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Identifying and quantifying environmental thresholds for ecological shifts in a large semi-regulated river

Shawn M. Giblin

Wisconsin Department of Natural Resources, La Crosse, Wisconsin, USA

ABSTRACT

Ecological shifts, between a clear macrophyte-dominated state and a turbid state dominated by phytoplankton and high inorganic suspended solids, have been well described in shallow lake ecosystems. While few documented examples exist in rivers, models predict regime shifts, especially in regulated rivers with high water retention time. Here I quantified ecological shifts in a large, semi-regulated floodplain river during a transition from a turbid- to a clear-water state using water quality, aquatic vegetation and fisheries data from a rigorous, standardized long-term data set. My findings indicate that significant changes occurred in total suspended solids concentration, aquatic macrophyte abundance, native and non-native fish biomass, fish functional feeding guild patterns, fish habitat guild assemblages and fish spawning guild assemblage patterns over a nearly 20-year period in Navigation Pool 8 of the Upper Mississippi River. Transitions in physical and biological indicators were examined to identify mechanisms underlying the ecological shifts. Environmental variables driving fish assemblage changes were identified (total suspended solids and aquatic vegetation) and management-relevant thresholds are presented. Awareness of management thresholds is critical for resource managers to implement measures to prevent the river from moving to a degraded state characterized by high non-native fish abundance and low predatory fish species abundance.

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Introduction

The Upper Mississippi River (UMR) near La Crosse, Wisconsin, USA (Figure 1), experienced increased turbidity and a collapse of submersed aquatic vegetation (SAV) in the late 1980s, resulting in a shift from mostly SAV-based primary production to phytoplankton-based primary production (Rogers 1994; Owens & Crumpton 1995). The collapse of SAV resulted in a dramatic decline in the recreational fishery (Rogers et al. 1995). In the early 2000s, SAV coverage expanded, and the recreational fishery recovered. Ecological shifts, between a clear water macrophyte-dominated state and a turbid, phytoplankton-dominated state, have been well described in shallow lake ecosystems (e.g. Scheffer 2004). The potential for shifts between macrophyte dominance and algal dominance in river environments with relatively long water residence time (WRT) is supported by both conceptual and spatially explicit mathematical models (Hilton et al. 2006; Hilt et al. 2011). There are, however, few published examples of this type of shift in free-flowing rivers (see Dent et al. 2002).

CONTACT Shawn M. Giblin shawn.giblin@wisconsin.gov

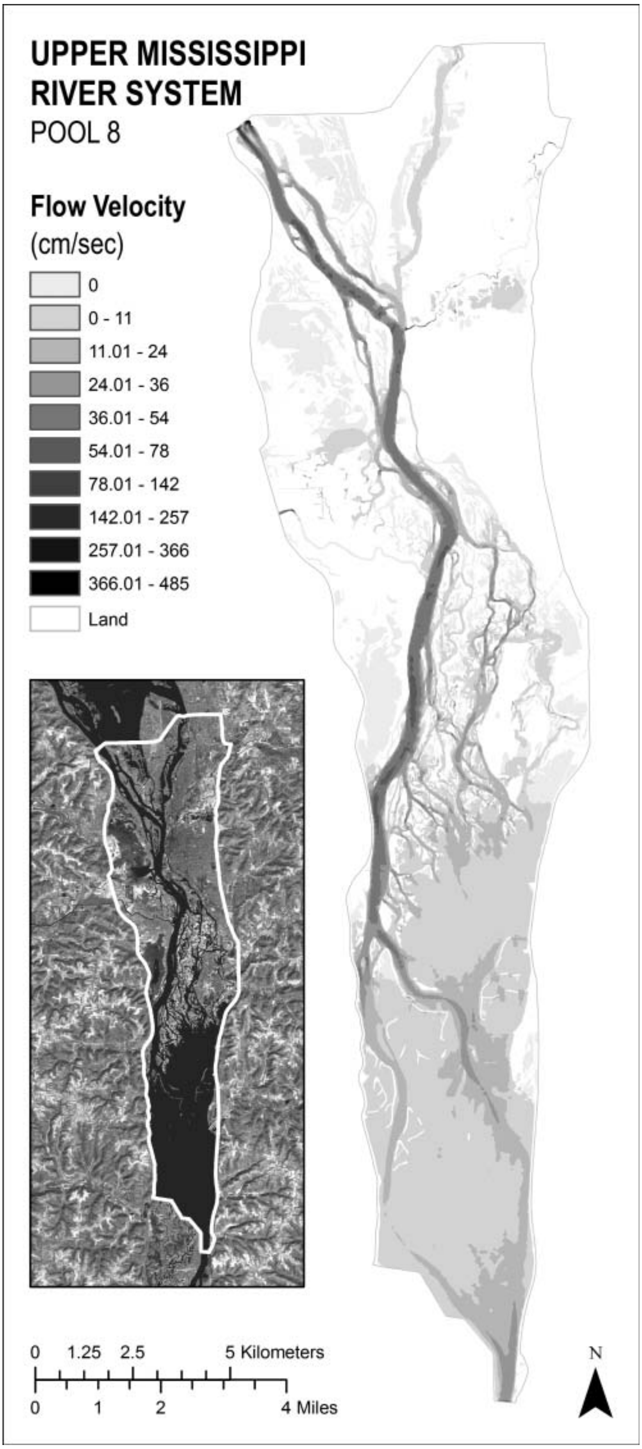

Figure 1. Navigation Pool 8 of the Upper Mississippi River extending from 1093.1 to 1130.6 km. The extent of water coverage and velocities are shown at a mean discharge of 1133 $m^3 s^{-1}$, and the inset is a shaded representation at the same discharge. The main navigation channel is maintained at a depth of at least 2.75 m through dredging and natural erosion. Backwaters, semi-connected lakes and the impounded areas are shallower, with average depths of <1.5 m.

The positive relationship between aquatic macrophytes and water clarity is well understood (Scheffer 1990) and the prevalence of aquatic macrophytes drives a variety of ecological processes in many aquatic ecosystems (Meerhoff et al. 2003). Proliferation of aquatic macrophytes influences a variety of feedback mechanisms in large rivers including reduced sediment resuspension (James et al. 2004), reduced phytoplankton biomass via competition for nutrients and sinking (James & Barko 1994), increases in invertebrate biomass (Engel 1988), increased refuge for zooplankton (Schriver et al. 1995), increased denitrification (Weisner et al. 1994), production of allelopathic substances (Jasser 1995) and increases in waterfowl abundance (Hargeby et al. 1994; Rybicki & Landwehr 2007).

