Effects of Main-Stem Impoundments on Hydrology and Larval Fish Communities in Major Tributaries of Two Large Midwestern Rivers

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Effects of main-stem impoundments on hydrology and larval fish communities in major tributaries of two large Midwestern rivers

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A thesis written in partial fulfillment of the requirements for the degree of

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Jordan Pesik, B.A.
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ABSTRACT

Anthropogenic modifications, like impoundments, have altered natural environmental conditions in most lotic systems and impacted fish ecology in many ways. We examined the effect of large river impoundments on fish reproductive behavior by studying the larval fish communities in tributaries of the impounded Illinois and unimpounded Wabash Rivers. We hypothesized that larval fish communities would be similar between the geographically proximal systems, but temporal structuring would depend largely on flow regimes. Biweekly larval densities were greatest among all taxa in the Wabash system, though overall communities were similar between systems. Of the six tributaries, the four smallest rivers were most similar in assemblage structure, and the two largest tributaries were more diverse. All tributaries demonstrated larval community shifts from spring to summer, but Illinois River tributaries exhibited greater temporal variability. The large rivers had distinctive hydrographs, with differences in peak amplitude, duration, timing, and rate of water level change. Regulation of flow on the Illinois River was shown to mediate river fluctuations in its tributaries. Consequently, fish that depend on high water events for spawning in tributaries may not receive a strong cue in Illinois River tributaries and instead spawn in the Illinois River. Subsequently, larval production in large, impounded lotic systems may be concentrated in the larger rivers of these systems, and more evenly distributed among rivers in free-flowing systems.
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I have had the great pleasure of working with and befriending many during my time at EIU. I have been extremely blessed to have met and been supported by so many outstanding people with a commitment to research, many of whom were integral to the success of this project.
I would like to especially recognize Bethany Hoster, Sam Gradle, Cassy Shaffer, Jess Thornton, Eric Hine, Jaelen Myers, Missy Eaton, Alicia Kellup, Brianne Horan, Megan Lomas, Chloe Derrick, Ariana Maulding, Amber Toenyes, Erin McKay, Devlon Sutton and Kaleb Wood. I will greatly miss being a part of the Fisheries and Aquatic Research Team (FART). I wish to also thank all the students and staff involved with the campus Newman Center for their support and fellowship. I have much to be thankful for and will take along many memories from my time spent at this extraordinary academic institution and community.

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BACKGROUND

Of all the species in the world, humans have been the most influential in reshaping the landscape, degrading biotic communities, and manipulating biogeochemical cycles on a worldwide basis (Vitousek, Mooney, Lubchenco, & Melillo, 1997). Large rivers are some of the most anthropogenically-altered ecosystems in the world, with impoundments affecting more than 58% of the world's large rivers (Nilsson, Reidy, Dynesius, & Revenga, 2005). Large rivers and lakes, as opposed to smaller streams, maintain a greater biotic diversity; the inherent buffering of a larger, more complex environment and high degree of spatial connectivity within these systems permit environmental stability (Jackson, Peres-Neto, & Olden, 2001). Although conditions in natural systems may fluctuate greatly and appear inherently unstable, the environmental stability created by dams and other anthropogenic modifications reduces the quality and natural buffering capacity of aquatic environments (Gorman & Karr, 1978). Therefore, it is important to understand the disruptive mechanisms underlying anthropogenic activities in lotic systems.

Dams degrade ecological functions of rivers as corridors to dispersal on spatial and temporal scales. As a physical barrier, dams most identifiably impede fish migrations and fragment the home ranges of certain species, resulting in ecological repercussions. Localized extinctions, as well as reductions in reproductive success and genetic health alter fish communities both above and below impoundments (Drinkwater & Frank, 1994; Neraas & Spruell, 2001; Winston, Taylor, & Pigg, 1991; Yamamoto, Morita, Koizumi, & Maekawa, 2004). Dams generally serve as a barricade to upstream movements, but in rare instances the pools formed upstream may facilitate dispersal in upper reaches by submerging natural barriers to fish passage (Hinrichsen, Hasselman, Ebbesmeyer, & Shields, 2013). Nevertheless, dams not only affect the movements of fish and other aquatic biota, they directly affect habitat quality and availability as well.
Dams on large rivers often coincide with other anthropogenic activities, such as channel regulation by dredging, flow diversion by wing dikes, and bank stabilization. The compounding effects of these alterations greatly reduce the environmental complexity and stability of these systems (Gorman & Karr, 1978; Jackson et al., 2001), thereby reducing community diversity and ecological stability. Nevertheless, many environmental consequences can be directly attributable to dams.

Annual hydrologic cycling is often associated with thermal cycling in many natural systems (Andresen, Hilberg, & Kunkel, 2012), but dam structure and water release methods may shift the downstream thermal regime, and subsequently favor a radically different fish community (Hinrichsen et al., 2013; Quinn & Kwak, 2003). In general, highly tolerant or nonnative species often thrive in the aquatic conditions created by dams (Bunn & Arthington, 2002; Butler & Wahl, 2010; Hinrichsen et al., 2013; Santucci, Gephard, & Pescitelli, 2005; Winston et al., 1991), thus outcompeting sensitive or native taxa and reducing biotic integrity of the system; however, this is not always the case. For example, the impoundment forming Lake Texoma has prevented movement of Red Shiner individuals between upstream tributary populations, and eventually resulted in localized extinctions of this highly abundant, highly tolerant, nonindigenous cyprinid. With the removal of Red Shiner, there was an increase in biotic integrity and community health in the system (Matthews & Marsh-Matthews, 2007).

Generally, community structuring is dictated by spatial scale of interest. Biotic interactions such as competition and predation typically dominate on small scales, whereas abiotic parameters are stronger drivers of large-scale community dynamics (Jackson et al., 2001). In large river systems mostly contained to their channel, abiotic conditions and species communities often evolve on predictable spatial gradients; however, the river continuum concept (Vannote, Minshall, Cummins, Sedell, & Cushing, 1980) becomes less applicable with greater
floodplain interaction (Johnson, Richardson, & Naimo, 1995; Mendonça, Magnusson, & Zuanon, 2005). As more rivers become altered and regulated by human activities, floodplain interactions often diminish as water levels are stabilized.

