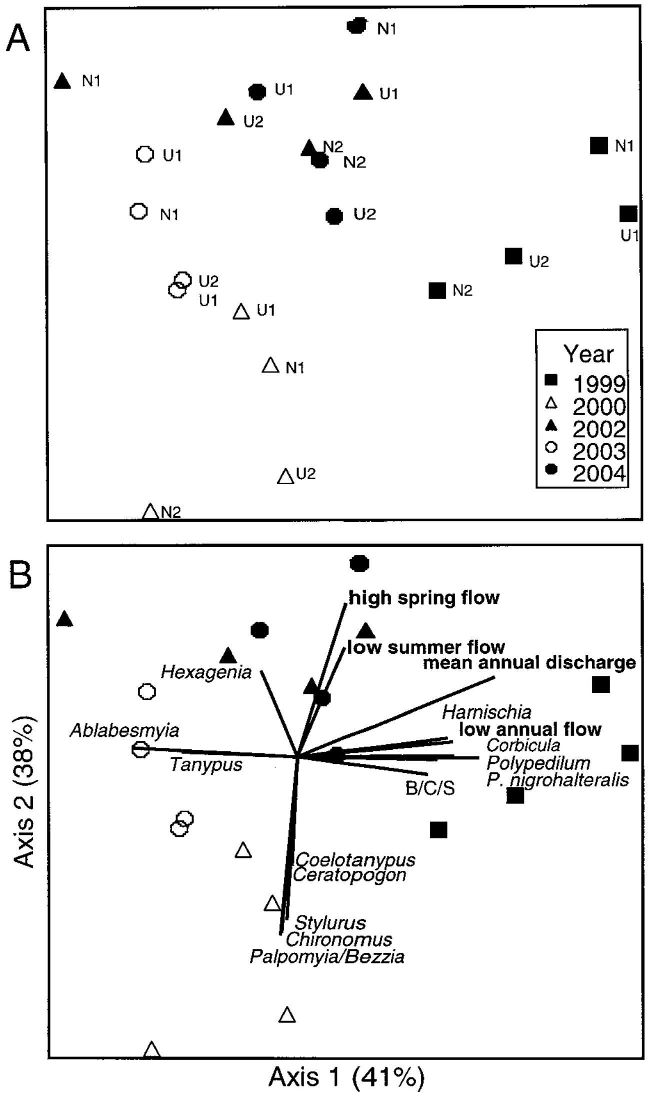

Fig. 3. Non-metric Multidimensional Scaling ordination of macroinvertebrates found in fine sediments of the Mississippi River near Cape Girardeau, MO. **A)** Illustrates spatial and temporal variability with symbols indicating un-notched (U1 & U2) and notched (N1 & N2) dikes in 1999, 2000, 2002, 2003 and 2004. **B)** Same ordination but includes vectors for individual taxa and preceding hydrologic conditions in relation to sites. B/C/S indicates the taxa Bivalvia, *Cryptochironomus*, and *Stictochironomus*, which had the shortest vectors. Hydrologic variables (USGS gage 7022000) were summarized as: mean annual discharge, high spring flow (highest average monthly discharge 12 prior to sampling; occurred in May or June), low annual flow (lowest average monthly discharge 12 months prior to sampling; occurred from Oct to Feb), and low summer flow (lowest average monthly discharge during Jul to Sep prior to sampling).

fer consistently across taxa from un-notched dikes (i. e., U1 and U2; Fig. 2). For example, dikes N1 and U1 had a higher total macroinvertebrate density than dikes N2 and U2 while dikes N1, N2, and U1 had a lower ceratopogonid density than dike U2.

Density for 15 of the 16 dominant taxa or groups of taxa (i. e., total macroinvertebrates, oligochaetes, *Hexagenia*, and all the dominant chironomid species) exhibited significant year-to-year variation, but this was not consistent across taxa (Table 1). For example, in 2002 total macroinvertebrate density was low compared to other years, but *Hexagenia* density was high. Dominance among the chironomid midges also varied year-to-year. The most common midges were *Cryptochironomus* and *Polypedilum* in 1999, *Chironomus* in 2000, *Ablabesmyia* in 2002 and 2004, and *Chironomus* and *Ablabesmyia* in 2003 (Table 1). Finally, differences among dikes varied among years such that 12 of the 16 dominant taxa or groups of taxa had significant dike by year interactions (Table 1).