The abundance of SAV is also one of the major factors driving the fish community characteristics across the UMR (Barko et al. 2005; Chick et al. 2005; Ickes et al. 2005). Widespread landscape disturbance, resulting in increased sediment loads, has been identified as driving declines in SAV abundance resulting in declines in backwater specialists and predators with phytophilic spawning strategies (Parks et al. 2014). Relatively clear, vegetated systems tend to be dominated by visual predators such as yellow perch (*Perca flavescens*), northern pike (*Esox lucious*) and largemouth bass (*Micropterus salmoides)* (Kipling 1983; Killgore et al. 1989). Piscivorous fish such as northern pike, bowfin (*Amia calva*), largemouth bass and longnose gar (*Lepisosteus osseus*) are often able to substantially reduce recruitment among planktivorous fish (Scarnecchia 1992; Sondergaard et al. 1997). A reduction in planktivorous fish can alter food webs and results in further increases in aquatic vegetation and water clarity (Persson et al. 1988). Alternatively, benthivorous fish such as common carp (*Cyprinus carpio*) tend to be abundant in turbid systems and can maintain a turbid state due to resuspension during their feeding activities (Miller & Crowl 2006). Once substantial populations of common carp and other benthivores are high, establishing SAV can become difficult due to poor water transparency (Havens 1991).

The UMR navigational pool examined here includes multiple habitat-type characteristics of this ecologically complex river: the main channel, extensive, natural floodplain backwaters extending kilometers laterally from the main channel, semi-connected shallow lakes and a shallow impoundment in the lower third of the pool (Figure 1). Thus, it is a relatively natural, connected floodplain ecosystem influenced by a combination of riverine and shallow lake processes, and may provide an unusual example of ecosystem shifts in a large semi-regulated river.

A shift from a turbid phytoplankton-dominated system to a clear macrophyte-dominated system was captured by long-term physical and biological monitoring by Long Term Resource Monitoring (LTRM) on the UMR. Comprehensive, quality-controlled, replicated data on water quality, fish and aquatic plant communities have been collected annually since 1993 (Moore et al. 2010). This long-term data set provides an opportunity to closely examine the mechanisms underlying large ecological shifts (Holling 1973; Scheffer & Carpenter 2003), including trophic interactions at large spatial and temporal scales.

My objective was to quantify and describe changes in water quality, vegetation and fish assemblage over an 18-year period spanning a transition from turbid to clear water in a 39-km reach of the UMR (Navigation Pool 8). Specifically, I (1) examined the environmental factors associated with the observed ecological changes; and (2) identified management-relevant environmental thresholds for shifts in biological and limnological responses.

Methods

Study area

The UMR consists of a series of navigation pools extending from Minneapolis, Minnesota, USA, to the confluence of the Ohio River at Cairo, Illinois, USA. The 27 navigation dams within this area are low-head dams built to maintain sufficient depth in the river for navigation during the low-flow season and were designed to have little impact on the discharge or water level during high-flow and flood conditions (Sparks 1995; Anfinson 2005). Navigation pools are unlike reservoirs in that they remain mostly riverine in nature.

The study was conducted in Navigation Pool 8 of the UMR (Figure 1). Pool 8 is located between Lock and Dam 7 (Dresbach, Minnesota, USA) and Lock and Dam 8 (Genoa, Wisconsin, USA). It is 39 km long and encompasses ~9000 aquatic ha. Pool 8, typical of many of the navigation pools of the UMR, is composed of a diverse array of aquatic areas (Wilcox 1993), and has been spatially stratified for sampling purposes into the main channel, side channel, contiguous backwaters, isolated backwaters and impounded areas (Soballe & Fischer 2004; Ickes et al. 2014). The main channel is >3 m deep and is characterized by relatively high water velocity (0.20–0.60 ms^{-1}). Side channels are lotic but exhibit depth and water velocity that are generally less than the main channel. Contiguous backwaters typically exhibit very low water velocity (often below detection) and are connected to the main or side channel habitat at normal river stage. Isolated backwaters typically exhibit undetectable water velocity and lack connection to the channel habitat at average river stage. The impounded area is a large expanse of open water located directly upstream of the lock and dam. The average WRT in Pool 8 is 1.7 days (Wasley 2000), but this number is heavily influenced by the very large volume of water moving quickly through the main channel – WRTs in contiguous backwaters, isolated backwaters and impounded areas may range from days to months.

The UMR is modified for navigation and is somewhat unique among rivers worldwide in that the contiguous backwaters remain connected to flowing channels even during low-flow conditions. More detailed descriptions of these contrasting aquatic areas can be found in Strauss et al. (2004).

Study design

Annual pool-wide weighted mean data from a spatially stratified random sampling design were used to generate water quality (Soballe & Fischer 2004) and fisheries trends (Ickes et al. 2014; Ratcliff et al. 2014) by season and/or year for analysis. Aquatic vegetation was also measured in representative strata, and was quantified using a percent frequency index (essentially a detection rate), measured and calculated over the entire navigation pool (Yin et al. 2000). Collection of the fish and water quality data presented here began in 1993 and continued through 2011, except for 2003, when no data were collected due to budgetary constraints. I used water quality data from three seasonal sampling episodes from each year: spring, summer and autumn. In each episode, water quality data were collected at 150 randomly selected sites, weighted for stratum. Spring episodes began the last week of April, summer episodes began the last week of July and fall episodes began the second week of October. Each seasonal sampling episode was generally completed in 10–14 days. Annual fish community data were indexed using standardized day electrofishing methods from 15 June to 31 October (Ickes et al. 2014; Ratcliff et al. 2014). Aquatic vegetation data were collected annually (between 15 June and 15 August). All sampling sites were selected randomly prior to each sampling episode according to published procedures under a stratified random sampling design (Yin et al. 2000; Soballe & Fischer 2004; Ratcliff et al. 2014).

Periods (1993–2001 and 2002–2011) were delimited to provide equal sample size between the earlier period, characterized by higher total suspended solids (TSS) and less aquatic vegetation and the later period, characterized by lower TSS and increased aquatic vegetation. Water quality, vegetation and fish community metrics were compared between the two periods. Associations and potential explanatory mechanisms linking fish community responses to environmental drivers were identified using the BIOENV procedure (Primer v. 6.0).

Sampling and data collection

My data have been derived from a long-term monitoring program on the UMR, which has been observing water quality, aquatic plant and fish communities since 1993. As part of the federally mandated Upper Mississippi River Restoration (UMRR) program, the LTRM element conducts annual assessments using a spatially stratified randomized sampling design and highly standardized sampling protocols to control sampling and non-sampling error sources (Gutreuter et al. 1995; Soballe & Fischer 2004, Ickes et al. 2014; Ratcliff et al. 2014). The statistical design of the monitoring effort, and the standardized nature of the observations it collects, produce annual design-based index estimators of the measured attributes with well-understood statistical properties (Ickes et al. 2014). Relevant sampling details and descriptions of attributes used in my paper are provided below, for each data source.