The force and variability of water flow dictates both in-stream conditions and floodplain habitats; impoundments purposefully disrupt the natural flow regime. Increased rates of sediment deposition in the pools preceding dams reduces upstream habitat quality (Ibáñez, Prat, & Canicio, 1996), and large, irregular pulses of water released below hydropower dams can directly affect growth and survival of young-of-year fish (Weyers, Jennings, & Freeman, 2003). Consequently, fish communities will shift in response to dam-generated habitat (Hastings, Meiners, Colombo, & Thomas, 2016; Santucci et al., 2005). Natural variations in the hydrologic regime often occur on seasonally predictable timetables (Ibáñez et al., 1996; Magilligan & Nislow, 2005; Zhang, Xia, Liang, & Shao, 2010). Nevertheless, water control structures may temporally redistribute daily and seasonal water flow, depending on dam structure and function. Altered hydrology may reduce the significance of individual events (Graf, 2006; Ibáñez et al., 1996; Koehn & Harrington, 2006; Magilligan & Nislow, 2005; Zhang et al., 2010) and inhibit critical habitat connectivity with riparian zones, floodplain wetlands, and tributaries (Graf, 2006; Kingsford, 2000; Neraas & Spruell, 2001). Connectivity with these habitats is regulated by the flood pulse in many temperate and tropical river systems. In low order streams and anthropogenically-modified systems, the pulse is typically short and unpredictable, limiting organismal use of habitats within the aquatic-terrestrial transition zone. During long and predictable flood pulse events, however, organismal adaptations take advantage of the induced rapid recycling of organic matter and nutrients within the submerged transition zone (Junk, Bayley, & Sparks, 1989). In systems where organisms are adapted to seasonal flood events, short and irregularly distributed cycles caused by anthropogenic flow regulation may prevent the completion of reproductive cycles (Johnson et
al., 1995). Consequently, closely linked fish behaviors and environmental characteristics decouple, negatively affecting reproductive success and population health in lotic systems.

Fish behaviors, movements, and distributions are influenced by broad-scale spatiotemporal environmental parameters (Turner, Trexler, Miller, & Toyer, 1994). Latitude is a main determinant of regional and seasonal climatic conditions, such as temperature and precipitation. Length of growing season is inversely related across a latitudinal gradient, with more restrictive temperature constraints on metabolic activity in poikilotherms at higher latitudes (Conover, 1992; Garvey & Marschall, 2003). A wide variety of taxa exhibit coincidental population and behavioral fluctuations amongst geographically separated populations (Liebhold, Koenig, & Bjørnstad, 2004). This generalized phenomenon is known as spatial synchrony. Three underlying drivers of spatial synchrony have been identified: the Moran effect and the influence of climatic conditions (Cattanéo, Hugueny, & Lamouroux, 2003; Engen & Saether, 2005; Ranta, Kaitala, Lindström, & Helle, 1997; Tedesco, Hugueny, Paugy, & Fermon, 2004), the dispersal of individuals between populations, and the trophic interactions of nomadic predators (Liebhold et al., 2004; Ripa, 2000). In aquatic systems, changing water temperature, photoperiod (Hubbs, 1985; Pankhurst & Porter, 2003; Papoulias, DeLonay, Annis, Wildhaber, & Tillitt, 2011), and pulses in discharge (Beamesderfer, Rien, & Nigro, 1995; Burdick & Hightower, 2006; Firehammer & Scarnecchia, 2006; Gehrke, Brown, Schiller, Moffatt, & Bruce, 1995) drive spawning behavior for many fish species, leading to predictable variability in community compositions throughout the year (Floyd, Hoyt, & Timbrook, 1984; Turner et al., 1994). Specific habitat characteristics can further affect and be used to predict population dynamics for individual species (Nelson, Hocking, Harding, Harding, & Reynolds, 2015). Despite this knowledge, our understanding of environmental factors affecting synchrony of fish populations in river systems is poorly developed.
Although most research has focused on adult stages, larval fish are greatly understudied despite their value as an indicator of environmental integrity and population health. Larval fish are sensitive to many of the environmental changes induced by anthropogenic activities (Humphries & Lake, 2000; Mapes, DuFour, Pritt, & Mayer, 2015). Thus, monitoring larval fish species diversity and abundance can be used to measure biotic community responses to environmental change and restoration efforts, as well as predict future stock health (Humphries & Lake, 2000; Jenkins & King, 2006; Mapes et al., 2015). Since many fish may have different life history characteristics as larvae (e.g. habitat preference, diet), the inclusion of larval fish in studies of population management and environmental health is paradigm.

During this study, we used an intensive sampling regimen to elucidate the ecological effects of large river impoundments on fishes in tributary rivers. Tributaries provide essential habitats for reproduction of many fishes in lentic and large lotic systems (Douglas & Douglas, 2000; Mansfield, 1984; Webber, Bestgen, & Haines, 2013). Although the effects of dams on hydrology (Ibáñez et al., 1996), spawning behaviors (Beamesderfer et al., 1995; Firehammer & Scarnecchia, 2006), and larval fish growth and survival (Agostinho, Gomes, & Zalewski, 2001; Weyers et al., 2003) are well documented in the main-stem reaches of these large rivers, the lateral extent of influence into their tributaries is not well understood. The purpose of this study is to determine the influence of main-stem dams and large-scale flow regime manipulation on fish reproduction in tributaries. To do so, we analyzed larval fish community composition and dissimilarity on spatial and temporal scales from tributaries of the impounded Illinois River and mostly unhindered Wabash River in the region of Illinois and Indiana.

