Interactive effects of hydrogeomorphology on fish community structure in a large floodplain river

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Abstract.   Biocomplexity is an emergent property of ecosystems that captures the interplay of structures and processes at multiple scales. These interactions can establish a dynamic habitat template that serves as a filter to define ecological organization across landscapes. Studies of biocomplexity in floodplain rivers typically focus on hydrological variability or geomorphic heterogeneity separately, with their interactions being an output rather than the direct focus of investigations. This study examines the interaction of hydrological variability and geomorphic heterogeneity across 25 off-channel habitats (OCHs) of the Upper Mississippi River, USA. Questions posed were as follows: What are the interactive effects of hydrological variability and geomorphic heterogeneity shaping the physical habitat template of OCHs? and How does the organization of the physical habitat template influence fish community composition within OCHs? Three distinct OCH groups emerged from this study: where hydrological variability defined Group 1 (Lake group); Group 2 was organized via geomorphic heterogeneity (Backwater group); and a combination of hydrological and geomorphological variables defined Group 3 (Slackwater group). Thus, the differential interaction of hydrology and geomorphology defined the dynamic physical habitat template of OCHs in this riverine landscape. No significant difference between the association matrices of the hydrogeomorphic template and fish community composition for the 25 OCH sites was recorded. A priori grouping of fish into the three OCH groups revealed marked differences in fish community composition. A subset of hydrogeomorphic variables that defined the physical character of the OCHs acted as an environmental filter for the fish community composition of the three OCH groups. A conceptual model explaining hydrogeomorphic–ecological interactions across the OCHs of this floodplain river system is provided.

Key words: biocomplexity; community; diversity; geomorphology; hydrology; mosaic; off-channel habitats; physical template; riverine landscapes.

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INTRODUCTION

Biocomplexity is defined as the "properties emerging from the interplay of behavorial, biological, chemical, physical, and social interactions that affect, sustain, and are modified by living organisms" (Michener et al. 2001). It is apparent from this definition that biocomplexity requires an interdisciplinary approach in order to gain an understanding of the organization and interactions within ecosystems (Delong and Thoms 2016a). Floodplain rivers are an excellent landscape for investigating ecosystem biocomplexity (Tockner et al. 2010a). Hydrological variability and spatial heterogeneity in physical character are primary abiotic drivers that define the landscape of these complex ecosystems (Stanford et al. 2005, Delong and Thoms 2016b, Thoms and Delong 2018). The flow regime of rivers operates across multiple temporal scales,

from seconds to centuries (Walker et al. 1995, Dollar et al. 2007), and can be characterized by variation in magnitude, frequency, timing, duration, and rate of change (Richter et al. 1996). Various components of the flow regime are responsible in shaping the geomorphological character of riverine landscapes (Schumm 1988), especially its physical heterogeneity (Scown et al. 2015). The geomorphological character of a riverine landscape is hierarchical, operating across multiple spatial and temporal scales (Thoms and Parsons 2002, Thorp et al. 2008). The interactive effects of hydrological variability and geomorphic heterogeneity—hydrogeomorphology— establish the dynamic habitat template of river ecosystems (Southwood 1988, Stanford et al. 2005, Tockner et al. 2010a).

Interactions of hydrological variability and geomorphic heterogeneity serve as scale-dependent filters that determine ecological form and function in riverine landscapes (Poff 1997). Identification of factors that define the composition of communities remains a challenge, particularly in complex ecosystems (Tockner et al. 2010b). The habitat template of floodplain-river ecosystems functions as an environmental filter that determines which species have adapted life-history traits that allow them to persist (e.g., Hoeinghaus et al. 2008, Arthington et al. 2010). A primary focus in understanding community composition in floodplain rivers has been the influence of hydrological processes, especially hydrological connectivity (e.g., Galat et al. 2004). Others have independently addressed the role of geomorphological character on community composition (Winemiller et al. 2000, Dembkowski and Miranda 2012, Scown et al. 2015). A limited number of studies have shown the influence of both hydrology and geomorphology on community composition (e.g., Hoeinghaus et al. 2008, Arthington et al. 2010). While these studies provide some insight, they do not incorporate the key component of interactions between hydrological variability and geomorphic heterogeneity within these complex ecosystems.

Floodplain rivers are characterized by the presence of multiple channels and numerous off-channel habitats (OCHs; Thoms et al. 2016a). OCHs are viewed as independent patches that vary both temporally and spatially across the riverine landscape (sensu Weins 2002), thus

contributing to the hydrogeomorphic complexity of floodplain rivers. Hydrological connectivity facilitates the flux of nutrients and organic matter, resulting in greater primary productivity (McGinness and McArthur 2011, Petit et al. 2017). Connectivity also allows passage for fish that spawn on the floodplain or within OCHs (Miyazono et al. 2010). Corridors formed by hydrological connectivity allow for dispersal of juvenile fish and invertebrates (Galat and Zweimuller 2001) as well as the movement of mobile predators that take advantage of the high abundance of prey in OCHs (Zeug et al. 2005, Robertson et al. 2008). Spatial heterogeneity is a major factor in the biodiversity of OCHs. Greater spatial heterogeneity increases the diversity of niches present, resulting in a concomitant increase in species richness (e.g., Post 2002). Collectively, hydrological variability and geomorphic heterogeneity influence the organization of food webs through increased primary production (Thoms et al. 2017, Thoms and Delong 2018), immigration/emigration of prey and predators (Robertson et al. 2008), and retentive zones for autotrophs and organic matter (Petit et al. 2017). Floodplain-river ecosystems, therefore, provide an excellent model for illustrating the interplay between the habitat template (hydrogeomorphology) and biocomplexity (Tockner et al. 2010b).

The interactive effects of hydrological variability and geomorphic heterogeneity on the ecological character of OCHs, at multiple scales, are investigated in the Upper Mississippi River, USA. Two questions are posed for this study: (1) What are the interactive effects of hydrological connectivity and geomorphic heterogeneity shaping the physical habitat template of OCHs? and (2) How does the organization of the physical habitat template influence fish community composition within OCHs? From these questions, we hypothesize that interactions between hydrological and geomorphological factors will define the physical habitat template of individual OCHs and that the template established for each OCH will determine fish community composition.