Water quality and discharge

Water quality data were gained from online data repositories housed at the United States Geological Survey (USGS) Upper Midwest Environmental Sciences Center (http://www.umesc.usgs.gov/data_library/water_quality/water_quality_page.html, accessed 11 November 2016). Water samples were taken at a depth of 0.20 m at each site to assess the water column TSS, total nitrogen (TN), total phosphorus (TP) and chlorophyll *a* (CHL) concentrations. TSS was determined gravimetrically following standard methods (APHA 1992). Samples for TN and TP analyses were collected from randomly selected subsets consisting of 33% of the sampling sites. TN and TP samples were preserved in the field with concentrated H_2SO_4, transported on ice and refrigerated until analysis. TN and TP concentrations were determined colorimetrically using standard methods (APHA 1992). CHL concentrations were determined fluorometrically. Further details regarding LTRM field methods can be found in Soballe and Fischer (2004). Discharge data were collected by the U.S. Geological Survey at Winona, Minnesota, USA.

Seasonal pool-wide means (spring, summer and fall) were generated annually for TSS, TP, TN and CHL for the period of record (1993–2011) for analysis. Pool-wide means are adjusted for non-proportional sampling and standard errors for both non-proportional sampling and stratification. These statistics are calculated according to established procedures, and are published on the LTRM online database. Mean annual discharge at Winona, Minnesota, USA, was used in the analysis.

Aquatic vegetation

Aquatic vegetation community data were gained from online data repositories housed at the USGS Upper Midwest Environmental Sciences Center (http://www.umesc.usgs.gov/data_library/vegetation/vegetation_page.html, accessed 11 November 2016). Standardized sampling procedures are described in Rogers and Owens (1995) and Yin et al. (2000). Aquatic vegetation community and relative abundance data are collected annually between 15 June and 15 August, the period of maximum standing stocks. Each year, 450 randomly selected sampling sites (weighted by stratum) are visited and vegetation is identified and quantified in six subsampling units, each ~1.5 m× 0.36 m. Recorded field data include species detect/non-detect and a relative abundance score that reflects either the biomass (SAV) or the percent cover over the water surface (rooted floating leaf and emergent). I used percent frequency occurrence (Yin et al. 2000) for analysis. Percent frequency occurrence is a measure of how often a species or life form is encountered. It is calculated by dividing the number of sites where a species or life form occurs by the total number of sites sampled and multiplying by 100. I used annual pool-wide design-based percent frequency estimators (Yin et al. 2000) for the submersed (SAVPf; *N* species = 18), rooted-floating leaf (RFPf; *N* species = 3) and emergent (EMPf; *N* species = 27) vegetation. This provided annual time series (1993–2001) of abundance indices for plant assemblages. Submersed, rooted floating-leaf and emergent vegetation class estimates derived from percent frequency estimators were then summed to generate a total aquatic plant index, referred to hereafter as VegSum (Yin et al. 2000). It was possible for all three life forms to overlap; therefore, VegSum can exceed 100%.

Fish

Fish community data were gained from online data repositories housed at the USGS Upper Midwest Environmental Sciences Center (http://www.umesc.usgs.gov/data_library/fisheries/fish_page.html, accessed 11 November 2016). I selected fishery-independent day electrofishing collections from a larger database, 1993–2011 (15 June–15 October each year; the average number of samples per year = 76). I retained data for all the observed species (N = 87, 1993–2011). Species catch and length data were relationally linked to a second database housing species-specific life-history traits and empirically derived allometric growth models (O'Hara et al. 2007). Using these two linked databases, I then generated estimates of mass per sample per species by applying species-specific growth models to length and catch data per sample. Species were then combined, per sample, into the following guilds as expressed in O'Hara et al. (2007): (1) native/non-native status; (2) exploitation status; (3) feeding guild; (4) habitat preference; (5) reproductive guild; and (6) trophic position (Table A1). Mass was summed by sample and guild for each year and an estimate of mean mass-per-unit-effort (g/15-minute electrofishing run) was calculated as per the statistical estimators expressed in Ickes et al. (2014) and Ratcliff et al. (2014). This resulted in annual time series of design-based functional mass expressions for each fish guild class that represent the aquatic environment of Navigation Pool 8, 1993–2011.

Analytics

Testing for changes in observed attributes

Water quality, aquatic plant and fish guild time series used in this study were parsed into two equal periods (1993–2001 and 2002–2011; both N = 9 due to no data collected in 2003) for analyses. Mann–Whitney Rank Sum Tests (SAS Institute 2008, SAS v. 9.2) were used to infer differences in water quality, fish guild and aquatic plant indices (Table 1) between the two periods. Differences in the observed medians between periods were calculated for each environmental variable and guild class and plotted (Figures 2 and 3) to both qualify and quantify the nature of significant shifts among all study variables (expressed as percent change in median).

Testing for fish guild shifts in relation to changes in environmental conditions

For each fish guild (N = 5; trophic position excluded), guild classes were treated as multivariate observations and the Bray–Curtis similarity metric was used to ascribe similarity scores among years in the guild structure. Non-metric multidimensional scaling (NMDS; Primer v. 6.0; Clarke 1993) was applied to the similarity matrices and patterns in guild structure were visualized in both two-dimensional and three-dimensional solutions and plots. I tested for shifts in guild structure between periods using an Analysis of Similarity (ANOSIM; Primer v. 6.0), with period (as described above) as the grouping factor in the analysis (Figure 4).

To identify and test which environmental attributes (discharge, water quality and aquatic plant variables) were most strongly associated with shifts in fish guild responses between the two periods, I used the BIOENV procedure (Table 2; Primer v. 6.0). To complement the similarity matrices described for the fish guild data, I generated similarity scores (Euclidean distance) among years based upon the environmental attributes data. For each fish guild, Primer's BIOENV routine was used to generate a canonical solution (maximum rank correlation) between the biological response similarity matrix and the environmental variable similarity matrix. Correlations were calculated using Spearman's rank correlation coefficient. To impose parsimony upon the maximal correlation determination, I constrained the number of environmental variables to a maximum of three variables for each fish guild analysis. Primer's BIOENV procedure is an unconstrained method and generates rank correlation solutions for all permutations of environmental variables (order and number

Table 1. Mann–Whitney rank sum test results indicating the *U*-statistic, *t*-value and *p*-value for all study parameters between environmental periods observed in Pool 8 of the Upper Mississippi River (1993–2011). The 25th percentile, median and 75th percentile for each parameter by environmental period are also presented.