Due to the environmental similarity and geographic proximity of the large river watersheds, we first hypothesize the overall community structuring will be similar between systems, though some within-system variability will likely exist. Conversely, we expect flow regime
alterations in tributaries of the Illinois River, and we secondarily hypothesize there will be temporal dissimilarities in community structuring between systems due to environmental-behavioral coupling in fish reproduction.
REFERENCES


INTRODUCTION

Large rivers are some of the most over-utilized and anthropogenically impacted ecosystems in the world; more than 58% of the world’s large rivers have been impounded (Nilsson, Reidy, Dynesius, & Revenga, 2005). In the United States alone, there are more than 90,000 dams, and not a single large river is left free-flowing along its entire length (Graf, 2006; United States Army Corps of Engineers, 2016).

All impoundments alter the flow of rivers. The force and variability of flow dictates the geomorphology of both in-stream conditions and floodplain habitats. Natural variations in the hydrologic regime often occur on predictable timetables (Ibáñez, Prat, & Canicio, 1996; Magilligan & Nislow, 2005; Zhang, Xia, Liang, & Shao, 2010); however, water control structures reform the temporal distribution of flow on daily and seasonal scales, often reducing the significance of individual and compounding events (Graf, 2006; Ibáñez et al., 1996; Magilligan & Nislow, 2005; Zhang et al., 2010). While dam structure, function, and position along the river corridor ultimately influence the exact hydrological and ecological effects of flow manipulation on the river system, dams generally affect four biologically-significant components of the flood-pulse: amplitude, duration, timing, and rate of change (Agostinho, Gomes, & Zalewski, 2001; Agostinho, Thomaz, Minte-Vera, & Winemiller, 2000). The flood-pulse is an important concept in lotic ecology from both nutrient cycling and habitat availability standpoints (Junk, Bayley, & Sparks, 1989; Kingsford, 2000), and many aquatic organisms have developed life-history adaptations to attributes of the flood-pulse.

Dams have been shown to affect adult fish populations and communities as a consequence to these altered habitat conditions (Butler & Wahl, 2010; Hastings, Meiners, Colombo, & Thomas, 2016; Santucci, Gephart, & Pescitelli, 2005). Subsequently, many studies have evaluated the impact of dams on reproduction in fishes (e.g. Weyers, Jennings, & Freeman,
2003). In lotic systems, many fishes correlate spawning activities with high water periods because of increased flows or floodplain access (Agostinho, Gomes, Verissimo, & Okada, 2004; Burdick & Hightower, 2006; Douglas & Douglas, 2000; Firehammer & Scarnecchia, 2006). In regulated river reaches, spawning success of individual species may be improved (Ruhr, 1957) or reduced (Beamesderfer, Rien, & Nigro, 1995; Firehammer & Scarnecchia, 2006), depending on the species and impoundment characteristics. Regulated systems favor invasive and tolerant species proportionally in the community. By contrast, unregulated systems more often support increased abundance of individuals from most taxa and greater community diversity (Gehrke, Brown, Schiller, Moffatt, & Bruce, 1995; Humphries & Lake, 2000).

Current knowledge of the effects of river regulation on fish communities and behavior is primarily limited to within the impounded river, yet few studies address fish reproduction beyond the immediate river corridor of the impounded river. Rivers, by their very nature, form fluidly-connected waterways, which biota actively interchange between. Due to this connectivity, hydrographic conditions in one river should, at the very least, affect conditions in the downstream portions of adjoining rivers. This understanding is similar to the way estuaries push salinity gradients upriver through interactions in tides, upriver conditions, and winds (Liu, Chen, Cheng, Hsu, & Kuo, 2007; Liu, Hsu, & Kuo, 2001). The mechanisms in purely lotic systems would replace tides with downriver or adjoining river conditions.

Tributaries often provide critical spawning habitat for population maintenance of many migratory species (Douglas & Douglas, 2000; Mansfield, 1984; Webber, Bestgen, & Haines, 2013) and may harbor resident populations of large-river and small-river taxa (Brown & Coon, 1994). Consequently, large river recruitment may source largely from tributaries. Furthermore, conditions in the tributaries, and not the larger river have been shown to trigger migratory movements in some species (Douglas & Douglas, 2000). However, the importance of tributaries
to the large river systems, as noted by Cowx et al. (2015), is rarely addressed in lotic studies. Therefore, this study will expand current knowledge on the implications of hydrological manipulation on fish reproduction in large tributaries of an impounded system.

The Illinois and Wabash Rivers are two large river systems located in Illinois. Both watersheds have a primarily limestone and sandstone geologic foundation (Gray, Ault, & Keller, 1987; Willman et al., 1967), with land-use dominated by agriculture and similar proportions of urban development (United States Geological Survey, 2011). Additionally, the temperate climate of the region supports an annual precipitation cycle. The majority of the yearly precipitation occurs during the warmer months (Andresen, Hilberg, & Kunkel, 2012), particularly during spring and early summer. Given the similarities in watersheds and climates, we presume many of the localized environmental conditions and in-stream habitat features are the same between these large river systems, and we hypothesize these systems support very similar adult and larval fish communities.

Though these systems have much in common, these large rivers represent a dichotomy in flow regimes. The Illinois River is a heavily modified river, featuring five impoundments along its channelized length, with additional impoundments present upriver in the Des Plaines River. By contrast, the lower 625km of the Wabash River are free from impoundments. Since hydrological conditions in the tributaries, especially the lower reaches, are likely dictated by the hydrology of the mainstem, we also hypothesize there will be different temporal patterns in larval community structuring per the Moran effect. Variability among these communities may be attributable to hydrological conditions or other environmental parameters. Through this study we hope to identify whether or not altered hydrology caused by large river dams has consequences to fish reproduction in large tributaries.
METHODS

Study Rivers

We sampled three major (6-7th order) tributaries for each of the Illinois and Wabash Rivers: the Mackinaw, Sangamon, and Spoon Rivers for the Illinois system; the Embarras, Little Wabash, and Vermilion Rivers for the Wabash system (Figure 1). The confluences of all three Illinois River tributaries are located within the LaGrange Reach, which is bounded by wicket dams in Peoria, IL, and LaGrange, IL. These wicket dams are not permanent impediments to flow or fish passage and may be fully lowered to the substrate during high water events to maximize drainage. The confluences of all three Wabash River tributaries are located within the lower 625km free-flowing reach. For simplicity, we refer to the grouping of tributaries of the same large river as a collective “system,” with “main-stem” referencing the Illinois or Wabash River.