Non-metric Multidimensional Scaling (NMS) ordination was used to examine spatial and temporal variability across macroinvertebrate taxa. The first three axes of the NMS accounted for 87 % of the variance in the ordination (Fig. 3). Annual differences in individual species abundances and community structure quantified by the ANOVA were evident in the NMS ordination as sites clustered more by year than by dike. Axis 1 differentiated years (especially 1999 from 2003) based on high densities of *Corbicula*, *Harnischia*, *Paralauterborniella nigrohalteralis* and *Polypedilum* in 1999 (r = 0.63–0.72) versus high densities of *Ablabesmyia* (r = –0.70) and *Tanypus* in 2003 (r = –0.58), and was positively correlated (r = 0.66) with low annual flow in the year preceding sampling (Fig. 3). Axis 2 differentiated years (especially 2000 from 2002 and 2004) based on high (2000) or low (2002 and 2004) densities of *Stylurus*, *Chironomus*, and *Palpomyia/Bezzia* (r > –0.72), and was positively correlated high spring discharge (r = 0.70) and low summer flow (r = 0.58; Fig. 3). The

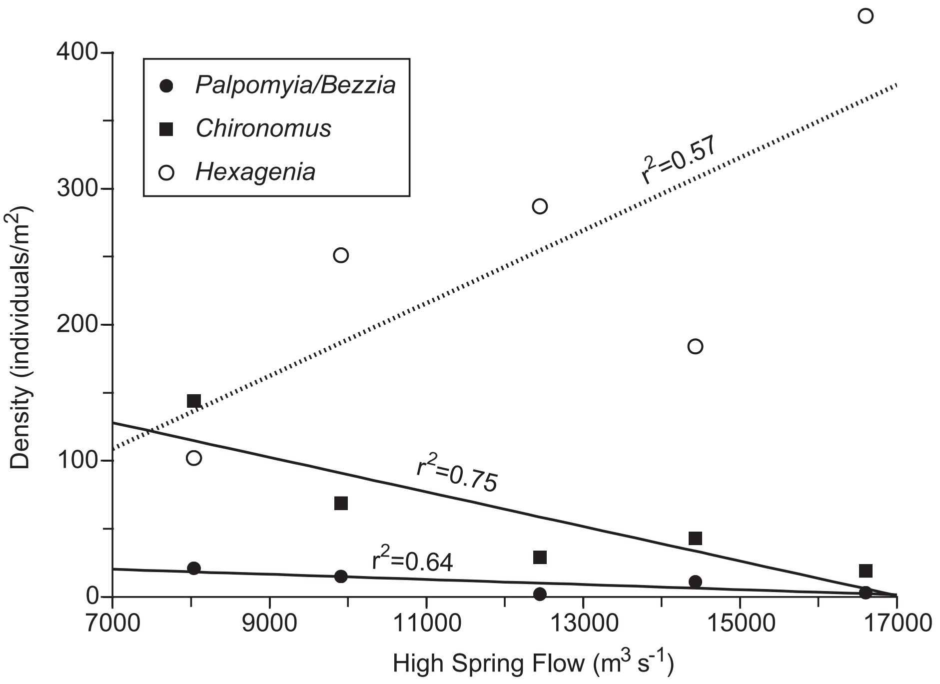

Fig. 4. Changes in density of three macroinvertebrate taxa from the NMS (see Fig. 3) that show a linear relationships to peak high flow during the preceding spring.

contrast in responses among taxa is clearest for changes in densities of *Hexagenia*, *Chironomus*, and *Palpomyia/Bezzia* relative to peak spring discharge (Fig. 4).

Rock substrates

A total of 50 macroinvertebrate taxa were collected in rock basket samplers placed on the upstream faces of the wing dikes in 1999 and 2001 (Appendix 1). Most (42) were insects such as 21 EPT taxa and 19 Diptera taxa, which included 17 chironomid midge taxa. Only 27 of the 50 taxa were also found in the fine sediments. Total macroinvertebrate density averaged ≈ 110,000 individuals/m^2 for the two years, but was nearly three times greater in 2001 than in 1999, although similar taxa were observed both years (Table 3). Differences in total density primarily reflect three times more hydropsychid caddisflies in 2001 (≈ 159,000 individuals/m^2) than in 1999 (≈ 48,000 individuals/m^2). Hydropsychid caddisflies were > 95 % of the total numbers, which resulted in the collector-gatherers being the dominant functional feeding group (Table 2). Chironomid midges were nearly 100 % of the total dipteran density and for both years the dominant midges were *Rheotanytarsus* and *Polypedilum*.

The 2-way ANOVA (dike, year, dike × year) on densities of the 18 dominant taxa or groups of taxa indicated that the density of only three taxa (Chironomidae, *Polypedilum*, and Oligochaeta) differed among dikes while the density of 13 taxa or groups differed among years (Table 3; Fig. 5). Total macroinvertebrates, Heptageniidae, Hydropsychidae, Unidentified Hydropsychidae, and *Thienemannimyia* were more abundant in 2001; Oligochaeta, *Dreissena polymorpha*, unidentified (i. e., small) Plecoptera, Perlodidae, Chironomidae, *Cricotopus/Orthocladius*, *Rheotanytarsus*, and *Thienemanniella* were more abundant in 1999. Only Oligochaeta, *Hydropsyche bidens/orris*, and *Thienemannimyia* exhibited a significant interaction term (dike*year), indicating that differences among dikes differed between years (Table 3).