	1993–2001			2002–2011					
Variable	25th	Median	75th	25th	Median	75th	*U*	*t*	*p*
Vegetation									
SAV[a] (% Freq.)	36.30	46.4	48.51	64.76	71.39	79.03	1	46	<0.001
RF[b] (% Freq.)	12.16	17.50	18.50	24.98	31.08	37.68	0	45	<0.001
EM[c] (% Freq.)	7.20	9.87	11.47	17.55	19.96	25.40	0	45	<0.001
VEGSUM[d] (% Freq.)	55.65	75.38	78.32	109.13	123	140.04	1	46	<0.001
Discharge									
Mean annual at Winona (m^3 s)	33,855	38,600	46,690	24,145	31,360	37,575	21	105	0.093
Water quality									
TSS[e] Spring (mg L)	20.40	25.12	27.46	12.93	14.86	21.83	12	114	0.013
TSS[e] Summer (mg L)	22.48	23.81	27.56	7.19	10.09	18.18	3	123	0.001
TSS[e] Fall (mg L)	16.83	19.80	24.10	7.44	10.10	18.47	16	110	0.034
CHL[f] Spring (μg L)	24.15	37.10	53.16	16.41	32.27	45.77	33	93	0.536
CHL[f] Summer (μg L)	14.99	25.04	55.15	12.89	21.51	34.21	36	90	0.724
CHL[f] Fall (μg L)	15.46	22.73	42.14	4.67	6.82	15.99	12	114	0.013
TN[g] Spring (mg L)	1.75	2.85	3.66	1.74	2.65	3.56	36	90	0.724
TN[g] Summer (mg L)	1.77	2.49	2.60	1.41	1.67	2.21	22	104	0.112
TN[g] Fall (mg L)	1.30	1.46	1.95	1.37	1.60	2.77	33	78	0.536
TP[h] Spring (mg L)	0.10	0.11	0.12	0.09	0.10	0.12	29	97	0.331
TP[h] Summer (mg L)	0.15	0.17	0.19	0.16	0.18	0.23	26	71	0.216
TP[h] Fall (mg L)	0.13	0.15	0.17	0.12	0.15	0.17	40	85	1.000
Fish MPUE									
Native	6070.96	7445.65	8524.23	8195.85	9814.95	13,144.96	8	53	0.005
Non-native	9472.25	12,642.28	16,216.79	5260.18	6304.35	7160.53	6	120	0.003
Exploitation status									
Recreational	1389.55	2581.95	2861.10	3368.10	4767.30	6125.07	0	45	< 0.001
Commercial	14,224.93	16,710.59	20,142.43	9899.41	11,299.64	13,997.18	9	117	0.006
Non-game	257.91	368.67	487.66	97.45	246.24	1025.66	31	95	0.427
Adult feeding guild									
Carnivore	637	731.22	801.24	973.14	1122.42	1885.73	3	48	0.001
Invertivore–carnivore	1829.55	2303.81	2559.72	3104.49	4012.74	5002.12	3	48	0.001
Invertivore–detritivore	9528.29	12,705.65	16,320.54	5339.21	6416.56	7250.48	6	120	0.003
Invertivore–planktivore	0.66	1.06	1.34	1.93	3.80	8.78	7	52	0.004
Invertivore–herbivore	35.96	107.76	129.42	17.37	22.31	45.39	14	112	0.022
Planktivore–invertivore	0.24	0.42	0.74	0.69	0.97	2.00	14	59	0.022
Detritivore	0.26	0.42	11.58	3.29	5.31	35.79	21	66	0.093
Invertivore	2677.72	3664.80	4375.28	3793.94	4266.26	5441.15	21	66	0.093
Planktivore–detritivore	25.44	35.09	137.22	0	36.77	62.10	30.5	95.5	0.399
Detritivore–invertivore	0	0.01	0.05	0	0.01	0.03	34	92	0.579
Herbivore	77.26	284.71	399.06	25.09	191.51	956.02	36	90	0.724
Planktivore	6.94	12.86	18.89	5.41	8.83	21.33	36	90	0.724
Habitat guild									
Limnophillic	1089.69	1536.16	2264.98	2805.82	4,025.70	6047.51	0	45	<0.001
Limnorheophillic	12,934.84	14,653.77	18,457.17	8140.20	9564.78	11,269.62	7	119	0.004
Pelagicrheolimnophillic	38.92	68.14	79.39	14.83	46.05	86.14	31	95	0.427
Pelagiclimnorheophillic	30.48	78.19	202.46	9.81	63.84	183.46	32	94	0.480
Rheolimnophillic	1184.14	1321.94	1521.70	1140.46	1329.54	1713.92	38	83	0.860
Rheophillic	90.83	200.92	245.51	113.03	184.78	218.10	39	87	0.930
Reproductive guild									
Polyphillic	935.85	1695	2210.53	2561.63	4047.78	5035.37	0	45	<0.001
Phytophillic	683.10	791.15	851.63	1071.34	1189.34	1923.26	4	49	0.001
Phytolithophillic	9620.32	12,771.18	16,370.70	5685.71	6593.01	7510.34	6	120	0.003
Pelagophillic	143.72	158.75	245.37	165.48	265.69	327.35	26	71	0.216
Lithophillic	2221.99	2697	3527.93	2725.97	3105.90	3860.88	29	74	0.331
Psammophillic	0	0.01	0.02	0	0.02	0.03	32	77	0.477
Lithopelagophillic	992.73	1095.14	1306.17	700.17	786.85	1681.23	33	93	0.536
Spleleophillic	329.31	364.61	539.95	293.62	431.79	507.59	39	84	0.930
Trophic status									
Fourth	2619.94	2917.59	3263.05	4179.92	5135.17	6887.85	2	47	< 0.001
Third	14,140.75	16,331.20	19,247.65	9670.18	11,691.53	13,837.96	8	118	0.005
First-CHL[f] fall	15.46	22.73	42.14	4.67	6.82	15.99	12	114	0.013
First-CHL[f] summer	14.99	25.04	55.15	12.89	21.51	34.21	36	90	0.724

(*continued*)

Table 1. (*Continued*)

Variable	1993–2001 25th	1993–2001 Median	1993–2001 75th	2002–2011 25th	2002–2011 Median	2002–2011 75th	*U*	*t*	*p*
First-CHL[f] spring	24.15	37.10	53.16	16.41	32.27	45.77	33	93	0.536
VegSum[d] (% Freq.)	55.65	75.38	78.32	109.13	123	140.04	1	46	< 0.001
Species of management interest									
Micropterus salmoides	390.43	569.19	1081.25	1793.21	2211.97	3353.93	1	46	< 0.001
Esox luscious	87.65	138.43	287.33	364.85	424.36	446.46	2	47	< 0.001
Lepomis macrochirus	136.95	393.42	457.57	430.29	782.72	1278.63	11	56	0.01
Cyprinus carpio	9472.25	12,642.28	16,216.79	5260.18	6304.35	7160.53	6	120	0.003

[a]Submersed aquatic vegetation.
[b]Rooted-floating vegetation.
[c]Emergent vegetation.
[d]Sum of submersed, rooted floating and emergent vegetation percent frequency.
[e]Total suspended solids.
[f]Chlorophyll α.
[g]Total nitrogen.
[h]Total phosphorus.