MATERIALS AND METHODS

Study area

The area of the Upper Mississippi River (UMR) studied (Fig. 1) extended 97-river km
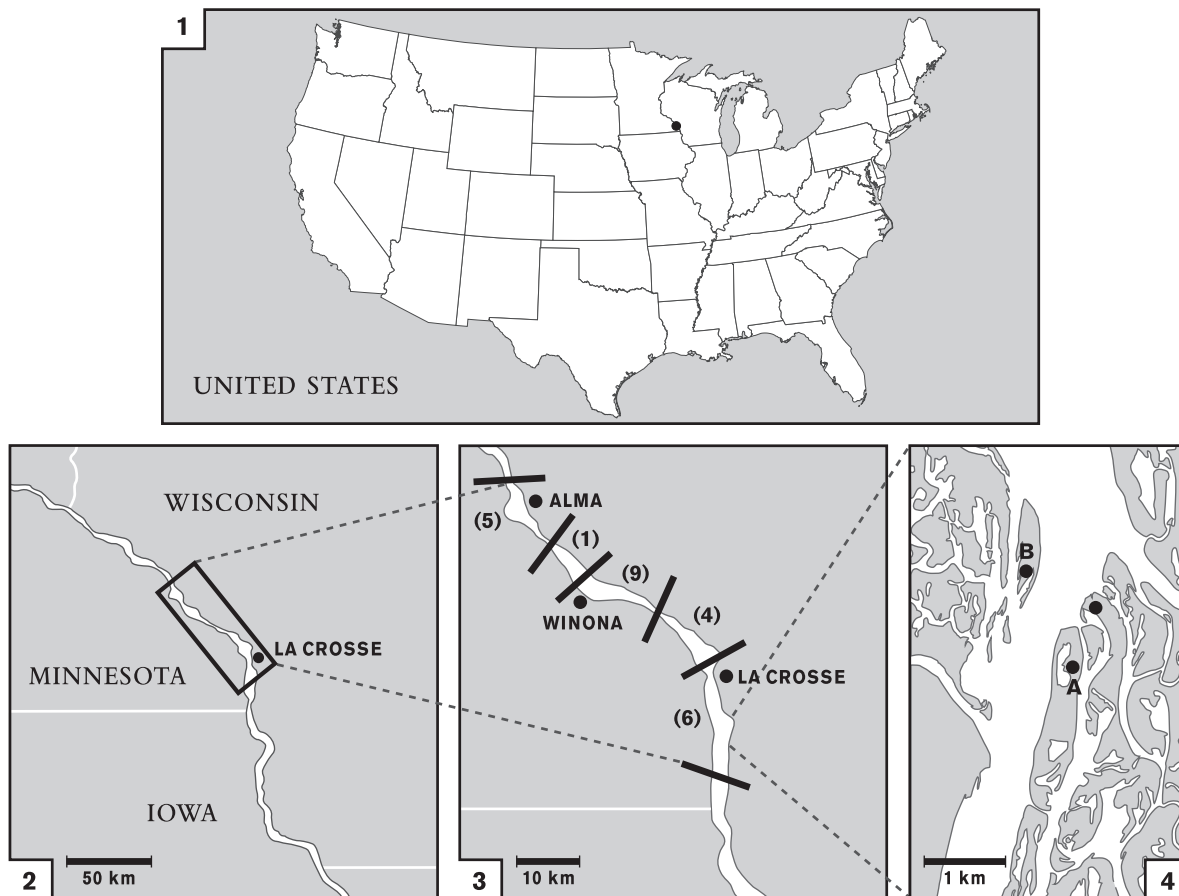
Fig. 1. (1) Map of the United States and location (dot) of the study area. (2) Map of the upper Midwest of the United States showing full study area of the Upper Mississippi River (black box). Scale bar = 50 km. (3) Full length of the 97-river km study (scale bar = 10 km). Black bars across the river denote location of low-head lock and dams, and numbers in parentheses are the number of sample sites in each navigation reach. Study area begins downstream of Alma, Wisconsin (44.3200° N, 91.914° W), and ends downstream of La Crosse, Wisconsin (43.6941° N, 91.2798° W). (4) An example of the physical complexity of the riverine landscape of this region of the Upper Mississippi River (scale bar = 1 km). The two habitats studied, floodplain lake (A) and connected backwaters (B), are shown as well as an additional site (•) used in this portion of Pool 8. Map created by Betty Kline, Kline Design, Winona, Minnesota, USA.

from Alma, Wisconsin (44.3200° N, 91.914° W), to Brownsville, Minnesota, USA (43.6941° N, 91.2798° W). This portion of the UMR lies within an incised valley up to 8.5 km wide, and nested within this is an anabranching riverine landscape with an extensive floodplain (mean width = 4.1 km). The floodplain is a complex mosaic of forest, prairie, wetlands, and various water bodies as well as natural levees and channels that are periodically wetted during higher flows. Included among these are floodplain water bodies or OCHs that are interspersed throughout the floodplain and on islands within the riverscape. Frequency of hydrological connectivity varies widely among these OCHs and other aquatic habitats. Backwater habitats that remain connected to channels are also abundant. With levees limited to only a few urban areas, over 95% of the floodplain is subjected to regular periods of inundation (Delong 2005). Average annual discharge of the UMR at Winona, Minnesota, USA, is 851 m^3/s (USGS gage 053785000;

1929–2015). Historically, the annual pattern of discharge of the UMR was characterized by a spring flood pulse beginning from snowmelt and rain in late March and continuing through late May. Discharge is generally lowest in winter and late summer. There are, however, within-bank-full flow pulses periodically throughout the summer as well as larger flood pulses that reconnect floodplain OCHs. Thus, the number of flood-plain OCHs that become hydrologically connected depends on the magnitude of a flood. A greater frequency of prolonged periods of both well-below average and above average flood pulses has been evident in recent years, including during the winter. The hydrology of the UMR is influenced by a series of 26 low-head dams (structures with a head of <5 m) for navigation. These structures maintain a minimum 2.7 m deep navigation channel during periods of low flow, but do not regulate the flow regime of the UMR. During high-flow events, the control gates of the dams are removed, creating a run of the river condition (Delong and Thorp 2006), and, as a result, do not impact river–floodplain interactions. The river maintains natural patterns of discharge and current velocities along the sections of river between the low-head dams, the exception being that upstream reach close to the next dam (Sparks 1995, Delong 2005).

Geomorphological and hydrological variables

The study included hydrogeomorphic data for 25 OCHs from across the study area. These sites are part of a larger, separate study on the hydrogeomorphic character of the UMR riverine landscape. The 25 OCH sites were selected based on their longitudinal location within the study area, distance below dams, and frequency of hydrological connectivity (3–100% connected over a 3-yr period) prior to collection of fish. Field research occurred from late June through mid-August, a period when summer conditions, including water temperature, are relatively stable. Twenty-four hydrogeomorphic variables that have been successfully used to describe the physical habitat template of river ecosystems (cf. Thoms and Parsons 2003, Thoms et al. 2005, 2017, Arthington et al. 2010) were determined for each OCH. Initially, the pathway of hydrological connection was determined by examination of elevation gradients via Google Earth Pro. The

location of connectivity pathways was field-verified and the coordinates of the point of hydrological connection to each OCH recorded. This ascertained the water-surface elevation at which hydrological connection would occur. The commence-to-fill (CTF) elevation was obtained from regional digital elevation data. Long-term ($n = 50$ yr) daily mean stage data were obtained from all gages in the study area (U.S. Army Corps of Engineers 2016). Hydrological data from the gaging station closest to each OCH were corrected for water-surface slope relative to each gage and were then used to calculate metrics of hydrological connectivity at three different hydrological scales: flow regime, flow history, and flood pulse (sensu Thoms and Parsons 2003). Flow regime represents the long-term statistical generalization of flow behavior and incorporates macroscale influences that occur over hundreds of years. Flow history represents the sequence of floods or droughts and incorporates mesoscale influences between 1 and 100 yr. Flood pulse represents a flood event. SPELL analysis was undertaken to create a suite of 11 hydrological variables reflecting flow regime, history, and pulse scales for each OCH (Table 1). SPELL used the CTF elevation of an OCH as the threshold for hydrological connection. SPELL output calculates the number of days an OCH is connected during a hydrological event, the rate of water withdrawal during recession of the event, and the number of days from disconnection to reconnection by a new event as well as the dates on which connection and disconnection occur (Thoms and Parsons 2003). Thirteen geomorphological variables were determined at three levels of organization or scale: the landscape, planform, and within-OCH levels of organization (Table 1). The geomorphological variables were quantified using remotely sensed data and field-based measurements. Both the hydrological and geomorphic variables quantified for this study were combined into a hydrogeomorphic data set for statistical analyses.