Discussion

Abundance and structure of macroinvertebrate assemblages in big rivers

Descriptions and predictions of the structure and function of macroinvertebrate assemblages in rivers are rare, especially for rivers as large as the Mississippi. We expected *a priori* that macroinvertebrates at our sites would be abundant, especially species that consume fine particles (i. e., collector-gatherers in fine sediments or collector-filters on rocks). This reflects the natural increase in abundance of food resources, such as terrestrial and aquatic sources of fine and dissolved organic matter, as river size increases (Vannote et al. 1980, Webster & Meyer 1997). Our results agree with our *a priori* expectations in that macroinvertebrates in the Open River section were abundant (≈ 7,000 individuals/m^2 in fine sediments

Table 3. Macroinvertebrate density (individuals/m^2 ± 1 SE) on rocks in the Upper Mississippi River in the fall of 1999 and 2001. Relative abundance (RA) is based on the 2-yr average. A 2-way ANOVA (dike, year, dike * year interaction) was done on taxa that comprised ≥ 0.3 % of the total and on other fairly common taxa. Year means followed by similar letters did not significantly differ from each other based on a Tukey's test.

Taxa	1999	2001	Average	RA	Dike Effect	Year Effect	Interaction term
Total Macroinvertebrates	57,776±4132^{b}	162,960±21277^{a}	110,368±52598		ns	***	ns
Oligochaeta	1744±975^{a}	224±58^{b}	992±758	0.9	***	***	*
Bivalvia							
Dreissena polymorpha	256±158^{a}	0±2^{b}	128±125	0.1	ns	***	ns
Ephemeroptera							
Heptageniidae	432±121^{b}	1088±173^{a}	768±330	0.7	ns	***	ns
Stenonema	304±53	224±36	256±41	0.1	ns	ns	ns
Plecoptera	432±6^{a}	208±27^{b}	320±115	0.3	ns	ns	ns
Perlodidae	224±22^{a}	32±4^{b}	128±95	0.1	ns	***	ns
Trichoptera							
Hydropsychidae	47,664±3127^{b}	158,608±21346^{a}	103,136±55472	93.4	ns	***	ns
Hydropsyche bidens/orris	15,920±526	27,008±6532	21,472±5546	19.5	ns	ns	*
Potamyia flava	3904±844^{b}	29,024±2333^{a}	16,464±12565	14.9	ns	***	ns
Unidentified Hydropsychidae[1]	27,408±2518^{b}	102,112±13528^{a}	64,752±37354	58.7	ns	***	ns
Diptera							
Chironomidae	6848±1489^{a}	2032±466^{b}	4432±2410	4.0	***[2]	***	ns
Cricotopus/Orthocladius	240±63^{a}	0±0^{b}	112±116	0.1	ns	***	ns
Nanocladius	464±78^{a}	32±13^{b}	240±212	0.2	ns	***	ns
Polypedilum	2016±593	1184±391	1600±413	1.5	***	ns	ns
Rheotanytarsus	3696±836^{a}	640±36^{b}	2176±1524	2.0	ns	***	ns
Thienemanniella	144±35^{a}	0±1^{b}	64±68	0.1	ns	ns	ns
Thienemannimyia grp.	64±29^{b}	112±56^{a}	80±26	0.1	ns	**	*

[1] Unidentified Hydropsychidae were small individuals that were believed to be primarily *Hydropsyche bidens* in 1999, and *Hydropsyche bidens* and *Potamyia flava* in 2001.

[2] Tukey's test failed to detect differences between means, most likely due to small sample size (Zar 1984)

ns – Not statistically significant; * 0.01 < p ≤ 0.05; ** 0.001 < p ≤ 0.01; *** p ≤ 0.001

and ≈ 110,000 individuals/m^2 on rock substrates), and a majority of the species consumed fine particles (i. e., collector-gatherer oligochaetes and chironomids in the fine sediments, and collector-filter hydropsychids and chironomids on hard substrates). There was also a consistent pattern of high dominance by a few taxa at each site.

Macroinvertebrate assemblages in the Open River were equal to or higher in total density relative to macroinvertebrate assemblages described from Mississippi River Basin sites (Tables 4 and 5). In some cases, our densities may have been higher because we used a fine-mesh sieve. For example, we found that the coarse-mesh (1.18-mm) sieve used for monitoring near our sites (Sauer 2004) collected only 15–25 % of the oligochaetes, 9–33 % of the chironomids, and 42–70 % of *Hexagenia* relative to the fine-mesh (0.355-mm) sieve used in our study (unpublished data). Our densities may have also been higher because we did not sample sand and gravel habitats that are frequently moved by the current and generally support lower macroinvertebrate densities (Fremling 1973, Neuswanger et al. 1982, Seagle et al. 1982, Beckett et al. 1983, Anderson & Day 1986, Elstad 1986, Koel & Stevenson 2002, Sauer 2004).