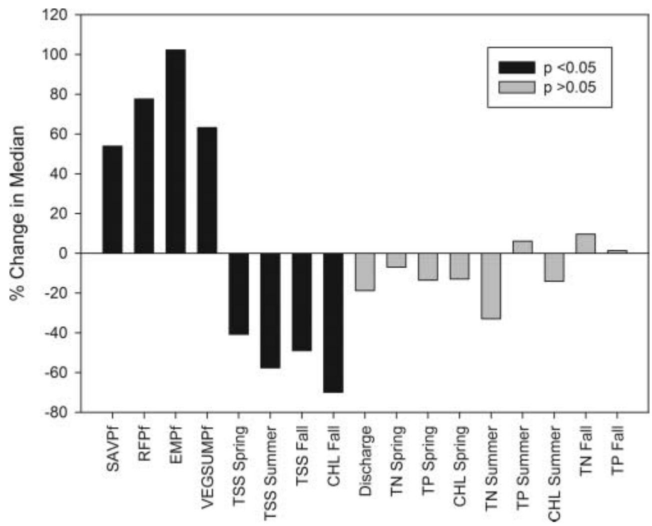

Figure 2. Change in median between the early environmental period (1993–2001) and the late environmental period (2002–2011) among the environmental variables in Pool 8 of the Upper Mississippi River. Changes significant at the $p < 0.05$ level are denoted with black bars.

of variables). Solutions were sorted by rank correlation order to identify the environmental variables most strongly associated with fish guild responses.

Identification of thresholds for environmental covariates driving fish guild responses

Once the environmental covariates associated with fish guild responses were identified, linear and piecewise regression techniques were used to determine the presence of TSS thresholds for fish guild metrics. Native/non-native and exploitation status guilds were selected for TSS threshold analysis due to their resource management importance. I selected TSS for threshold determination due to it being a more easily measured, and more management-relevant target than aquatic vegetation percent frequency (Table 3; Figure 5). Furthermore, TSS and aquatic vegetation (VegSum) tend to be tightly coupled (Figure 6; $r^2 = 0.807$). Linear regression was used to determine if TSS could predict fish guild metrics and generate statistics comparable to the piecewise regression method. Piecewise

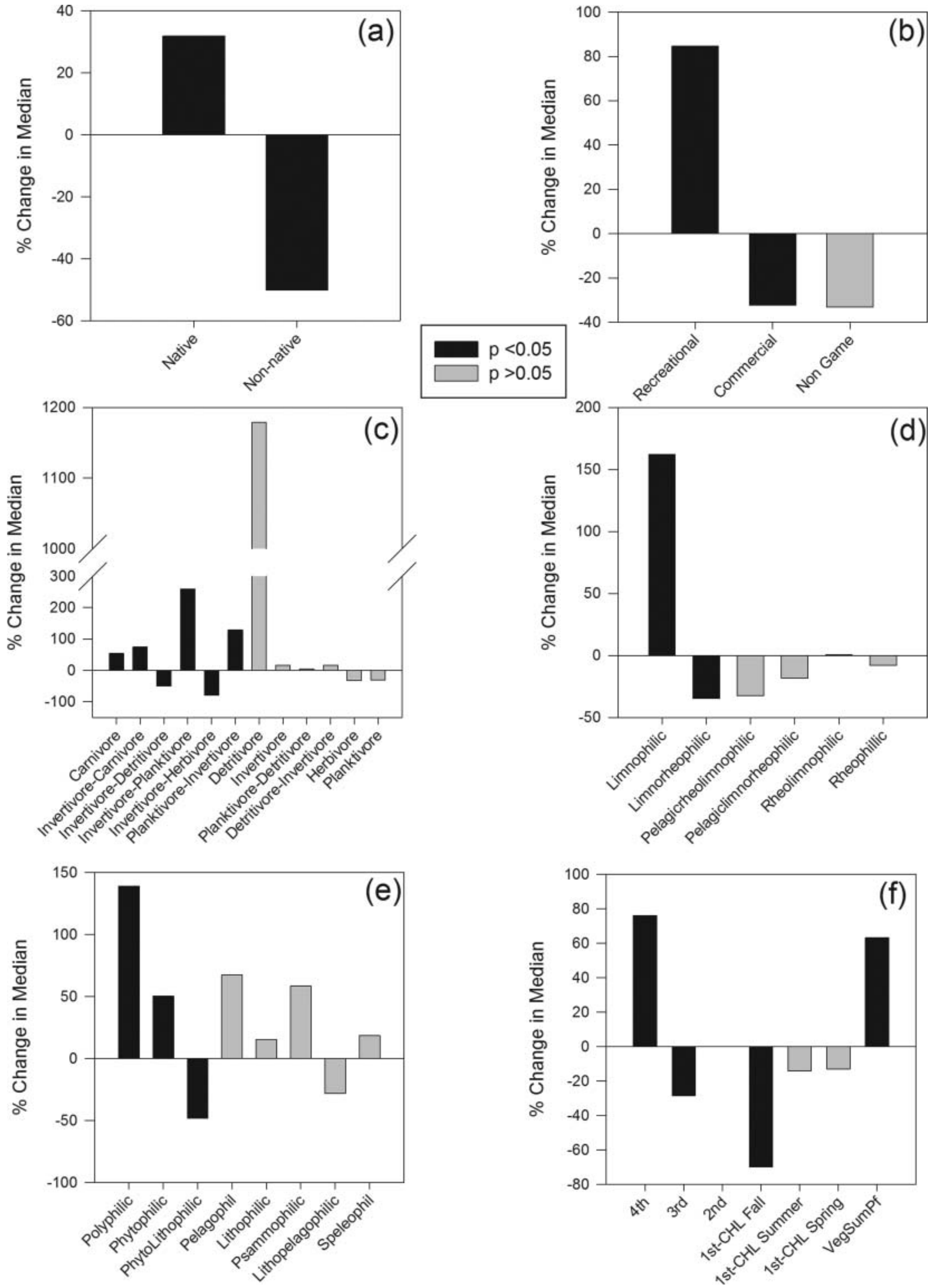

Figure 3. Change in median between the early period (1993–2001) and the late period (2002–2011) among (a) native/non-native status; (b) exploitation status; (c) feeding guild; (d) habitat guild; (e) reproductive guild; and (f) trophic position in Pool 8 of the Upper Mississippi River (1993–2011). Changes significant at the $p < 0.05$ level are denoted with black bars.