Fish collection

Fish were collected using fyke and mini-fyke nets and an electrofishing boat. Fyke and mini-fyke nets (mesh diameter = 15 mm) were set up in each OCH that could not be accessed by boat. Fyke and mini-fyke nets were randomly placed within the inaccessible OCHs, where they

Table 1. The hydrogeomorphic variables used in the study of 25 off-channel habitats in the Upper Mississippi River.

Variables	Level of organization or scale	Lake group	Slackwater group	Backwater group
Total number of days connected (N = 50 yr); TNDC	Regime	1008–4321	12,922–18,261	18,262–18,262
		2640.60	17,530.40	18,262.00
Maximum duration of a disconnection event (N = 50 yr); MxDC	Regime	518–1244	1–602	0–0
		891.4	82.1	0
Minimum duration of a disconnection event (N = 50 yr); MnDC	Regime	2 Jan	0–1	0–0
		1.1	0.9	0
Short-term connection (percent of days over 3-yr period); STC	History	7.4–80.3	80.9–100	100–100
		23.3	98	100
Month of greatest connection; MC	History	March–September	January–December	†
		April	August	†
Month of greatest disconnection; MDC	History	April–September	January–December	†
		May	September	†
Mean number of days for a connection event (MDIC)	Pulse	22 May	14–9130	18,262–18,262
		16.9	2745.00	18,262.00
Mean number of days for a disconnection event (MDDC)	Pulse	38.4–221.2	6-Jan	0–0
		116.7	3.7	0
Maximum number of days for a connection event (MxDIC)	Pulse	60–170	399–15,767	18,262–18,262
		122	6722.2	18,262
Minimum number of days for a connection event (MnDIC)	Pulse	1 Jan	1–7997	18,262–18,262
		1	1534.5	18262
Mean number of days for a drawdown to disconnection in an event (MDD)	Pulse	14 Apr	8.6–7744	0–5273
		10.6	2347.9	4476
Geomorphology variables				
Distance from closest upstream dam (km)	Landscape	0.7–21.2	2.4–12.3	4.2–18.6
		9.1	7.8	12.3
Perimeter (m)	Planform	298–2242	292–4000	367–6300
		912.2	1961.40	4652.00
Surface area (m^2)	Planform	4300–100,262	4000–353,500	6300–2,637,200
		25,192.00	62,468.10	493,850.00
Area: Perimeter ratio	Planform	9.3–44.8	9.7–61.0	15.7–135.1
		23.2	23.2	52.1
Circularity ratio	Planform	0.177–0.609	0.044–0.590	0.087–0.814
		0.351	0.302	0.369
Elongation	Planform	0.340–0.858	0.241–0.921	0.053–0.885
		0.584	0.716	0.582
Shoreline development index (SDI)	Planform	1.28–2.38	1.30–4.76	1.11–3.39
		1.76	2.21	2.12
Mean depth (m)	Within site	0.4–1.5	0.1–1.2	0.4–1.3
		0.7	0.8	1
Depth variance (Cv)	Within site	29.4–184.8	34.1–120.0	60.4–115.0
		81.5	87.2	86.9

(Table 1. Continued.)

Variables	Level of organization or scale	Lake group	Slackwater group	Backwater group
Maximum width (m)	Within site	46.7–164.4	33.8–375.9	44.3–508.6
		105.9	125	244.7
Maximum length (m)	Within site	125.4–1103.7	123.4–1399.5	91.8–2944.7
		326.1	490.3	1050.40
Commence-to-fill elevation (m)	Within site	192.99–202.13	192.06–200.94	190.58–200.57
		196.95	195.66	193.59

Notes: Levels of organization reflect the spatial (geomorphology) and temporal (hydrological) scales of the variables used. Range (upper row) and mean of variable measurements for the three habitat groups are provided. These variables were selected based on the previous studies of Thoms and Parsons (2003), and Arthington et al. (2010).

† In rows for months with greatest frequency of connection and disconnection because OCHs in the Backwater group remained fully connected over the 50-yr hydrological record used to generate the hydrology variables.

remained for 20 h. Fish were removed from nets then identified, measured for total and standard length, and weighed before returning them to the water. The exception was fish too small to identify in the field, which were euthanized and preserved with 70% ethanol for later identification. Electrofishing was done by boat in accessible OCHs using a 600-v pulsed direct current. Electrofishing was done along 150-m transects with multiple transects (n = 3–8 transects) within each OCH. Each transect within an OCH was limited to 5- to 8-min electrofishing time to maximize coverage of each OCH and to minimize fish mortality. The same processing and handling of fish used for fyke and mini-fyke nets were applied. Sampling bias is inherent to all sampling gear (e.g., Hubert and Fabrizio 2007), including electrofishing and nets, where bias toward the size of fish collected is a primary concern. Examination of the species found (cf., Table 2), range of the size of fish collected (cf., Fig. 3C), and the range of diversity measures (Appendix S1: Fig. S1) reflect the expected community composition of OCHs in the UMR. OCHs with a low frequency of hydrological connectivity are generally characterized by smaller-sized fish, most of which are juveniles, because these frequently disconnected OCHs function as nursery habitats (cf., Zeug et al. 2005). In addition, larger species, including piscivorous fishes, are commonly found in these habitats. OCHs that are permanently or rarely disconnected from the river are used by large rheophilic fish as well as small and large species of rheophilic and rheophobic species (e.g., Knights et al. 2008, Yildirim and Pegg 2009). Based on this reasoning, we suggest the gear used captured a valid representation of the fish community across the different OCHs of the study area. We do acknowledge that biases among gear types may occur and these are likely to be consistent across the OCHs (Reynolds 1983, Hubert and Fabrizio 2007).

The fish data set was structured for calculation of catch-per-unit-effort (CPUE; number of fish/hr for both nets and electrofishing) depending on which gear type was used for an OCH. Data were standardized for each sampling method by converting CPUE to relative abundance. Standardizing is one of the procedures for pre-treating data in the PRIMER statistical package (Clarke and Gorley 2006). Data were standardized for each OCH by taking the sum of CPUE for all species found in an OCH and dividing the CPUE of each species by the total CPUE for that OCH. This standardization resulted in a conversion of CPUE to relative abundance. Descriptive statistics were generated using all species within each OCH group. Measures of species diversity used were Shannon diversity, Simpson diversity, Simpson dominance, Simpson evenness, and Berger-Parker dominance (Brower et al. 1998, Morris et al. 2014). Fish species were also categorized into three reproductive strategies (equilibrium, opportunistic, and periodic) following Winemiller and Rose (1992). Reproductive life-history traits (e.g., age at maturity, fecundity, and egg size; see Table 1 of Winemiller and Rose 1992) of species collected were obtained from journal literature and Internet sources where reliable information was available. Species for which

Table 2. List of fish species collected and the off-channel habitat groups in which they were found in the Upper Mississippi River.