Dominance by a few taxa appears to be a community structure characteristic that is common among studies from the Mississippi River Basin (Tables 4 and 5). For fine bottom sediments, oligochaetes were the dominant macroinvertebrate group, i. e., 42–89 % of the total numbers in nine of 14 studies (Table 4). Chironomids were dominant (24–98 % of total abundance) in the remaining five studies. For hard substrates in relatively high velocities, ≤ 5 taxa frequently represented 75–95 % of the total numbers (Table 5). For example, our study found four insects, *H. bidens/orris, P. flava*, unidentified (i. e., small) Hydropsychidae, and *Rheotanytarsus,* comprised 95 % of the total density. Hydropsychids caddisflies were often the dominant group (60–93 % of the total numbers) in the studies from the Mississippi River Basin that we examined (Table 5), and hydropsychids consistently were comprised of one or more of the following species: *H. bidens, H. orris, P. flava,* and

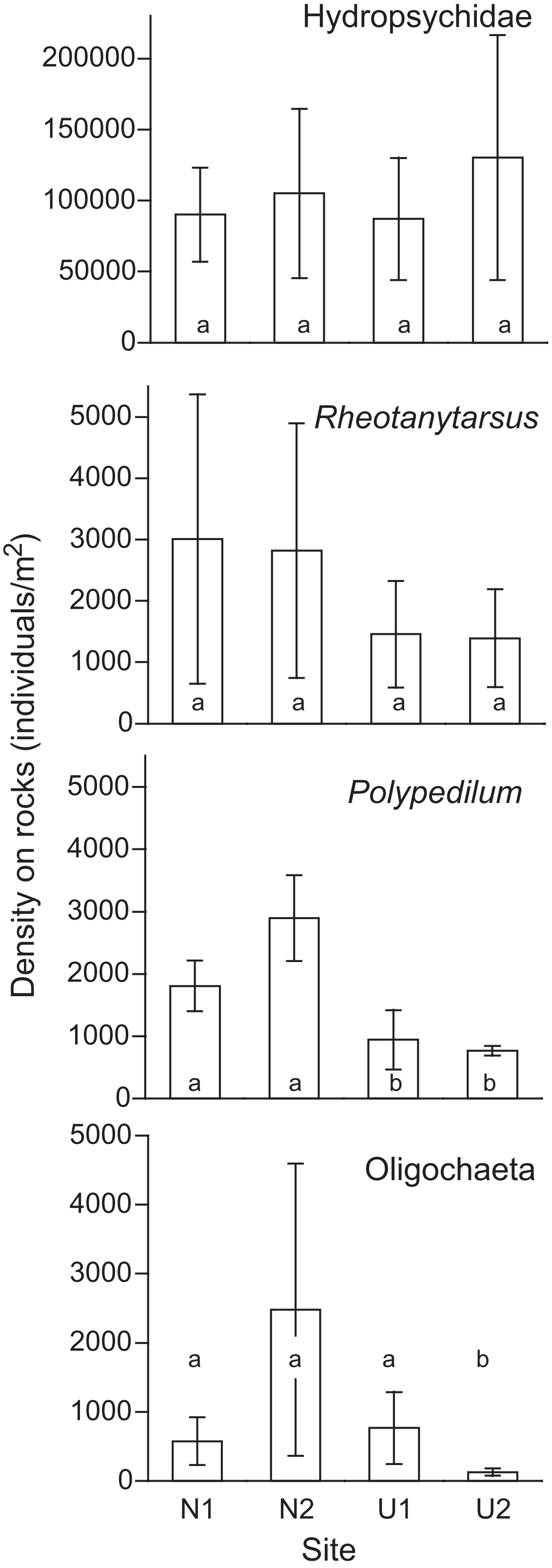

Fig. 5. Densities (mean ± 1 SE) of four common taxa on rock substrate. Significant differences based on 2-way ANOVA (see Table 3, df = 7) and Tukey's test; columns with the same letter do not differ significantly from each other ($p > 0.05$).

Cheumatopsyche (Hall 1982, Mathis et al. 1982, Seagle et al. 1982, Wright 1982, Way et al. 1995, Ecological Specialists 1999). Differences in hydropsychid composition among studies may reflect microhabitat sampled, season, sample method, or substrate sampled (Seagle et al. 1982, Neuswanger et al. 1982, Way et al. 1995). In a few cases, the common or dominant group on rock substrates was the filter-feeding caddisfly *Cyrnellus fraternus* (Illinois and Ohio Rivers; Mason et al. 1971, Seagle et al. 1982), the amphipod *Corophium lacustre* (Lower Mississippi River; Payne et al. 1989, Way et al. 1995), or oligochaeta (Ohio River; Mason et al. 1971).