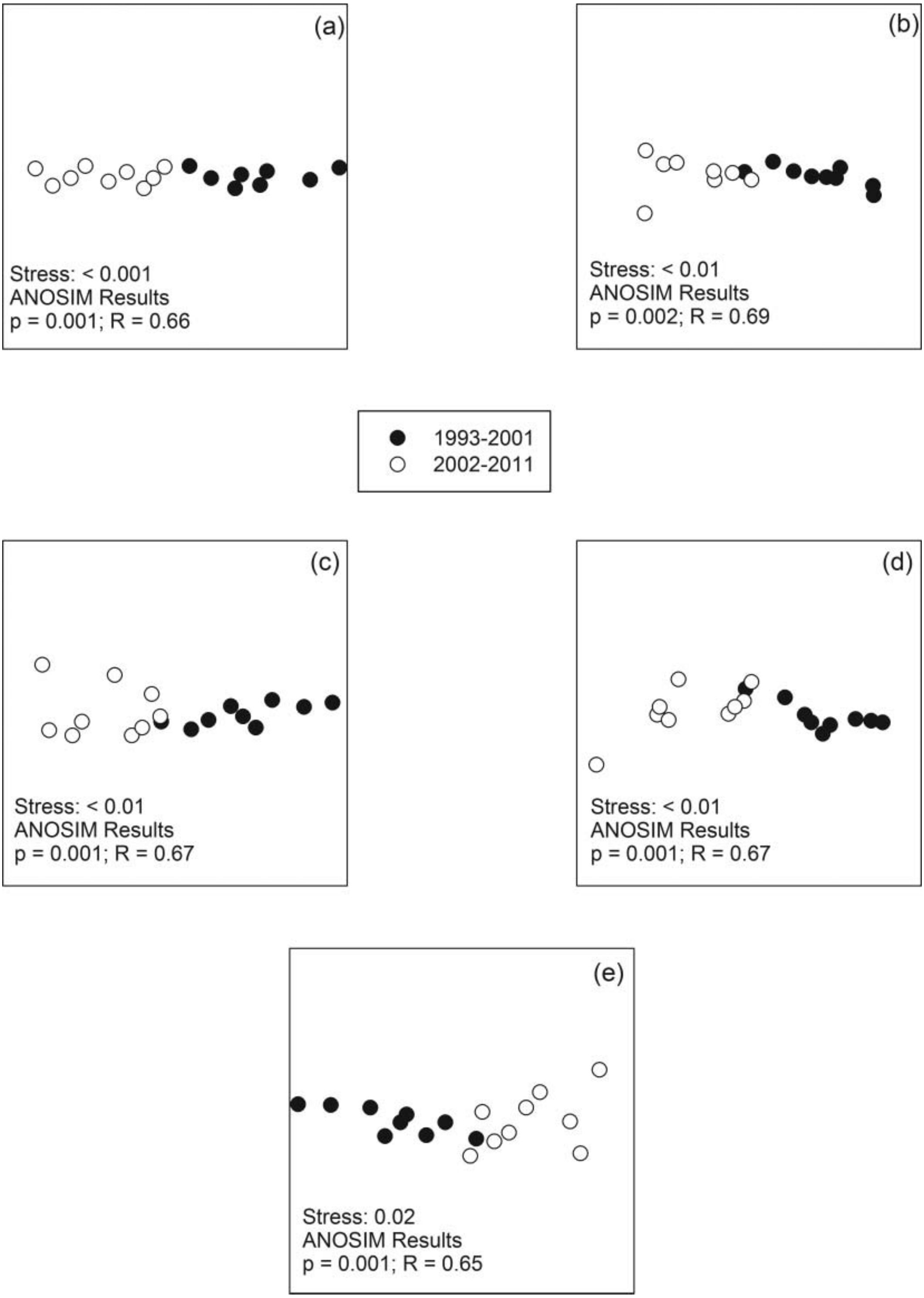

Figure 4. Two-dimensional non-metric scaling ordination (NMDS) between the early period (1993–2001) and the late period (2002-2011) among (a) native/non-native status; (b) exploitation status; (c) feeding guild; (d) habitat guild; and (e) reproductive guild in Pool 8 of the Upper Mississippi River (1993–2011). The ANOSIM results comparing the two time periods are also given.

Table 2. Primer BIOENV results indicating the top three environmental variables associated with fish guild shifts between periods in Pool 8 of the Upper Mississippi River (1993–2011). *R* indicates the maximal rank correlation for each three-variable solution.

Biological variable	First environmental variable	Second environmental variable	Third environmental variable	*R*
Native/non-native	VegSum[a] (% Freq.)	TSS[b] summer (mg L)	TSS[b] fall (mg L)	0.466
Exploitation status	VegSum [a] (% Freq.)	TSS[b] summer (mg L)	CHL[c] summer (μg L)	0.415
Adult feeding guild	VegSum [a] (% Freq.)	TSS[b] summer (mg L)	TSS[b] fall (mg L)	0.499
Habitat guild	VegSum [a] (% Freq.)	TSS[b] summer (mg L)	TSS[b] fall (mg L)	0.421
Reproductive guild	VegSum [a] (% Freq.)	TSS[b] summer (mg L)	TSS[b] fall (mg L)	0.358

[a]Sum of submersed, rooted floating and emergent vegetation percent frequency.
[b]Total suspended solids.
[c]Chlorophyll α.

Table 3. Thresholds for fish guild responses to mean summer TSS in Pool 8 of the Upper Mississippi River (1993–2011), and adjusted r^2 values as determined from two regression techniques. All parameter estimates are significant at the 0.05 level.

	Piecewise regression			Linear regression
Fish guild	Threshold	95% confidence interval	Adj r^2	Adj r^2
Non-native	19.26	14.235–24.275	0.6928	0.555
Native	12.55	6.424–18.666	0.4324	0.24
Commercial	19.15	12.401–25.889	0.4692	0.367
Recreational	12.29	8.155–16.414	0.5833	0.341

or ‘broken-stick’ regression models were used to identify thresholds or breakpoints (Toms & Lesperance 2003). Successful piecewise regression models have r^2 values >0.2 and greater than calculated r^2 values from corresponding linear regressions (Toms & Lesperance 2003; Black et al. 2011). For each identified threshold value, 95% confidence intervals were also calculated. Linear and piecewise regressions were performed in SigmaPlot 11.0 (Systat 2008).

Results

Shifts in water quality, aquatic plant and fish guild indices

Substantial shifts were observed among the environmental variables in this study. Eight of the 17 water quality, aquatic macrophyte and discharge variables demonstrated significant shifts ($p < 0.05$; Figure 2). Percent frequency of submersed, rooted-floating leaved, emergent and VegSum (all three life forms combined) increased significantly from the early-to-late environmental period (Table 1; Figure 2). Conversely, spring TSS, summer TSS, fall TSS and fall CHL decreased significantly from the early-to-late environmental period (Table 1; Figure 2). The remainder of the discharge and water quality variables exhibited no statistically significant change between the periods.