Species	Common name	Feeding guild	Reproductive trait	Lake	Slackwater	Backwater
Ambloplites rupestris	Rock bass	Invertivore/Piscivore	Equilibrium	X	X	X
Ameiurus melas	Black bullhead	Benthic Invertivore	Equilibrium	X	X	
Amia calva	Bowfin	Piscivore	Equilibrium	X	X	X
Aplodinotus grunniens	Freshwater drum	Benthic Invertivore	Periodic		X	X
Cyprinella spiloptera	Spotfin shiner	Pelagic Invertivore	Opportunistic		X	
Cyprinus carpio	Common carp	Benthic Omnivore	Periodic	X	X	X
Dorosoma cepedianum	Gizzard shad	Planktivore	Periodic	X	X	X
Esox lucius	Northern pike	Piscivore	Periodic	X	X	X
Ictalurus punctatus	Channel catfish	Benthic Invertivore	Equilibrium		X	
Ictiobus bubalus	Smallmouth buffalo	Benthic Omnivore	Periodic		X	
Ictiobus cyprinellus	Bigmouth buffalo	Planktivore	Periodic		X	
Lepisosteus osseus	Longnose gar	Piscivore	Periodic	X	X	X
Lepisosteus platostomus	Shortnose gar	Piscivore	Periodic	X	X	X
Lepomis cyanellus	Green sunfish	General Invertivore	Equilibrium	X	X	
Lepomis gibbosus	Pumpkinseed	General Invertivore	Equilibrium	X	X	X
Lepomis macrochirus	Bluegill	General Invertivore	Equilibrium	X	X	X
Micropterus dolomieu	Smallmouth bass	Invertivore/Piscivore	Equilibrium		X	
Micropterus salmoides	Largemouth bass	Piscivore/Invertivore	Equilibrium	X	X	X
Minytrema melanops	Spotted sucker	Benthic Omnivore	Periodic	X	X	X
Morone chrysops	White bass	Piscivore/Invertivore	Periodic			X
Moxostoma anisurum	Silver redhorse	Benthic Invertivore	Periodic	X	X	X
Moxostoma carinatum	River redhorse	Benthic Invertivore	Periodic	X	X	X
Moxostoma erythrurum	Golden redhorse	Benthic Invertivore	Periodic	X		
Moxostoma macrolepidotum	Shorthead redhorse	Benthic Invertivore	Periodic		X	
Notemigonus crysoleucas	Golden shiner	Pelagic Invertivore	Periodic	X	X	X
Notropis atherinoides	Emerald shiner	Planktivore	Opportunistic	X	X	X
Notropis hudsonius	Spottail shiner	Benthic Omnivore	Opportunistic		X	X
Perca flavescens	Yellow perch	Benthic Invertivore	Equilibrium	X	X	X
Percina caprodes	Logperch	Benthic Invertivore	Opportunistic		X	
Pomoxis nigromaculatus	Black crappie	Invertivore/Piscivore	Equilibrium	X	X	X
Pylodictis olivaris	Flathead catfish	Piscivore	Equilibrium			X
Sander canadensis	Sauger	Piscivore/Invertivore	Periodic	X	X	X
Sander vitreus	Walleye	Piscivore/Invertivore	Periodic		X	X

Note: Assignment of functional feeding guild and reproductive strategy are based on characteristics described by Welcomme et al. (2006) and Winemiller and Rose (1992).

no reproductive information could be found were inferred to have the same traits as a related member of the same genus.

Data analysis

The large data set on the hydrogeomorphic character of OCHs (25 sites by 24 variables) was analyzed using a suite of multivariate statistical analyses that initially identified groups of OCHs with a similar hydrogeomorphic character using PATN and PRIMER software (Belbin 1993, Warwick and Clarke 1993), both of which include nonparametric multivariate analyses used in this study. The data set was classified using the flexible unweighted pair-group method with arithmetic average fusion strategy, as recommended by Belbin (1993) based on the 24 hydrogeomorphic variables. The Gower association measure, which is a range-standardized measure and recommended for non-biological and non-parametric data sets (Belbin 1993), was used. Groups of OCHs with similar hydrogeomorphic character were selected by viewing the dendrogram representation of the classification, and the least number of groups with the maximum similarity chosen. Similarity percentage analysis (SIMPER) was then undertaken to determine which hydrogeomorphic variables contributed most to the within-group similarity of each group of OCHs. In addition, variability in

hydrogeomorphic character within the OCH groups was determined according to the rank dissimilarity used to compute the comparative index of multivariate dispersion (IMD), as described by Warwick and Clarke (1993).

For the fish data set, a resemblance matrix using fish community composition was calculated based on the Bray-Curtis dissimilarity measure (Warwick and Clarke 1993). This was followed by a Mantel test to establish the correlation between the hydrogeomorphic and fish community data sets. Given there was no significant difference between the hydrogeomorphic and fish matrices, site data for fish community composition were assigned a priori into the same OCH groups identified for the hydrogeomorphic data. This approach was applied to better define the role of hydrogeomorphic character of OCHs in shaping fish community composition. An analysis of similarity (ANOSIM) was applied to the fish community composition matrix to ascertain whether differences existed between the a priori groups. This was followed by SIMPER to establish which species of fish accounted for similarity in community composition with each a priori group as well as degree of dissimilarity through pairwise comparisons between OCH groups. An IMD was also undertaken to define the extent of variability in community composition within each a priori group. Finally, the relationship between hydrogeomorphic variables and fish community composition, of the three OCH groups in ordination space, was investigated using principal axis correlation (Belbin 1993). Principal axis correlation (PCC) generates a correlation value (R^2) for each of the 24 hydrogeomorphic variables, with high values indicating a strong association between a variable and the position of the OCH fish community composition in ordination space. A Monte Carlo permutation test (Belbin 1993) was performed, to test the significance of the correlation values. Only significant variables with an $R^2 > 0.75$ were included as vectors on the ordination plot.

Results

Hydrogeomorphic organization of off-channel habitats

Cluster analysis of the hydrogeomorphic variables placed the 25 OCHs into three distinct groups, which explained 75% of the similarity between OCHs. The first group (the Lake group) was comprised of 10 floodplain lakes. Floodplain lakes within this group were characterized by a lower frequency and duration of hydrological connectivity, as shown by the total number of days these OCHs were hydrologically connected over the 50-yr period (mean = 2460.6 d) and a low mean duration of each connection event (mean = 16.9 d). OCHs in the Lake group were also smaller in size, with a mean perimeter of 912.2 m, area of 25,192.0 m², and a lower shoreline development index (SDI) (mean = 1.76) compared to the other OCHs studied. The second hydrogeomorphic group identified in the cluster analysis was comprised of six backwater OCHs (the Backwater group). All of these OCHs were hydrologically connected to a channel over the entire 50-yr period of stage data. OCHs in this group were relatively large, having the longest perimeter (mean = 4652.0 m), largest area (mean = 493,850.0 m²), and greatest A/P ratio (mean = 52.1) of the 25 OCHs. The third group identified was a mixed collection of OCHs comprised of two floodplain lakes and seven backwaters, which are referred to collectively as the Slackwater group—aquatic habitats within the riverine landscape that are commonly characterized by little or no flow. OCHs within the Slackwater group experienced periods of hydrological disconnection, but these were of a lower frequency compared to the Lake group. Collectively, mean duration of hydrological connection for the Slackwater group was 2745.0 d, with mean maximum duration of connection of 6722.2 d. Slackwater OCHs were generally larger in size than floodplain lakes of the Lake group but smaller than those OCHs in the Backwater group (perimeter mean = 1961.4 m; area mean = 62,468.1 m²). Shoreline development index was greatest in the Slackwater group, as was their elongation ratio. The mean area/perimeter ratio of the Slackwater group was the same as that of the Lake group.