It is well known that differences in conditions such as substrate, food, and current affect macroinvertebrates in small streams (see Vinson & Hawkins 1998), and similar mechanisms presumably contribute to the differences between fine sediments and rocks in big rivers (Beckett et al. 1983, Anderson & Day 1986, Beckett & Pennington 1986, Elstad 1986, Jahn & Anderson 1986, Poulton et al. 2003). However, the similarity of dominant taxa throughout the Mississippi River Basin is a striking contrast to patterns observed for small streams (Vinson & Hawkins 1998). One would not expect the same dominant species for small streams in Missouri or Louisiana versus Minnesota or Wisconsin, but that is to some degree what has been observed for the Mississippi River and its larger tributaries (Tables 4 and 5). Some of the similarity among big river faunas may result from taxonomic issues (e. g., specimens identified only to genus or unrecognized taxonomic problems). However, the pattern suggests that conditions in the Mississippi River and its larger tributaries favor the same species across a large geographic range. We believe the faunal similarities among these big river sites reflect a common, similar food/energy resource (i. e., fine organic matter transported from upstream sources; Patrick 1998, Delong 2005), huge macroinvertebrate populations per km of river, few barriers for long-distance dispersal, a long history of human impacts (i. e., nutrient inputs, dredging, pollution), and limited local habitat influence relative to small streams (i. e., water chemistry, flow, and food resources in the big river reflect upstream conditions more than local geology, topography, and vegetation). In the few instances where rock substrate faunas were different (e. g., predominantly *Cyrnellus fraternus, Corophium lacustre,* Oligochaeta), it may have resulted from local conditions such as greater sediment deposition, slower current (Seagle et al. 1982), greater sampling depths (Payne et al. 1989), or even local pollution sources.

Table 4. Summary of studies on large rivers in the Mississippi River Basin (e. g., Mississippi, Ohio, Illinois and Missouri Rivers) that examined macroinvertebrates in sediments. Total macroinvertebrate density (individuals/m^2) and relative abundance provided for three common taxa. If the relative abundance could not be determined for a study then it was left blank (–), but this does not mean that the taxon was not present. Study locations provide nearest landmark and approximate river mile(s) when possible.

River	Upper Mississippi River							
Location	Pool 8[a]	Pool 8[b]	Pool 26[c]	Pool 20[d]	Pool 13[e]	Open River[f]	Open River[g]	Open River[h]
River Mile(s)	1093–1131	679–716	210–223	350	527–556	66–71	0–169	20
Total density (no./m^2)	645	2504–7621 *	1673	345	7261	6131	602	965
% Oligochaeta	20	58	45	6	25	88	42	89[#]
% Chironomidae	24	–	18	47	69	5	–	–
% *Hexagenia*	4	4	16	18	2	4	–	–
Study details:								
Mesh-size (mm)	0.25	0.6	0.6	0.6	0.5	0.355		0.6
Substrate			sand, mud			fine sediment		sand
Sample time	summer 1990	summer 1975	summer 1978	summer 1981	Feb–Mar 1983	fall 1999–00, 2002–04	Aug–Sept 1972	summer 1996

River	Ohio		Illinois			Missouri	
Location	Cincinnati, OH[i]	Louisville, KY[j]	Cairo, IL[j]	[k]	[l]	Kansas City, MO[m]	Clay County, SD[n]
River Mile(s)		600	980	80–159	3	377, 530 & 560	
Total density (no./m^2)	1858	14	22	56	1098	4328	550
% Oligochaeta	69	51	89	–	83	61	98
% Chironomidae	29	–	–	57	14	18	–
% *Hexagenia*	–	–	–	7▼	–	–	1
Study details:							
Mesh-size (mm)	0.42	0.6	0.6	1.0	0.6	0.5	
Substrate	silt	sand, gravel, silt	sand, rubble, mud	silt-clay, sand		fine sediment	sand, sandy loam
Sample time	Aug 1970	Aug 1967	Aug 1967	fall 1997 & 1998	summer 1981	fall 1996	monthly 1971–1972

* avg. total of less & more eutrophic sites

[#] *Barbidrilus paucisetus*

▼ Identified as Ephemeroptera only

[a] Brewer et al. 1995, [b] Elstad 1986, [c] Seagle et al. 1982, [d] Neuswanger et al. 1982, [e] Hubert et al. 1984, [f] This study, [g] Johnson et al. 1974, [h] Ecological Specialists 1999, [i] Mason et al. 1975, [j] Mason et al. 1971, [k] Koel & Stevenson 2002 (based on locations with no dredge material), [l] Seagle et al. 1982, [m] Poulton et al. 2003 & unpublished data, [n] Modde & Schmulbach 1973