Many statistically significant differences were observed among the fish guild metrics between the two time periods. Notably, native fish biomass indicated a significant increase, while non-native fish biomass indicated a significant decrease (Table 1; Figure 3(a)). For exploitation status, recreational fish biomass increased significantly, while commercial fish biomass decreased significantly (Table 1; Figure 3(b)). Within the adult feeding guild, carnivore, invertivore–carnivore, intertivore–planktivore and planktivore–invertivore guild classes all increased significantly, while the invertivore–detritivore and invertivore–herbivore guild classes decreased significantly (Table 1; Figure 3 (c)). For the habitat preference guild, limnophils increased significantly, while limnorheophils decreased significantly (Table 1; Figure 3(d)). For the reproductive guild, polyphils and phytophils increased significantly, while phytolithophils decreased significantly (Table 1; Figure 3(e)). For the trophic position guild, the fourth trophic level increased significantly, while the third trophic level decreased significantly (Table 1; Figure 3(f)). Furthermore, ANOSIM analysis demonstrated significant differences in fish community between the two time periods for all fisheries guilds examined (Figure 4).

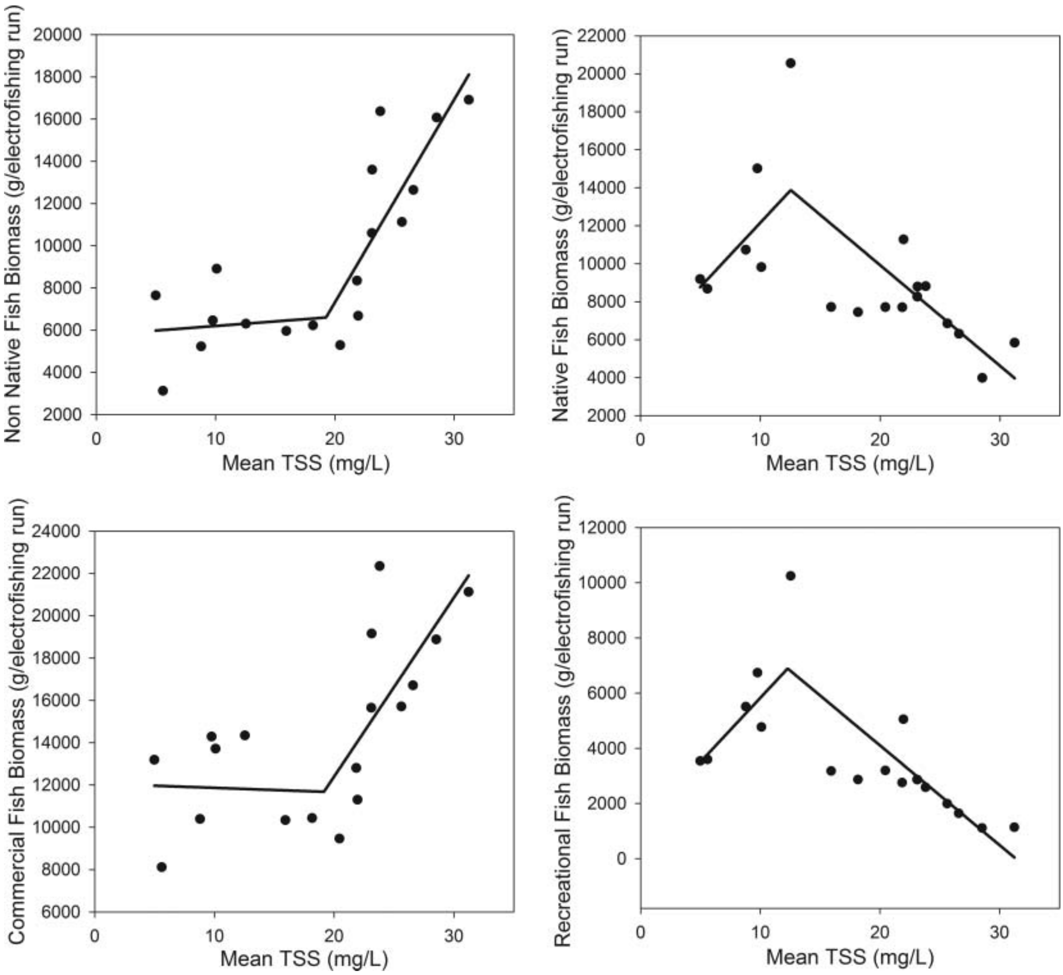

Figure 5. Relation between mean annual fish guild biomass per electrofishing run and mean summer TSS in Pool 8 of the Upper Mississippi River (1993–2011). Thresholds are indicated by the breakpoint in the piecewise regression line.

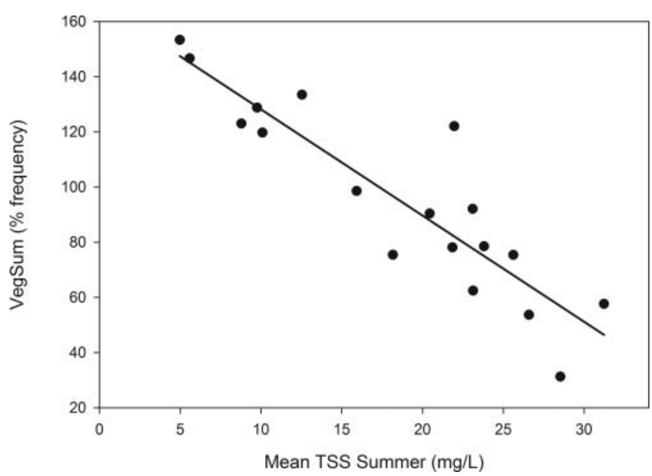

Figure 6. Relation between VegSum (percent frequency) and mean summer TSS in Pool 8 of the Upper Mississippi River (1993–2011). The line indicates the linear regression result ($y = -3.85x + 166.64$; $r^2 = 0.807$).

Environmental drivers of fish guild responses

Canonical rank correlation results from the BIOENV procedure, performed for five fish guilds considered, identified the primary environmental variables associated with fish guild responses (Table 2). For each fish guild, a three-variable solution produced the maximal rank correlation (range 0.358–0.499 among guilds; Table 2). The aquatic plant abundance index (VegSum) contributed to the canonical solution for every fish guild. Mean summer TSS also contributed to all five solutions. Mean fall TSS contributed to four of five solutions (exploitation status was the only exception). Mean summer CHL only contributed to the exploitation status guild solution. No additional environmental variables made contributions to the canonical solutions.