Both main-stem rivers are considered floodplain rivers, though they have their distinctions. The Illinois River has extensive backwater lakes connected to the river, whereas the Wabash River generally lacks this feature. Additionally, the Illinois River is heavily channelized by dredging; the Wabash River is largely confined to its channel by extensive levees. The tributaries of these main-stem rivers are generally medium-gradient streams with floodplain interactions only on rare occasions. With the exception of the Mackinaw, all tributaries have at least one impoundment along their length. Most of these are small impoundments (low-head dams) that may be completely submerged during high water events, though the Little Wabash and Sangamon Rivers both have large dams. Of these dams, only the large Sangamon River dam, which forms Lake Decatur, can be manipulated for water release. The Sangamon River is the largest tributary by discharge in this study, and the Little Wabash River is second in size.
Hydrograph Data

River gauge data for 2016 was standardized as a percentage of the all-time maximum recorded gauge data adjusted for the all-time minimum recorded gauge data nearest each site. This standardization method presented data as historically-relevant to each river gauge and allowed for direct comparisons of relative rates of change between sites. The equations for standardizing discharge and height followed the same design, and is as follows:

\[
\text{Standardized discharge} = \frac{(\text{Mean daily discharge} - \text{Minimum gauge discharge})}{(\text{Maximum gauge discharge} - \text{Minimum gauge discharge})}
\]

Flood-pulse regimes were distinguishable between systems. High water events on the main-stem Illinois River were temporally very broad and lasted upwards of several weeks, whereas pulses on the main-stem Wabash were brief and often less than two weeks in duration (Figure 2). The influence of dams on the Illinois River were highlighted during inter-pulse periods where river heights leveled-off at gauges immediately above these dams (Peoria and Beardstown). Not only were the duration and rate of change of flood-pulses altered in the Illinois River, but timing of the annual pulse appeared altered as well. All gauges in the Wabash system showed significant mean water level reduction from spring into summer (Correlation: \( t \leq -13.56, -0.79 \leq r \leq -0.69, P < 0.0001 \), Table 1), indicating the annual water pulse occurred in spring. However, river gauges in the Illinois system demonstrated relatively evenly distributed water levels throughout the year (Correlation: \(-1.37 \leq t \leq 2.61, -0.09 \leq r \leq 0.18, P \geq 0.01 \), Table 1).

The most downstream river gauges in the tributaries (Wabash system: between 10.8 km and 51.5 km upriver from confluence; Illinois system: between 28.8 km and 61.3 km upriver from confluence) showed different hydrologic regimes as well (Figure 2). The Wabash River tributaries exhibited very similar dynamics to the main-stem Wabash, but Illinois River tributaries exhibited
different dynamics from either main-stem. Illinois River tributaries had very few large flood-pulses throughout the sampling timeframe compared to the Wabash River tributaries, and pulses tended to have lower amplitudes and different shapes from typical pulses in Wabash River tributaries, especially during spring and early summer. Following peaks in pulses, the point of reduced rate of drainage generally occurred at a relatively higher percentage of the maximum gauge height (around 25%) in the Illinois River tributaries than the Wabash River tributaries, which occurred much closer to base flow (around 15%). All tributary gauges in the Wabash system showed evidence for the annual spring flood-pulse (Correlation: $t = -4.38$, $r = -0.29$, $P < 0.0001$, Table 1), but Illinois River tributaries exhibited some variability. The Mackinaw (Correlation: $t = 0.41$, $r = 0.03$, $P = 0.68$, Table 1) and Spoon (Correlation: $t = -0.78$, $r = -0.05$, $P = 0.44$, Table 1) Rivers did not show evidence of the expected annual distribution, while the Sangamon River did (Correlation: $t = -5.24$, $r = -0.34$, $P < 0.0001$, Table 1).

Sampling Protocol

We sampled the Illinois and Wabash systems alternating biweekly from mid-March 2016 to the end of September 2016. Tributaries were sampled at three locations to capture larval communities from lower, middle, and upper river conditions. We sampled with three gears in an attempt to more thoroughly sample the larval fish community. Rectangular stream drift nets (Aquatic Research Instruments, 0.25m x 0.45m mouth, 1.0m tapering 500µm mesh net) were anchored and buoyed just beneath the surface near the left bank, mid-channel, and right bank. Sampling duration was dependent on flow velocity and amount of particulate debris in the water at the time of sampling. A flow counter (General Oceanics) was positioned in the mouth of every net for an estimate of water volume filtered. Drift nets sampled fish larvae drifting near the surface. We also sampled larvae using two quatrefoil light traps (Aquatic Research Instruments) with green glow sticks. This gear was placed in slack water areas along the banks for overnight
sampling, and it primarily sampled for species and developmental stages of larvae exhibiting phototactic responses. We incorporated boat-mounted, conical ichthyoplankton "push" nets (Wildlife Supply Company [Wildco], 0.5m diameter, 3.0m tapering 500µm mesh net) only at lower river sites owing to the necessity of large boat access. Pushes were conducted into the current for five minutes to filter a target volume of water (determined by net-mounted flow counter) in each third of the channel width (see Claramunt, Shoup, & Wahl, 2005, for method development of push net). Push nets were similar to drift nets in sampling for larvae drifting near the surface; however, this active sampling technique increased catch of more developed larvae which could exhibit gear avoidance of the passive drift net.

We recorded depth and flow for all samples of each gear, as well as water temperature, dissolved oxygen, Secchi depth, conductivity, specific conductivity, stream width, and pH. Mean daily river discharges and heights were taken from the nearest river gauge. Both raw and standardized discharge data were used in ordination analyses.