Similarity percentage analysis revealed differences in hydrogeomorphic variables explaining within-group similarity for the Lake, Backwater, and Slackwater groups. Hydrological variables dominated the within-group similarity of the Lake group, accounting for 52.1% of similarity between sites of this group (Fig. 2). Hydrological
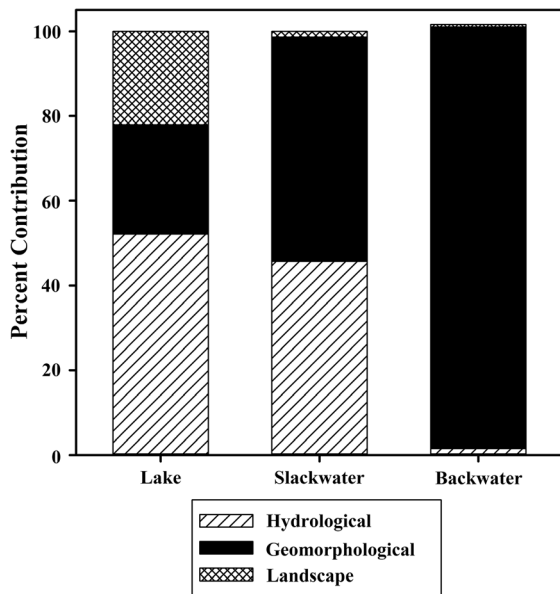
Fig. 2. Results of similarity percentage (SIMPER) analysis to depict the percent contribution of the 24 hydrogeomorphic variables to the similarity between habitats placed into three OCH groups. Figure depicts the cumulative contribution of hydrological, geomorphological, and landscape variables.

variables that strongly influenced this similarity included the longer-term flow regime variables (cf. Thoms and Parsons 2003), specifically minimum and maximum duration of disconnection (Fig. 2). Distance of an OCH site from the closest upstream dam, a landscape-scale variable, explained 22.0% of the within-group similarity of the Lake group. Other geomorphological variables accounted for 25.8% of the within-group similarity of the Lake group: mean depth, variability of depth (within-location-scale variables), and circularity ratio, a planform-scale variable. By comparison, the planform-scale geomorphological variables dominated the within-group similarity of the Backwater group (99.4%; Fig. 2). Surface area alone accounted for 65.6% of this similarity, with perimeter and A/P ratio contributing substantially as did length, a variable at the within-location scale (Fig. 2). No hydrological variables contributed substantially to the within-group similarity of the Backwater group. In contrast, a combination of hydrological and geomorphological variables, across a

range of scales, contributed to the within-group similarity of the Slackwater group (Fig. 2). Geomorphic variables accounted for 51.7% of the similarity while hydrological variables accounted for 32.4% of the within-group similarity. The main geomorphological variables were the planform-scale variables of perimeter, length/width ratio, width, length, and surface area. The main hydrological variables were mean number of days of drawdown after the peak of a connection event, maximum duration of disconnection, maximum duration of connection, mean number of days for each connection and mean depth—all flow regime- and pulse-scale variables.

Group variability, as measured by the IMD, for the hydrogeomorphic character within the Slackwater (1.11) and Backwater groups (1.02), was similar compared to a much lower variability of the Lake group (0.58). Pairwise comparisons using the multivariate dispersion measure (MvDisp) revealed clear differences in the variability of hydrogeomorphic characteristics of the Lake group to both the Slackwater (IMD = 0.65) and Backwater groups (IMD = 0.50). In contrast, differences in hydrogeomorphic character between the Backwater and Slackwater groups were not apparent (IMD = 0.10).

Fish community composition

Results of the Mantel test revealed no difference between the two matrices ($\alpha = 0.05$, $r = 0.26$). This indicates fish community composition in these 25 OCHs is shaped by the hydrogeomorphic character of the OCHs. Fish community composition (33 total species collected; Table 2) of the three a priori groups was different. A pairwise ANOSIM determined the greatest difference in fish community composition was between the Backwater and Slackwater groups ($R = 0.39$), followed by the Lake and Slackwater groups ($R = 0.32$), and then Backwater and Lake groups ($R = 0.30$). The five measures of diversity exhibited similar patterns for the three OCH groups (Appendix S1: Fig. S1). Of note is the overlap of ranges within and between the OCH groups. Given the similar patterns, Shannon diversity was included below as a descriptive statistic of community organization because it accounts for both abundance and evenness (cf. Morris et al. 2014).

The Lake group had the lowest total number of species present (*n* = 21), and all of these species were present in the other two OCH groups. The mean number of species across sites in the Lake group (mean = 8.2 ± 0.98 SE) and mean species diversity (mean = 1.46 ± 0.12) were the lowest among the three groups (Fig. 3). Most fish collected from the Lake group had a small body size (mean = 97.5 mm total length; 75th percentile = 120 mm TL). By comparison, 23 species were present in OCHs comprising the Backwater group, with *Pylodictis olivaris* and *Morone chrysops* specific to this group (Table 2). Mean number of species for in the Backwater group was 11.67 ± 2.47, and mean species diversity was 1.8 ± 0.25. The Slackwater group had the greatest number of species present (*n* = 30), with *Ictalurus punctatus, Ictiobus cyprinellus, Percina caprodes, Moxostoma macrolepidotum, Micropterus dolomieu, Ictiobus bubalus*, and *Cyprinella spiloptera* being specific to this group. Mean number of species (mean = 11.33 ± 1.52) and species diversity (mean = 1.82 ± 0.15) were comparable within the Backwater group (Fig. 3). Mean body size of fish (mean = 131.24 ± 4.07 mm TL) was intermediate to that of the other two groups (Fig. 3). Organization of species into the three reproductive strategies revealed differences among the three groups (Fig. 4). Equilibrium strategists dominated (83%) the communities in the Lake group, whereas periodic strategists represented only 14%. Both the Backwater and Slackwater groups possessed comparable abundances, with equilibrium strategists representing, respectively, 59% and 55% of the community. Both periodic and opportunistic strategists were more abundant among habitats in the Backwater and Slackwater groups.

Similarity percentage analysis revealed, from high to low percent contribution, that *Lepomis macrochirus, Pomoxis nigromaculatus, Micropterus salmoides, L. gibbosus, L. cyanellus*, and *Esox lucius* accounted for 85.2% of similarity in fish community composition of OCHs in the Lake group (Fig. 5). By comparison, similarity in community composition within the Slackwater group (61.6%) was largely accounted for by *P. nigromaculatus, M. salmoides*, and *L. macrochirus*. Four species of fish represented 91.5% of community similarity within the Backwater group, with *Dorosoma cepedianum* accounting for 67% of
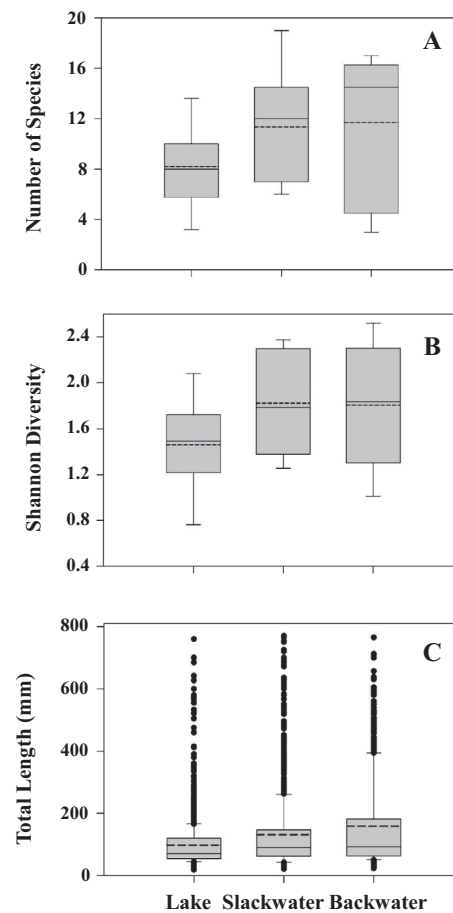