Annual variability in macroinvertebrate populations and assemblages

Multi-year studies of stream and river macroinvertebrates remain limited in both frequency and duration (Jackson & Füreder 2006). Many studies on the Mississippi River have reported seasonal (e. g., winter versus summer) variability in macroinvertebrates assemblages (Mathis et al. 1982, Wright 1982), but only a few have examined how these assemblages change annually. These multi-year studies have generally resulted from biomonitoring programs that focused on the mayfly *Hexagenia*, a group of species that have been used as sentinel indicator species throughout the Mississippi River Basin, and the Laurentian Great Lakes region (e. g., Fremling 1964, 1973, 1989, Carlander et al. 1967, Fremling & Johnson 1990, Krieger et al. 1996, Schloesser et al. 2000, Schloesser & Nalepa 2001, Sauer 2004, USGS 2004). In Pool 19, Carlander et al. (1967) reported that *Hexagenia* densities varied from 89 to 603 individuals/m^2 during 1959 to 1963. Long-term data from the 1950 s to 1980 s were used to describe the recovery of *Hexagenia* populations in the UMR (Fremling 1964, 1973, 1989, Fremling & Johnson 1990). Independent of known pollution sources, recent work from 1994–2000 noted annual variation in the UMR between river miles 0–80 for *Hexagenia* (range of 31–131 individuals/m^2, mean = 61 individuals/m^2) and Chironomidae (range of 8–99 individuals/m^2, mean = 46 individuals/m^2) in silt-clay substrate (Sauer 2004, USGS 2004).

Our study suggests that annual variation in the macroinvertebrates in fine sediments is influenced by such hydrologic conditions as spring discharge, which is determined by snow pack and spring rains, and low annual flow, which occurs in the autumn/winter (Oct–Mar) and is caused by low precipitation and either evapotransporation or freezing. For

Table 5. Summary of studies on large rivers in the Mississippi River Basin (e. g., Mississippi, Ohio, Illinois and Missouri Rivers) that examined macroinvertebrates on rock substrates. Macroinvertebrate density (to the nearest thousand) and relative abundance provided for common taxa. If the relative abundance could not be determined for a study then it was left blank (–), but this does not mean that the taxon was not present. Study locations provide nearest landmark and approximate river mile(s) when possible.

River	Upper Mississippi River						Lower Mississippi River
Location	Pool 13[a]	Pool 26[b]	[c]	Open River[d]	Open River[c]	[e]	[f]
River Mile(s)	547–548	212	164	66–71	30	447	480–530
Total density (no./m^2)	20,000	15,000	27,000	110,000	16,000	4000	
%Hydropsychidae	91	–	–	93	–	–	–
%Potamyia flava & *Hydropsyche* spp.*	53	≈ 80–90	90	35	78	74	86
%Chironomidae	–	≈10	–	4	–	–	–
%Rheotanytarsus	–	–	–	2	–	9	5
%Polypedilum	–	–	–	2	–	–	4
%Cyrnellus fraternus	–	–	–	–	–	–	–
%Corophium lacustre	–	–	–	–	–	15	–
Study details:							
Habitat	wing dikes	wing dikes	bendway weirs	dikes	bendway weirs	bank	dikes
Method	basket samplers	rock baskets	rock baskets	rock baskets	rocks	grooved concrete blocks	rocks
Mesh-size (mm)	0.5	0.6	0.6	0.355	0.6	0.25	
Sample time	fall 1978	summer 1981	summer 1996	fall 1999 & 2001	summer 1996	summer 1989	spring-fall 1978

River	Lower Mississippi River		Ohio			Illinois	Missouri
Location	[g]	[h]	Louisville, KY[i]	Evansville, IN[i]	Cairo, IL[i]	[b]	Kansas City, MO[j]
River Mile(s)	510–515	504–566	600	787	980	3	377, 530 & 560
Total density (no./m^2)	11,000	102,000				<700	
%Hydropsychidae	–	–	–	–	–	–	80
%Potamyia flava & *Hydropsyche* spp.*	23	68	–	63	60	–	70
%Chironomidae	–	–	27	9	17	8–11	–
%Rheotanytarsus	2	19	–	–	–	–	–
%Polypedilum	–	5	–	–	9	–	–
%Cyrnellus fraternus	–	–	17	12	–	80	–
%Corophium lacustre	31	–	–	–	–	–	–
Study details:							
Habitat	dikes	dikes			lock/dam	wing dikes	revetments & dikes
Method	rocks	rock baskets	rock baskets	rock baskets	rock baskets	rock baskets	rock baskets
Mesh-size (mm)	0.25	0.5	0.6	0.6	0.6	0.6	0.5
Sample time	Oct 1987 & 1988	Feb–June 1979	Oct–Nov 1965–1967	Oct–Nov 1965–1967	Oct–Nov 1965–1967	summer 1981	fall 1996