We defined specimens as larval fish from hatching to complete absorption of the median fin-fold. All samples were preserved in 95% ethanol and fish larvae were identified to the family taxonomic level (Auer, 1982). Specimens in the family Cyprinidae were further identified to one of four subgroups: the big-headed carps (Hypophthalmichthys spp.), Grass Carp (Ctenopharyngodon idella; Chapman, 2006), Common Carp (Cyprinus carpio), and small-bodied, native cyprinids (all others; Auer, 1982). These large-bodied cyprinid species were identified beyond the family-level taxonomy because of their exotic origins, high abundances in these river systems, and distinctive larval characteristics. Furthermore, our classification of all small-bodied cyprinids as "native" likely contains some error, but the vast majority of these species are native to the region.
Taxonomic groups that did not represent at least 0.05% of the total larvae captured and were not present in at least 2% of the samples were excluded from community comparisons because of their potentially high rarity leverage and the selectivity of the study sampling gear. For example, Ictaluridae and Lepisosteidae represent a substantial portion of the adult fish communities in these rivers, but the benthic nature of Ictaluridae young-of-year and effective locomotor control of Lepisosteidae young-of-year hinder sampling efficiency with the gear types we selected. Consequently, these larvae were rarely captured.

Statistical Analysis

Statistical data analysis was conducted in R version 3.4.0 (R Core Team, 2017). To compare larval densities between systems, we aggregated biweekly fish counts of all gears on each tributary. Thus, a sampling effort consisted of nine drift net, six light trap, and three push net samples. Pooling catch data into larger temporal blocks provided a means for direct comparison between the Illinois and Wabash systems and has been implemented for similar purposes in other larval fish studies (Koehn & Harrington, 2006). Biweekly counts were directly compared between the large river systems using Wilcoxon Rank Sum because of the lack of residual normality.

Larval fish communities were compared at a variety of levels of organization, including by site (classified by Strahler Stream Order), tributary, and system. All community comparisons were made using nonmetric multidimensional scaling (NMDS) ordinations based on Bray-Curtis dissimilarity of the most abundant taxa, similar to Mendonça, Magnusson, & Zuanon (2005). The number of dimensions used in ordinations was determined by the fewest dimensions needed to produce stress levels less than 0.15.

Ordinations were conducted using quantitative (proportional abundance) larval data. In addition to NMDS, we incorporated permutational multivariate analyses of variance (perMANOVA) using the adonis function in the Vegan package in R (Oksanen et al., 2017) to relate
larval assemblages to Strahler Stream Order and tributary. Additionally, we used similarity percentage (SIMPER) analysis to identify dissimilarities in larval communities between systems.

Using NMDS, we made temporal comparisons of larval communities between river systems on a biweekly basis. Additionally, we overlaid environmental variable vectors onto the NMDS plots using the function envfit (Oksanen et al., 2017) to identify environmental associations with community composition.

RESULTS

A total of 22,902 fish larvae were collected from 1,368 samples during this study. Of these larvae, 176 larvae (0.77%) were unable to be visually identified due to degradation. Although we collected larvae from eleven different families of fishes, five of the families (Aphredoderidae, Atherinopsidae, Hiodontidae, Lepisosteidae and Sciaenidae) represented only 0.28% of the fish collected and were not included in ordination analyses of community assemblages. This left nine taxonomic groups used in ordination analyses (Catostomidae; Centrarchidae; Clupeidae; Cyprinidae, genus Ctenopharyngodon; Cyprinidae, genus Cyprinus; Cyprinidae, genus Hypophthalmichthys; native Cyprinidae; Table 2). Total larval densities were statistically higher in the Wabash system than the Illinois system (Wilcoxon Rank-Sum: V = 91, P = 0.0002). Median biweekly larval density was 9.29-fold greater in the Wabash system than the Illinois system over the course of the sampling season. Densities of every taxonomic group were higher in the Wabash system than the Illinois system.

Despite apparent differences in reproductive potential between the two large river systems, summative larval communities were similarly structured between systems (Figure 3). Sites displayed considerable overlap in community structuring with the exception of all 7th Order (Strahler method) and one 5th Order site. These four sites all come from the Little Wabash and
Sangamon Rivers. This association between larval fish community structuring and stream size was supported by a perMANOVA \( (F_{3,467} = 12.42, \text{Permutations} = 999, R^2 = 0.071, P = 0.001) \). Likewise, the perMANOVA of tributary indicated individual tributaries exhibited unique community compositions \( (F_{5,467} = 2.99, \text{Permutations} = 999, R^2 = 0.029, P = 0.001) \). Small-bodied, native cyprinid fishes generally dominated the larval communities in these systems. Smaller rivers were typically dominated by taxonomic groups of smaller-bodied species, including native cyprinids, percids, and centrarchids, while the increased larval diversity observed within the larger rivers appeared attributable to increased presence of larger-bodied taxa, such as moronids, catostomids and exotic cyprinid groups.

Community dissimilarities between the large river systems were driven primarily by the three most abundant taxonomic groups: native Cyprinidae, Catostomidae and Centrarchidae. On average, these three taxa described 73.8% of the structural differences in community compositions between the Illinois and Wabash River systems (SIMPER). Native cyprinids were on average slightly more abundant in the Wabash River tributaries (42.7%) than the Illinois River tributaries (40.2%), whereas catostomids and centrarchids were more abundant in Illinois River tributaries (25.5% and 17.6%) than Wabash River tributaries (20.4% and 9.7%).

While larval communities were spatially similar between systems, they were distinguishable temporally. Wabash River tributary community assemblage structuring was strongly temporally divided along NMDS axis one (Figure 4); however, temporal structuring was less clear-cut in the Illinois system (Figure 5). Illinois River tributaries displayed great variation in composition on a biweekly basis, though they showed the same long-term pattern as the Wabash system. In general, centroids had greater spread along NMDS axis one in the Wabash system than the Illinois system. During the first five weeks of the study, larval communities were dominated by percids, clupeids, moronids and catostomids. These taxa were associated with higher values of
dissolved oxygen (First 5 weeks = 9.09 ± 0.24 mg/L vs. Last 8 weeks = 7.30 ± 0.19 mg/L; Community correlation: $R^2 = 0.22$, $P = 0.001$) and specific conductivity (First 5 weeks = 569.2 ± 19.8 mho/cm vs. Last 8 weeks = 534.1 ± 22.2 mho/cm; Community correlation: $R^2 = 0.07$, $p = 0.004$). Structuring shifted over to a cyprinid (both exotic and native) and centrarchid dominated community during the last eight weeks of the study. Water temperature is typically greatest during this part of the year (mid-summer) and was the only variable strongly negatively associated with axis one (Last 8 weeks = 25.1 ± 0.4 °C vs. First 5 weeks = 15.9 ± 0.8 °C; Community correlation: $R^2 = 0.36$, $P = 0.001$).