Fig. 3. Box-and-whisker plot of number of species (A), species diversity (B), and total length (C) of fish collected from sites within each of the three hydrogeomorphically defined habitat groups. Data are presented as median (solid line), mean (dashed line), 25th and 75th percentiles (bottom and top of gray box), and 10th and 90th percentiles (vertical bar). Black dots reflect the length of individual fish that fall outside the 10th and 90th percentiles.

community similarity (Fig. 5). *Perca flavescens, L. macrochirus*, and *M. salmoides* represented most of the remaining similarity of community composition within the Backwater group. A pairwise comparison, SIMPER, revealed high degrees of dissimilarity between the three OCH groups. The greatest dissimilarity was between the Lake and Backwater groups (77.45%; Table 3), followed closely by the Lake and Slackwater groups (76.2%; Table 4). Community composition of Slackwater and Backwater OCHs also
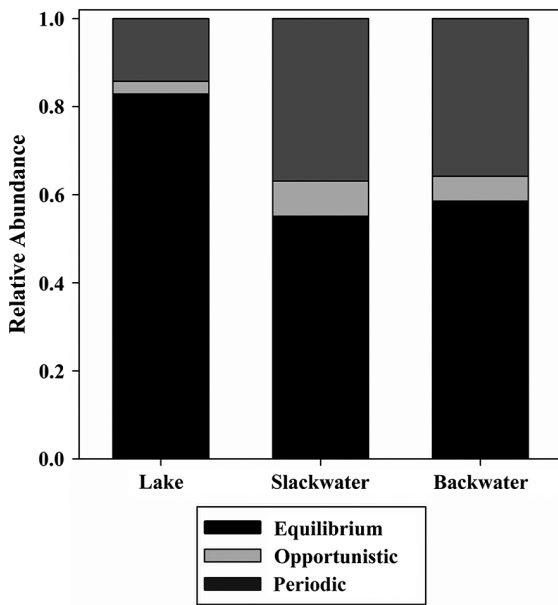
Fig. 4. Relative abundance of fish communities based on reproductive strategies defined by Winemiller and Rose (1992) for the sites within each of the three hydrogeomorphically defined habitat group.
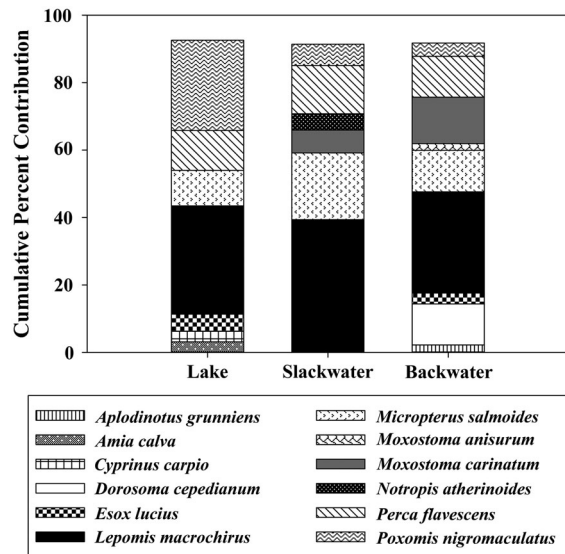

Fig. 5. Relative contribution of species contributing the most in explaining the similarity of fish community composition within each off-channel habitat group. Data were generated using similarity percentages (SIMPER) on the fish data set.

exhibited a high dissimilarity (61.2%; Table 5), thus indicating that all groups possessed marked difference in fish community composition.

Differences in the variability of fish community composition within the three groups were also recorded (Backwater group, 1.42; Slackwater group, 1.08; Lake group, 0.74). The IMD defined differences in fish community composition between the Lake group and both the Slackwater (0.40) and Backwater groups (0.37). Differences were also recorded in fish community composition of OCHs in a pairwise comparison of Backwater and Slackwater groups (0.12).

The a priori fish community groups display a degree of separation in ordination space (Fig. 6). Overall, OCHs of the Slackwater and Backwater groups had greater overlap within each other than with OCHs of the Lake group. The PCC vectors reflected a gradient of hydrological character across the ordination of the three groups. Specifically, the groups were separated along a horizontal axis of duration of disconnection and number of times of connection from the Lake group to the permanently connected Backwater group. OCHs of the Slackwater group separated

along this axis, with the two floodplain lakes grouping with the Lake group and the other OCHs associating with OCHs of the Backwater group. Thus, the three groups fall along a horizontal axis associated with flow regime- and flood pulse-scale influences. Geomorphological variables, particularly SDI and OCH perimeter (planform-scale variables), characterize a vertical gradient that separates OCHs of all three groups.

DISCUSSION

Understanding and predicting the composition of biological communities across landscapes is a challenge for ecosystem science (cf. Poff 1997, Thorp et al. 2008). The results of this study contribute to this understanding in two areas. First, the differential interaction of hydrology and geomorphology defines the physical habitat template of OCHs in the UMR. Hydrological variables defined the Lake group, whereas the OCHs of the Backwater group were characterized almost exclusively by geomorphological variables. In contrast, a dynamic interaction of both hydrological and geomorphological variables defines the Slackwater OCHs. Collectively,

Table 3. Pairwise comparisons of composition of fish communities occupying off-channel habitats (OCHs) of the Lake and Backwater groups of the Upper Mississippi River.

Species	Lake mean abundance	Backwater mean abundance	Percentage of contribution dissimilarity	Percentage of cumulative dissimilarity
Pomoxis nigromaculatus	0.26	0.05	16.66	16.66
Lepomis macrochirus	0.16	0.19	14.72	31.38
Dorosoma cepedianum	0.03	0.18	13.08	44.46
Perca flavescens	0.1	0.13	8.93	53.39
Micropterus salmoides	0.07	0.11	7.36	60.75
Moxostoma carinatum	0.01	0.07	4.53	65.27
Esox lucius	0.06	0.02	4.11	69.38
Lepomis gibbosus	0.05	0.02	3.84	73.23
Cyprinus carpio	0.04	0.02	3.62	76.85
Notropis atherinoides	0.03	0.03	3.38	80.23
Moxostoma anisurum	0	0.04	2.45	82.68
Amia calva	0.03	0.02	2.12	84.8
Aplodinotes grunniens	0	0.03	1.94	86.74
Ameiurus melas	0.03	0	1.87	88.61
Ictiobus cyprinellus	0.03	0	1.67	90.28
Minytrema melanops	0	0.02	1.38	91.66
Moxostoma macrolepidotum	0.01	0	1.05	92.71
Lepomis cyanellus	0.02	0	1.03	93.75
Notropis hudsonius	0	0.02	1.02	94.77
Cyprinella spiloptera	0	0.01	0.77	95.54

Notes: Average dissimilarity defines the extent of differences between communities. First two columns contain mean relative abundance of species each OCH group. Dissimilarity in community composition between Lake and Backwater groups = 77.45%.

this illustrates a non-uniform distribution of hydrogeomorphic drivers shaping the physical habitat template of OCHs across this riverine landscape. Second, this study also revealed that the influence of hydrogeomorphic drivers on the physical habitat template and community composition operate across multiple but different scales. Hydrological variables at the flow regime and flood pulse scales, and the landscape, planform, and within-OCH scales were determinants of the physical habitat template. By comparison, organization of fish communities is determined by hydrogeomorphic variables at the flow regime, history, flood pulse, and planform scales. Thus, a subset of the hydrogeomorphic drivers shaping the physical habitat template act as environmental filters for fish community composition in OCHs of this floodplain river landscape.