* Mostly *Hydropsyche bidens/orris*

[a] Hall 1982, [b] Seagle et al. 1982, [c] Ecological Specialists 1999, [d] This study, [e] Way et al. 1995, [f] Wright 1982, [g] Payne et al. 1989, [h] Mathis et al. 1982, [i] Mason et al. 1971, [j] Poulton et al. 2003 & unpublished data

example, certain taxa (e. g., *Chironomus*, *Palpomyia/Bezzia*, and *Stylurus*) respond negatively to high spring discharge (e. g., 2002, 2004) but thrive under minimal spring flooding (e. g., 2000) while other taxa (e. g., *Hexagenia*) exhibit the opposite response (Figs 3 and 4). Similarly, some taxa (e. g., *Ablabesmyia*) respond positively to conditions associated with lower discharge in autumn/winter while other taxa (e. g., *Harnischia*, *Corbicula*, *Polypedilum*, and *P. nigrohalteralis*) respond positively to less extreme minimum flows. The negative relationship between *Chironomus* and *Hexagenia* that we documented (Fig. 4) is surprisingly similar to their opposing responses to organic pollution (e. g., Jacobsen 1966, Cooper 1980), suggesting that natural dynamics (e. g., Plant et al. 2003) must be considered in biomonitoring programs involving certain taxon (e. g., *Chironomus* and *Hexagenia*).

One measure of annual variability for macroinvertebrate assemblages on rock substrate is the nearly

2.8-fold difference in density between 1999 and 2001. While these two years are not sufficient for a detailed analysis of this variation, it is possible the 2 m increase in the water level during the 2001 exposure period may have contributed to higher macroinvertebrate densities relative to 1999 by changing the position of the samplers in the water column (Delong & Payne 1985). It is also possible that the increase in hydropsychid density between 1999 and 2001 reflects a competitive release associated with a decrease in zebra mussel density (Table 3). Fremling (2005) noted a similar decline in zebra mussel abundance throughout the UMR between 1999 and 2002. Because both are filter-feeding macroinvertebrates, and zebra mussels have apparently impacted the Mississippi River (Fremling 2005), it is not unreasonable to suspect that some of the interannual differences we observed reflect direct and/or indirect responses to changes in the abundance of zebra mussels (Ricciardi et al. 1997, see caddisfly *Cyrnellus*) or other introduced non-native species, (e. g., Asian carp) that are now common in the UMR (Chick & Pegg 2001).

Dominance, temporal variability, and biological monitoring in big rivers

The use of macroinvertebrates to assess water quality is well established for wadeable streams (Barbour et al. 1999), but not for big rivers. A primary challenge for monitoring macroinvertebrates in big rivers is that the assemblage is skewed toward a few dominant taxa. In smaller streams, a single taxon comprising >60 % of the total numbers would frequently be evidence of water quality or habitat degradation as it affects measures of richness, diversity, and evenness (Barbour et al. 1999). However, this condition appears frequently in big rivers (Tables 4 and 5) and may be considered the natural or reference condition (Vannote et al. 1980), even though few big rivers, including the Mississippi, can be considered pristine given their long history of anthropogenic influence (e. g., snag removal, dam construction, agriculture, sewage effluent, introduction of nonnative species; Benke & Cushing 2005). An additional complication is that some dominant big river taxa (e. g., oligochaetes and most chironomid midges) are fairly tolerant of pollution (i. e., tolerance value ≥6; Barbour et al. 1999). Thus, assessing water quality using a pollution tolerance index would primarily reflect the presence of these abundant pollution-tolerant taxa and obscure the information provided by more pollution-sensitive taxa. Finally, annual variability such as we observed for the fine sediments and rocks may confound efforts to discern if assemblages are responding to natural hydrological conditions or pollution.

Based on the data from our sites, we believe that this portion of the Open River has improved significantly over the last several decades. Data from 1957–1963 indicate that water quality had degraded to the point that there were no mass emergences of *Hexagenia* on the UMR below St Louis, MO (Rkm 0–290, which encompasses our study area; Fremling 1964, 1973). Current conditions are significantly better than in the 1960's. *Hexagenia* are present annually at relatively high densities (250 individuals/m^2 in the fine sediments, Table 1) that are similar to other locations on the Mississippi River (Neuswanger et al. 1982, Beckett et al. 1983, Elstad 1986, Sauer 2004). In addition, the macroinvertebrate assemblages that we found in the UMR do not appear to exhibit pollution stress (e. g., low total richness) similar to that observed at selected sites on other big rivers such as the Ohio (Mason et al. 1971), Illinois (Seagle et al. 1982; see Delong 2005), or Missouri (Poulton et al. 2003).