River discharge was the only significant environmental variable associated with NMDS axis two (Community correlation: $R^2 = 0.05$, $P = 0.007$); however, size-standardized discharge was not significant (Community correlation: $R^2 = 0.04$, $P = 0.054$). Community structuring appeared more diverse along NMDS axis two in the Illinois system than the Wabash system. Overall, the taxonomic groups Centrarchidae, Catostomidae, and Hypophthalmichthys appeared most strongly associated with high discharge events. Comparing between systems, catostomids showed strong dominance of the larval community from biweeks 3-5 in the Wabash system, but not the Illinois system.

Aside from the hydrographs, the environments of both systems were generally the same. All water chemistry (dissolved oxygen, conductivity, pH) and physical parameters (temperature, water depth, channel width, flow velocity) measured in the tributaries were similar between systems. Data from the National Weather Service indicated there was only an 18% difference in mean rainfall between the tributary watersheds of the Illinois (71.8 ± 0.8 cm) and Wabash (84.6 ± 4.7 cm) Rivers during this study.
DISCUSSION

We found both magnitude and pattern of reproduction in fishes differed between the large tributaries of the Illinois and Wabash River basins. Larval fish communities were similarly structured spatially between the larger river systems because of similarities in geology, landscape composition, and climate, as well as geographic proximity. Small-bodied, native cyprinids, catostomids and centrarchids dominated the larval fish communities in these systems.

Hydrographs of the Illinois River demonstrated how a series of wicket-gate impoundments on a single river can manipulate flow and flood-pulse characteristics within the river system. We found evidence for suppressed or altered hydrological dynamics regarding pulse amplitude, duration, timing, and rate of change in both the main-stem and large tributaries of the impounded large river. These suppressed hydrological dynamics have been identified in many regulated rivers around the world (Graf, 2006; Ibáñez et al., 1996; Koehn & Harrington, 2006; Magilligan & Nislow, 2005; Zhang et al., 2010), and have been shown to negatively affect many fish populations. For example, species dependent on large spring flows (e.g. migratory species) have reduced spawning success in many impounded systems (Agostinho et al., 2004; Beamesderfer et al., 1995; Firehammer & Scarnecchia, 2006). As environmental and reproductive cycles become decoupled in increasingly regulated rivers, species diversity and abundance have declined (Gehrke et al., 1995; Scheidegger & Bain, 1995). In neotropical systems, the frequency of floodplain inundation has been shown to be associated with recruitment success of all reproductive strategies (Agostinho et al., 2001, 2000). While flood-pulses were largely contained to the channel in these Midwestern tributaries, abundances of larvae from all taxonomic groups were also greater in the unimpounded system.

All three Illinois River tributaries showed altered hydrographs, though only the Sangamon River demonstrated seasonal water-level fluctuation with higher average levels in the spring.
Despite joining the Illinois River directly upstream of the LaGrange Dam and having its own large dam upstream the sampling sites, the Sangamon appeared to be less affected by flow modulation from these two sources, which may be attributable to its size. Coincidentally, the Sangamon River had greater total larval fish abundance than both other Illinois River tributaries combined, though was still a fraction of any single Wabash River tributary.

The altered hydrological dynamics within these tributaries likely drives the temporal dissimilarities in larval community structuring we hypothesized and observed. The timing of flood-pulses has been found to be an important driver of larval community structure in other lotic systems (Bednarski, Miller, & Scarnecchia, 2008). Fish reproduce when the environmental conditions are satisfactory (Moran effect); therefore, the seemingly sporadic and less productive nature of fish reproduction in Illinois River tributaries is likely a consequence of modified environmental characteristics, such as spring flood-pulses. A study conducted by Nannini, Goodrich, Dettmers, Soluk, & Wahl (2012) provides strong evidence fish are reproducing in the main-channel and backwater habitats of the Illinois River, suggesting these habitats may provide more preferred conditions for fish reproduction than the tributaries in the Illinois system. With flood-pulse cues from the tributaries being mediated, it is possible that migratory fish are being tricked to spawn below the dams and not in the tributaries (T. Straub, personal communication, April 27, 2018). In anticipation of water-level rise, dam operators may release water from the dams, creating an earlier or greater flood-pulse than what would come from the tributaries, influencing fish to migrate upriver in search of the tributary sourcing the flood-pulse (see Douglas & Douglas, 2000). However, these fish would likely migrate upriver until they reached one of the Illinois River dams, then reproduce below the dam instead of in a tributary because upstream movement was prohibited. Therefore, fish populations in the tributaries of the impounded Illinois River may largely source from the main-stem, where it appears fish may source from both the
tributaries and the main-stem in the Wabash system. However, since this study did not include a genetic analysis we can only hypothesize this difference in population dynamics.

In our study, we found abundances of catostomids, Hypophthalmichthys and centrarchids were strongly associated with high discharge events. Reproductive patterns are very similar among species within these families of fishes; however, of these three taxa we only expected elevated densities of catostomids and Hypophthalmichthys larvae with flood pulse events (Douglas & Douglas, 2000; Lohmeyer & Garvey, 2009). Unlike these two taxa, centrarchids seek out shallow, slack water locations where males build nests in the substrate. Due to the steeply sloping banks and lack of backwater habitat in these tributaries, we expected larval abundances of centrarchids to be higher during lower water periods with coinciding slower flows along the substrate and potentially more flow refugia (Turner, Trexler, Miller, & Toyer, 1994). Instead, our abundance trends were similar to what others have found with densities of centrarchids directly corresponding to water-level. High water may provide access to littoral habitats with an abundance of flow refugia and more suitable spawning substrates, thus promoting greater spawning activity (Martin, Mengel, Novotny, & Walburg, 1981; Raibley, O’Hara, Irons, Blodgett, & Sparks, 1997). Although high water probably provided access to a limited amount of spawning habitat in the study rivers, these pulses more likely flushed larvae out of low water nesting locations (pools) and refugia in slack water areas along banks.