Hydrogeomorphic character of off-channel habitats

Traditional models describing the physical template of floodplain rivers are relatively simple (Thoms et al. 2016*b*). The physical and ecological character of aquatic habitats of floodplain river landscapes depicts linear longitudinal and lateral gradients (cf. Vannote et al. 1980, Junk et al. 1989). Hydrology, particularly hydrological connectivity, is viewed as the ultimate arbiter of the physical and ecological organization of riverine landscapes (Walker et al. 1995, Amoros and Bornette 2002). This perception is based on the underlying assumption that geomorphic character of a river and its floodplain is dictated by the temporal dynamics of hydrology, specifically the magnitude, frequency, duration, timing, and rate of change of hydrological connections, which systematically vary downstream and laterally across the riverine landscape (e.g., Poff 1997). However, the seminal works of Southwood (1977, 1988) emphasized that the physical landscape provides the template on which biological and evolutionary processes act. From this arose the recognition that physical habitats, such as OCHs, in the riverine landscape, are organized both spatially (geomorphic heterogeneity) and temporally (hydrological variability; Townsend 1989, Poff and Ward 1990, Resh et al. 1994,

Table 4. Pairwise comparisons of composition of fish communities occupying off-channel habitats (OCHs) of the Lake and Slackwater groups of the Upper Mississippi River.

Species	Lake mean abundance	Slackwater mean abundance	Percentage of contribution dissimilarity	Percentage of cumulative dissimilarity
Pomoxis nigromaculatus	0.26	0.1	18.2	18.2
Lepomis macrochirus	0.16	0.22	16.48	34.68
Micropterus salmoides	0.07	0.15	9.5	44.17
Perca flavescens	0.1	0.12	8.66	52.83
Notropis hudsonius	0	0.08	5.24	58.08
Notropis atherinoides	0.03	0.05	4.37	62.44
Esox lucius	0.06	0.02	4.15	66.59
Moxostoma carinatum	0.01	0.06	4.13	70.72
Lepomis gibbosus	0.05	0.01	3.79	74.51
Dorosoma cepedianum	0.03	0.02	2.68	77.19
Cyprinus carpio	0.04	0	2.64	79.83
Minytrema melanops	0	0.03	2.36	82.19
Cyprinella spiloptera	0	0.03	2.21	84.4
Amia calva	0.03	0.01	2.07	86.48
Notemigonus crysoleucas	0	0.03	2.06	88.54
Ameiurus melas	0.03	0	1.83	90.36
Ictiobus cyprinellus	0.03	0	1.7	92.06
Moxostoma macrolepidotum	0.01	0	1.21	93.27
Lepomis cyanellus	0.02	0	1.05	94.33
Moxostoma anisurum	0	0.02	1.05	95.37

Note: Dissimilarity in community composition between Lake and Slackwater groups = 76.26%.

Townsend and Hildrew 1994). This study of the physical character and fish community composition of OCHs in the UMR suggests a more complex mosaic of physical habitat patches influenced by the differential interactions of both hydrology and geomorphology. As such, OCHs are an important part of the hierarchical organization of the riverine landscape, with their internal processes defined across multiple scales (Dollar et al. 2007, Thorp et al. 2008).

Hydrogeomorphic organization of fish communities

The composition of fish communities within the three OCH groups of the UMR is organized via a unique interaction of hydrological and geomorphological variables. These differences are evident in the species diversity, species richness, size distribution, and life-history strategies of the communities inhabiting the three groups of OCHs. This is further supported by the high level of dissimilarity (>60%) in community composition identified by pairwise comparisons of the OCH groups. The regional species pool of this portion of the UMR includes 119 species (Gutreuter et al. 1997), all of which have

preferential habitats defined by a suite of hydrogeomorphic factors evident at specific but different spatial and temporal scales.

The composition of fish communities of the Lake group is organized by hydrogeomorphic variables across the flow regime, flood pulse, and planform scales. The critical variables acting as a filter for OCHs in the Lake group consisted of measures of duration of disconnections, which reflect amount of time isolated from channels; SDI; and perimeter. Periods of disconnection lead to protracted periods of isolation that provide long-term environmental stability with only occasional disturbance from high flows (Arthington et al. 2005). Characterized as having low species diversity and richness, the fish community of floodplain lakes is dominated by rheophobic species (e.g., *Lepomis* spp., *Micropterus salmoides*, and *Pomoxis nigromaculatus*). Prolonged periods of isolation also lead to intense competition and high rates of predation by piscivorous fishes, with the outcome of these interactions contributing to low species diversity and richness (Arthington et al. 2005). Another distinguishing feature of the community is the predominance of juvenile fish inhabiting floodplain lakes.

Table 5. Pairwise comparisons of composition of fish communities occupying off-channel habitats (OCHs) of the Slackwater and Backwater groups of the Upper Mississippi River.

Species	Slackwater mean abundance	Backwater mean abundance	Percentage of contribution dissimilarity	Percentage of cumulative dissimilarity
Dorosoma cepedianum	0.02	0.18	15.31	15.31
Lepomis macrochirus	0.22	0.19	11.83	27.14
Perca flavescens	0.12	0.13	9.81	36.95
Micropterus salmoides	0.15	0.11	9.39	46.35
Pomoxis nigromaculatus	0.1	0.05	9.19	55.53
Notropis hudsonius	0.08	0.02	6.34	61.87
Moxostoma carinatum	0.06	0.07	5.5	67.37
Notropis atherinoides	0.05	0.03	4.06	71.43
Minytrema melanops	0.03	0.02	3.73	75.17
Moxostoma anisurum	0.02	0.04	3.25	78.41
Cyprinella spiloptera	0.03	0.01	3.14	81.56
Notemigonus crysoleucas	0.03	0.01	2.46	84.01
Aplodinotus grunniens	0.01	0.03	2.2	86.21
Esox lucius	0.02	0.02	2.07	88.28
Cyprinus carpio	0	0.02	1.97	90.25
Lepomis gibbosus	0.01	0.02	1.6	91.85
Amia calva	0.01	0.02	1.57	93.42
Sander canadensis	0.01	0.01	0.95	94.38
Percina caprodes	0.01	0	0.84	95.21

Note: Dissimilarity in community composition between Slackwater and Backwater groups = 61.20%.