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Appendix 1. Macroinvertebrates collected in fine sediments and on rocks in the Mississippi River at Cape Girardeau, MO during 1999–2004. For the sediments macroinvertebrates were indicated as rare* ($<15\,m^{-2}$), frequent** ($15–249\,m^{-2}$), and common*** (250 to $>6500\,m^{-2}$). For the rock habitat macroinvertebrates were indicated as rare* ($<55\ m^{-2}$), frequent** ($55–1600\,m^{-2}$), and common*** (1601 to $>65{,}000\,m^{-2}$). Densities from sediments and rock habitat are based on the average of 5 yrs and 2 yrs of data, respectively. Functional feeding group (FFG) is as follows: CF = collector-filterer, CG = collector-gatherer, SC = scraper, SH = shredder, and P = predator (Merritt & Cummins 1996, Pennak 1989).

Taxa	**FFG**	**Sediments**	**Rocks**
NON-INSECTS			
Planariidae		*	**
Nematoda		**	*
Oligochaeta	CG	***	**
Hirudinea		*	
Crustacea			
Isopoda	CG	*	*
Asellidae	CG	*	
Amphipoda	CG	*	*
Decapoda		*	*
Acari			*
Gastropoda		*	*
Pelecypoda			
Bivalvia			
Corbicula		**	
Dreissena polymorpha		*	**
EPHEMEROPTERA			
Caenidae			
Brachycercus	CG	*	
Caenis	CG	*	*
Caenis latipennis	CG	*	
Baetidae			*
Ephemerellidae			
Ephemerella	CG	*	
Eurylophella	CG	*	
Ephemeridae			
Hexagenia	CG	***	
Heptageniidae			**
Heptagenia flavescens	SC		*
Heptagenia grp.	SC		*
Leucrocuta	SC	*	
Stenonema	SC	*	**
Stenonema integrum	SC		**
Stenonema terminatum	SC		*
Isonychiidae			
Isonychia	CF		*
Neoephemeridae			
Neoephemera	CG		*
Potamanthidae			
Anthopotamus	CF	*	
ODONATA			
Anisoptera		*	
Gomphidae			
Dromogomphus	P	*	
Gomphus	P	*	
Stylurus	P	*	
Corduliidae			
Macromia georgiana/illinoense	P	*	
PLECOPTERA			
Taeniopterygidae			
Taeniopteryx	SH		*
Perlidae	P		
Acroneuria abnormis	P		*
Acroneuria mela	P		*
Attaneuria ruralis			*
Neoperla	P		*
Perlesta	P		*
Perlodidae			**
Hydroperla	P	*	*
Hydroperla fugitans			**
TRICHOPTERA			
Hydropsychidae			
Cheumatopsyche	CF	**	
Hydropsyche bidens/orris	CF	*	***
Hydropsyche nr. *simulans*	CF		*
Hydropsyche venularis	CF		**
Potamyia flava	CF	**	***
Hydroptilidae		*	
Hydroptila			*
Leptoceridae		*	*
Polycentropodidae			
Neureclipsis	CF	*	*
COLEOPTERA			
Elmidae			
Stenelmis	SC	*	*
Staphylinidae	P	*	
DIPTERA			
Ceratopogonidae		**	
Ceratopogon		*	
Culicoides	P	*	
Monohelea		*	
Palpomyia/Bezzia complex	P	*	
Probezzia	P	**	
Chaoboridae			
Chaoborus	P	*	
Chironomidae			
Tanypodinae			
Ablabesmyia	P	**	
Ablabesmyia annulata	P	**	
Coelotanypus	P	**	
Procladius	P	**	
Tanypus	P	*	
Telopelopia	P		*
Thienemannimyia	P		*
Thienemannimyia grp.	P	*	**
Orthocladinae			
Corynoneura	CG		*
Cricotopus	SH		*
Cricotopus/Orthocladius		*	**
Epoicocladius	CG	*	
Hydrobaenus	SC		*
Lopescladius	CG	*	
Nanocladius	CG	*	**
Orthocladius	CG	*	
Smittia	CG	*	
Thienemanniella	CG	*	**
Chironominae			
Chironomus	CG	**	*

Appendix 1. Continued.

Taxa	FFG	Sediments	Rocks
Cladotanytarsus	CG	*	
Cryptochironomus	P	**	*
Cryptotendipes		*	
Dicrotendipes	CG	*	*
Glyptotendipes	SH		*
Harnischia	CG	*	
Microchironomus	CG	*	
Microtendipes	CF		*
Paracladopelma		*	
Paralauterborniella nigrohalteralis	CG	*	
Polypedilum	SH	**	***
Polypedilum convictum	SH	*	
Polypedilum scalaenum grp.	SH	*	
Rheotanytarsus	CF	*	***
Robackia	CG	*	
Stempellina	CG	*	
Stenochironomus	CG	*	*
Stictochironomus	CG	*	
Stictochironomus caffrarius grp.	CG	*	
Tanytarsus	CF	*	*
Empididae			
Hemerodromia	P		*
Psychodidae			
Psychoda	CG	*	
Simulidae			*
Scatophagidae	SH	*	
Tipulidae	SH	*	