Other taxonomic groups in these, including clupeids and moronids (Burdick & Hightower, 2006), are known to reproduce in connection with large discharge events, yet failed to demonstrate strong associations to discharge within the ordination analyses. Since this study was conducted during a relatively weak year for flood-pulses throughout both river systems, interannual variation in flood pulse dynamics may likely explain the weak ties of these species to
discharge in the data we collected, as only extremely large events may trigger substantial spawning by these species.

Several other environmental variables were strongly associated with temporal larval community structuring in both systems, including water temperature, dissolved oxygen and specific conductivity. Temperature is widely understood as a spawning cue in many fishes (Lohmeyer & Garvey, 2009; Monteleone, 1992), and is strongly tied to photoperiod, another well-recognized environmental driver of spawning behavior (Hubbs, 1985; Pankhurst & Porter, 2003; Papoulias, DeLonay, Annis, Wildhaber, & Tillitt, 2011). Studies indicate mixed impacts on the importance of dissolved oxygen to fish egg and larvae growth and development (Brungs, 1971; Hamor & Garside, 1976; Jones & Reynolds, 1999; Ringler & Hall, 1975). Although the ionic environment may influence fertilization success in some fishes (Billard & Cosson, 1992), its importance to spawning behavior and larval fish abundance is not fully understood. Nevertheless, both dissolved oxygen and specific conductivity can be associated with the annual cycling of water temperature. Subsequently, temperature regime and flood pulse dynamics may be the most reproductively influential environmental variables for fishes in tributaries of large midwestern rivers.

Through this study, we develop a more thorough understanding of the scope of impact of impoundments on large river systems. Many lotic fishes have evolved to take advantage of the fundamental differences between lentic and lotic aquatic environments, but impoundments have substantially affected flow regimes and fish communities that depend on them in rivers all around the world. To mediate the negative effects of dams, many have recommended that water regulation entail natural flow patterns at seasonal scales and magnitudes (Agostinho et al., 2004, 2001; Ibáñez et al., 1996). While such changes to water way regulation would likely improve the ecological integrity of these systems, they may rarely be practical because of the industrial and
economic ramifications of enforcing such measures. Understanding the full scope of ecological effects by anthropogenic activities must be a priority to determine the necessary changes to future river-way regulation.
REFERENCES


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## Tables

Table 1. Results of standardized gauge height correlation analyses. Locations correspond with data in Figure 2. Significant temporal correlations (Corr.) are denoted with an * adjacent its corresponding P-Value, and mean temporal change in gauge height is given as an increase (+), decrease (-), or no change (0).

<table>
<thead>
<tr>
<th>System</th>
<th>River</th>
<th>Gauge Location</th>
<th>t</th>
<th>df</th>
<th>Corr.</th>
<th>P-Value</th>
<th>Change</th>
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<tr>
<td>Illinois</td>
<td>Illinois</td>
<td>Meredosia</td>
<td>-1.37</td>
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<td>0</td>
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<tr>
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<td>0.75</td>
<td>0</td>
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</tr>
<tr>
<td>Illinois</td>
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<td>0.02</td>
<td>0.72</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Illinois</td>
<td>Kingston Mines</td>
<td>0.03</td>
<td>211</td>
<td>0.002</td>
<td>0.98</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Illinois</td>
<td>Peoria</td>
<td>2.61</td>
<td>212</td>
<td>0.18</td>
<td>0.01 *</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Sangamon</td>
<td>Oakford</td>
<td>-5.24</td>
<td>212</td>
<td>-0.34</td>
<td>&lt; 0.0001 *</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Spoon</td>
<td>Seville</td>
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<td>212</td>
<td>-0.05</td>
<td>0.44</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Mackinaw</td>
<td>Green Valley</td>
<td>0.41</td>
<td>212</td>
<td>0.03</td>
<td>0.68</td>
<td>0</td>
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</tr>
<tr>
<td>Wabash</td>
<td>Wabash</td>
<td>New Harmony</td>
<td>-17.74</td>
<td>192</td>
<td>-0.79</td>
<td>&lt; 0.0001 *</td>
<td>-</td>
</tr>
<tr>
<td>Wabash</td>
<td>Terre Haute</td>
<td>-14.81</td>
<td>201</td>
<td>-0.72</td>
<td>&lt; 0.0001 *</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Wabash</td>
<td>Mt. Carmel</td>
<td>-17.41</td>
<td>196</td>
<td>-0.78</td>
<td>&lt; 0.0001 *</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Wabash</td>
<td>Montezuma</td>
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<td>&lt; 0.0001 *</td>
<td>-</td>
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<tr>
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<td>199</td>
<td>-0.70</td>
<td>&lt; 0.0001 *</td>
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</tr>
<tr>
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<td>212</td>
<td>-0.42</td>
<td>&lt; 0.0001 *</td>
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</table>
Table 2. Taxonomic groups used in community ordination analyses.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Family</th>
<th>Taxonomic Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cat</td>
<td>Catostomidae</td>
<td>Buffaloes, Carpsuckers, Redhorses, Suckers</td>
</tr>
<tr>
<td>Cen</td>
<td>Centrarchidae</td>
<td>Black Basses, Sunfishes, Crappies</td>
</tr>
<tr>
<td>Clu</td>
<td>Clupeidae</td>
<td>Shad, Herring</td>
</tr>
<tr>
<td>Cyp</td>
<td>Cyprinidae</td>
<td><em>Cyprinus carpio</em> (Common Carp)</td>
</tr>
<tr>
<td>Ctn</td>
<td>Cyprinidae</td>
<td><em>Ctenopharyngodon idella</em> (Grass Carp)</td>
</tr>
<tr>
<td>Hyp</td>
<td>Cyprinidae</td>
<td><em>Hypophthalmichthys spp.</em> (Silver &amp; Bighead Carp)</td>
</tr>
<tr>
<td>Nat</td>
<td>Cyprinidae</td>
<td>Native small-bodied cyprinids, Shiners, Chubs, Minnows</td>
</tr>
<tr>
<td>Mor</td>
<td>Moronidae</td>
<td>Temperate Basses</td>
</tr>
<tr>
<td>Per</td>
<td>Percidae</td>
<td>Darters, Yellow Perch, Walleye, Sauger</td>
</tr>
</tbody>
</table>
Figure 1. Study river systems with sampling locations and impoundments. Lowest sites on tributaries were located 0.81-1.61km upstream from confluence with main river, where flow unquestionably originated from tributary. Large river dams and large dams on tributaries are shown.
Figure 2. River gauge heights for Illinois River, Illinois River tributaries, Wabash River, and Wabash River tributaries (top to bottom) during the study period. Gauge heights were standardized among sites as a proportion of the maximum height ever recorded at that site. River kilometer is given next to the site name for main-stem sites. Tributary hydrographs are from the most-downstream gauges, respectively. Illinois River sites Peoria and Beardstown were immediately upriver wicket dams.
Figure 3. Nonmetric multidimensional scaling plots of proportional abundance data with centroids (mean ± SE) of samples demarcated by A) sampling site (each site is represented by its Strahler Stream Order classification) and B) tributary. Species coordinates are plotted to describe assemblage characteristics.
Figure 4. Nonmetric multidimensional scaling plots of Wabash River tributary proportional abundance community data. Centroids (mean ± SE) define biweekly sampling units. Plots display the same centroids, but additional data include: A) standard error bars, B) Species points, C) environmental vectors significantly associated with species assemblage characteristics and corresponding $R^2$ values, and D) temporal ordering of samples following numerical progression.
Figure 5. Nonmetric multidimensional scaling plots of Illinois River tributary proportional abundance community data. Centroids (mean ± SE) define biweekly sampling units. Plots display the same centroids, but additional data include: A) standard error bars, B) Species points, C) environmental vectors significantly associated with species assemblage characteristics and corresponding $R^2$ values, and D) temporal ordering of samples following numerical progression.
CONCLUSIONS