Floodplain lakes serve as nurseries for many fish species, with isolation from mobile predators provided by prolonged disconnection from channels (Zeug et al. 2005). Another contributor to the preponderance of juveniles is the thick masses of aquatic vegetation present in many of these lakes, which compensates for their limited geomorphic complexity, providing essential refugia from predators (Gomes et al. 2012). Reconnection of floodplain lakes allows for dispersal of mature fish to other habitats present across the riverine landscape (Stoffels et al. 2016, Tonkin et al. 2018). The low frequency of connection characteristic of the Lake group promotes long-term stability within these habitats. The stable environment created by prolonged isolation has led to communities dominated by species employing an equilibrium reproductive strategy (Winemiller and Rose 1992). Equilibrium strategists, among which includes many Centrarchidae, tend to follow K-strategist traits, including greater investment in energy put into egg production, parental care, and smaller clutches. In addition, equilibrium strategists generally increase in abundance as frequency of hydrological connectivity decreases (Miyazono et al. 2010, Mims and Olden 2012).
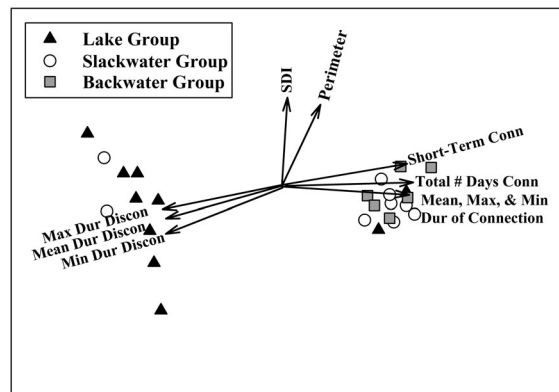

Fig. 6. Ordination of fish community composition for the three off-channel habitat groups identified in the Upper Mississippi River and the association between hydrogeomorphic variables ($R^2 > 0.75$) as determined by principal axis correlation (PCC). The ordination was significant with a stress <0.2 in two dimensions. Abbreviations are Dur Disconn, duration of disconnection; Conn, connection; SDI, Shoreline Development Index.

Fish community composition of OCHs of both the Backwater and Slackwater groups is organized by hydrogeomorphic variables representing all three hydrological scales and the planform

scale. In contrast, variables reflecting duration of connection in conjunction with geomorphic variables at the planform scale (SDI and perimeter) functioned as the filters determining community composition. The OCHs of both groups were either permanently connected (Backwater group) to a channel or disconnected occasionally for very short periods (≤6 d) over the 50-yr hydrological record used in this study. OCHs in the Backwater and Slackwater groups possess an SDI and perimeter greater than most of the OCHs of the Lake Group. This, in addition to the high degree of variability of the physical habitat variables, indicates greater geomorphic complexity within the habitat template.

Physical heterogeneity provides a broader range of mesohabitats within OCHs, thus expanding the availability of niches and the capacity to support more species (Zeug et al. 2005). Geomorphic factors, including large surface area, a long perimeter, greater depth, and high variability in depth, are key characteristics of geomorphological complexity (Thoms et al. 2005). Both habitats in the Backwater and

Slackwater groups of this study fit these parameters. The availability of a greater variety of habitats opens opportunities as refugia for juvenile fish (Zeug et al. 2005, Zeug and Winemiller 2008) and for riverine species avoiding high flows in channels (Pease et al. 2006, Price et al. 2013). In addition, physically heterogeneous environments also promote autochthonous production and the retention of other resources and prey, thus providing greater access for food resources (Sheldon and Thoms 2006).

Long durations of hydrological connection provide a corridor for rheophilic fish to move from channels into OCHs which can be used as refugia from disturbance in channels (Galat and Zweimuller 2001), access for spawning (Mims and Olden 2012) or the acquisition of food resources (Zeug et al. 2005). The OCHs of both the Slackwater and Backwater groups exhibit long duration or permanent connection to a channel. In addition, both Backwater and Slackwater OCHs are subjected to fluctuations in water levels during flow pulses, increases in stage with water remaining in a channel, or
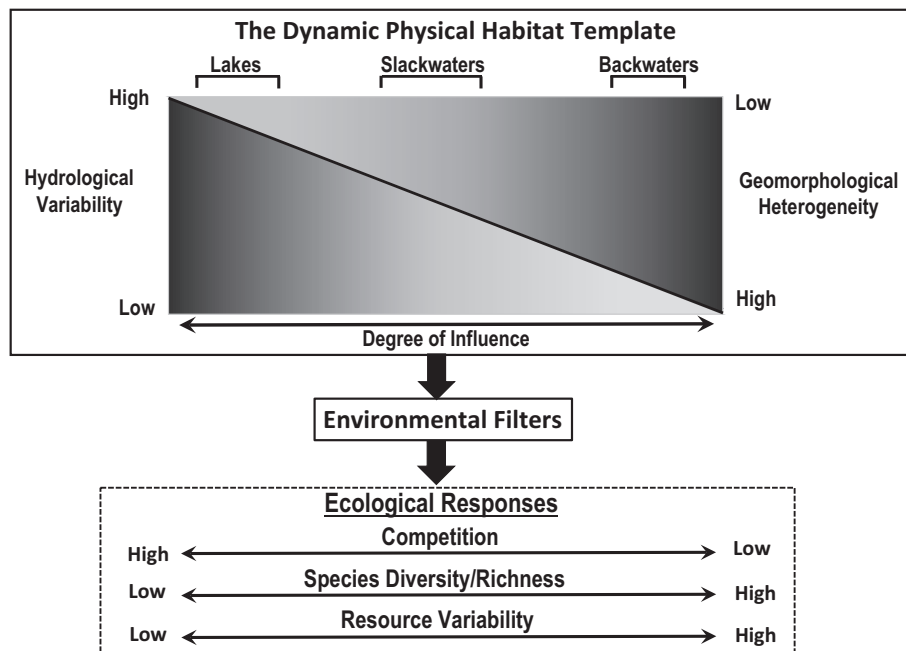

Fig. 7. A conceptual framework of the interplay of hydrogeomorphological and ecological organization within off-channel habitats (OCHs) of a floodplain river. Examples of the type of ecological processes illustrate differences in the nature of response as a function of the habitat template created by the hydrogeomorphic character of OCHs.

flood pulses. These fluctuations can be gradual, with marked changes occurring when higher-magnitude flow events introduce overland flow to an OCH. These fluctuations are advantageous for species that have adopted a periodic reproductive strategy (Zeug and Winemiller 2008). Fish following a periodic reproductive strategy delay reproduction until optimal conditions develop (Winemiller and Rose 1992). In the case of periodic strategists, floodplain inundation sets the stage for moving onto the floodplain to release their vast quantity of eggs. The relative stability of hydrological connection, between high-flow events, in backwaters and slackwaters, is sufficient to provide conditions suitable for spawning by equilibrium strategists, which still account for >50% of the fish community.

Conceptual model of a dynamic physical habitat template

Hydrogeomorphic processes operating over multiple spatial and temporal scales influence the organization of aquatic habitats within ecosystems, such as floodplain rivers. The drivers of this organization have received little attention because of the complexity of physical and ecological interactions (Tockner et al. 2010*a*). We provide a conceptual model that addresses the level of influence of geomorphology and hydrology on the ecological organization of OCHs (Fig. 7). Hydrological variability and geomorphic heterogeneity, operating across multiple spatial and temporal scales, are the primary drivers that establish the physical habitat template. Their degree of influence on the physical habitat template of OCHs is not uniform. Instead, the physical habitat templates of groups of OCHs are established via differential interactions, with these interactions ranging from predominantly driven by hydrologically variability to geomorphological. Variables that lead to the establishment of this dynamic habitat template are also responsible in shaping community composition. However, a subset of these hydrogeomorphic variables serve as environmental filters for the species that comprise a community, and they operate across multiple but different spatial and temporal scales. Ultimately, the communities established by the hydrogeomorphic filters will dictate the ecological responses of the community relative to the type of OCH in which they inhabit.

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