Water regulation of our world’s large rivers is an inherently complex task where managers must attempt to balance both human and ecological needs. Nevertheless, it would appear that these ecological requirements often fall by the wayside. Up to now, the majority of efforts to identify and categorize the physical and ecological impacts of damming river systems have focused at the immediate reach or river corridor scale (Koehn & Harrington, 2006; Quinn & Kwak, 2003; Weyers, Jennings, & Freeman, 2003; Zhang, Xia, Liang, & Shao, 2010), and fewer have expanded their scope of study to the larger system (Drinkwater & Frank, 1994; Matthews & Marsh-Matthews, 2007). River systems range across wide geographic expanses of various geochemical attributes and have high degrees connectivity and interaction throughout both the aquatic and terrestrial realms. Reiterating the words of others before us (Fausch, Torgersen, Baxter, & Li, 2002; Power et al., 1988), we need to continue to address ecological questions at a variety of spatial and temporal scales. By analyzing larval community assemblages in tributaries of large rivers we are hopefully taking a step in that direction, though long-term monitoring is vital to building a comprehensive understanding of the greater ecological implications of anthropogenic activities. Since environmental conditions exhibit variability from year to year, continuous monitoring over multiple years is necessary to solidify claims.

In this study, impoundments not only impacted hydrology in the main-stem large river, but also influenced the flow regime and fish reproduction in its tributaries. In comparing large tributaries of the Illinois and Wabash River basins, we found larval fish communities were structured quite similarly amongst all rivers, with some variation attributable to size of river. However, abundance of all taxa, representing a variety of life histories and reproductive strategies, were much lower in tributaries of the impounded river. Additionally, the temporal arrangement of community structuring exhibited differences between systems, seemingly in
association with hydrological features. Although most environmental characteristics, including bedrock composition, temperature, pH, dissolved oxygen levels, and flow velocities were quite similar between basins, flood-pulses were altered in impounded river tributaries. Given this single distinctive element, it is apparent main-stem impoundments alter the flood-pulse regime and have a large impact on the success of reproduction in these river systems.

Dam removal efforts have gained popularity in recent years, yet many call for ecological evaluations on the potential of removals as a restoration strategy (Doyle et al., 2005; Pizzuto, 2002; Poff & Hart, 2002). Depending on the number, size, age and function of impoundments, removal of certain dams may not be feasible (Poff & Hart, 2002) or produce the desired ecological results (Doyle et al., 2005). With respect to the many dams with controlled water release, researchers have suggested dam operational procedures that maintain more natural flow patterns, especially at the seasonal scale (Agostinho, Gomes, & Zalewski, 2001; Ibáñez, Prat, & Canicio, 1996). If implemented, these modifications would hopefully enable access to floodplain habitats and increase the success of spawning events closely tied to seasonal changes in discharge; however, this is likely not practical in all river systems, particularly those that must maintain navigation channels. The protection of specific in-stream habitats can mitigate some of the ecological implications of impoundments as well (Wydoski & Wydoski, 2002). Although there are many propositions, it is important to continue to consider additional measures for ecological improvements as potential resolutions to the often-conflicting ideals of humanity and the environment.

With impending forecasts of climate change, ecological implications of dams may soon be exacerbated by shifting freshwater distribution and increased water demands for human needs (Christensen, Wood, Voisin, Lettenmaier, & Palmer, 2004; Schröter et al., 2005). However, we can begin to approach these questions by continuing to develop our understanding of lotic ecology.
With regard to further developing this study, long-term monitoring is imperative to effectively isolate environmental parameters governing reproduction in fishes. By varying the temporal and spatial scale at which samples are collected, we can address behavioral adaptations of fish to environmental cues in greater detail (e.g. Species are stimulated to spawn during the initial stages of a flood-pulse; Agostinho, Thomaz, Minte-Vera, & Winemiller, 2000). Ultimately, rivers are large and complex systems that require a more comprehensive understanding of anthropogenic impacts in order to develop balanced and effective ecological management practices.
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