Thresholds for fish guild responses to environmental drivers with emphasis on native and exploitation status

Thresholds were detected in the relations between fish guild metrics and summer TSS. Fish guild response thresholds ranged from 12.29 to 19.26 mg/L summer TSS (Table 3; Figure 5). Non-native fish biomass increased and native fish biomass decreased as summer TSS increased (Table 3; Figure 5). Similarly, recreational fish biomass decreased and commercial fish biomass increased as summer TSS increased (Table 3; Figure 5).

Discussion

It is evident that portions of the UMR have undergone a shift from a turbid system with sparse vegetation during the early 1990s, to a clear water system with abundant aquatic vegetation in the recent years. There are likely multiple factors driving TSS levels within Pool 8 which makes it difficult to identify the ultimate driver of these changes, but TSS is clearly associated with changes in vegetation and fish communities in the UMR. As this shift from a turbid to vegetated condition has occurred, a number of positive and negative feedbacks have reshaped the ecosystem. The increase in vegetation has likely resulted in a decrease in wind-induced sediment resuspension due to buffering of wave action (Dent et al. 2002) and sediment stabilization. Phytoplankton production decreased, although only statistically significant in the fall, and was likely the combined result of many drivers, including allelopathic exudates from rooted vegetation inhibiting phytoplankton growth (Sondergaard & Moss 1998), higher algal sinking rates within the low-velocity environment of the plant beds that remove phytoplankton from the photic zone (Sand-Jensen 1998; Kohler et al. 2010), increased algal predation by zooplankton that use refuge within plant beds and reduce phytoplankton standing stocks (Hillbricht-Ilkowska 1999), trophic shifts resulting in suppression of planktivores by abundant top predators (Wootton & Power 1993) and nitrate becoming locally less available due to denitrification within the plant beds (Veraart et al. 2011).

The indexed mass of benthivorous, non-native, common carp decreased by approximately 50% over the transition, perhaps due to the less favorable vegetated environment that developed (Breukelaar et al. 1994). Common carp were the most abundant fish species in Pool 8, in terms of indexed mass, throughout the entire study period. Therefore, a 50% reduction in common carp likely reduced bioturbation in the system, leading to a strong positive feedback between this non-native fish and turbidity/TSS.

Indexed native fish mass showed a significant increase, while indexed non-native fish mass showed a significant decrease as TSS declined (Figure 5). Aquatic vegetation and TSS were the most explanatory variables driving native/non-native fish assemblage (Table 2). This is consistent with the results of many studies demonstrating a significant positive relationship between common carp mass (non-native to North America) and TSS concentration (Meijer et al. 1989; Meijer et al. 1990; Havens 1991; Breukelaar et al. 1994). Conversely, many studies have shown an increase in native fish biomass as TSS is reduced and vegetation coverage increases (Grift 2001; Zambrano et al. 2001;

Parks et al. 2014). Because TSS had such a pronounced effect on the dominance between native and non-native indexed fish mass, I expect that TSS reductions will be critical to native fish conservation in the upper impounded Mississippi River.

Recreational fish indexed mass increased significantly by nearly 80%, while commercial fish indexed mass decreased significantly as TSS declined and aquatic vegetation increased (Figure 5). The increase in recreational fish indexed mass was overwhelmingly tied to increases in largemouth bass, northern pike (both visual predators) and bluegill (*Lepomis macrochirus*; a visual invertivore; Table 1). Many studies have documented the link between an increase in these three species and increased vegetation (Killgore et al. 1989; Grimm & Backx 1990; Bettoli et al. 1993; Grift 2001). The reduction in commercial fish indexed mass closely mirrored the reduction in non-native fish indexed mass, and was likely driven by the observed decline in common carp, a non-native but commercially important species.

The carnivorous fish guild increased significantly, while the invertivore–detritivore fish guild decreased significantly as TSS declined and aquatic vegetation increased. The positive relationship between aquatic vegetation and visual predator species like largemouth bass and northern pike is well known, but an understanding of the ecological importance of formerly reviled fishes such as gars and bowfin has only recently come to light (Scarnecchia 1992). Having the full complement of carnivorous fishes is critical to ecosystem function, especially for controlling recruitment of ecosystem generalists of the invertivore–detritivore guild, with the most prominent of this group being the common carp (Parks et al. 2014).

Limnophilic fish showed a significant increase, while the more channel-dwelling limnorheophils decreased significantly as TSS declined and aquatic vegetation increased. This result supports recent research documenting ecological shifts in the opposite direction (from clear to turbid states) in which a decline in backwater specialists was observed in agriculturally impacted Midwestern rivers (Parks et al. 2014). TSS concentration was lower, and vegetation coverage within Pool 8 was greater, than the highly impacted rivers in Iowa, USA, studied by Parks et al. (2014). It seems likely that the expansion of vegetation beds in Pool 8 has increased areas of low water velocity within the pool, and is a possible reason for the decline in limnorheophils (Sand-Jensen 1998).

Polyphilic and phytophilic fish guilds increased significantly, while the phytolithophilic fish guild decreased significantly as TSS declined and aquatic vegetation increased. The increase in fish with phytophilic spawning strategies is encouraging and suggests that the reduction of TSS can contribute greatly to the restoration of ecological structure of North American rivers affected by agriculture. My results again corroborate those of Parks et al. (2014) who noted substantial declines in fish with phytophilic spawning strategies in Iowa, USA. Rivers as flow regimes were altered, water quality degraded and river corridors were fragmented following the onset of intensive row crop agriculture.

Significant trophic shifts in fish were observed as TSS declined and aquatic vegetation increased. Indexed mass of the fourth trophic level increased significantly; likely due to the increase in visual predators (especially northern pike and largemouth bass) experiencing increased feeding efficiency with greater water transparency (Killgore et al. 1989; Grimm & Backx 1990; Bettoli et al. 1993). Additionally, many of the top trophic-level species (northern pike, longnose gar and bowfin, specifically) are also phytophilic spawners, so they may have benefited both from increased clarity and increased vegetation abundance (Parks et al. 2014). The increase in the fourth trophic level likely resulted in the reduction of the third trophic level due to increased predation.

This study demonstrates TSS as a useful indicator for changes in ecosystem structure and function. I found it was associated with increases in aquatic vegetation (Figure 6) and important functional changes in fish community. Identification of ecological thresholds is critical to sound management of aquatic resources. Once particular thresholds are crossed, aquatic systems can move away from desired ecological conditions and it can become very difficult to shift the system back to the desired state (Groffman et al. 2006). Managers need to know where these thresholds exist due to the very high stakes associated with crossing the ecological tipping points (Sparks et al. 1990; Scheffer & Carpenter 2003). I identified thresholds ranging between 12.29 and 19.26 mg/L mean summer TSS for the UMR. The mean of the summer TSS thresholds was 16 mg/L and I suggest this value as an important management target for native fish conservation in the UMR. This value appears to be consistent with thresholds identified by other researchers in a variety of environments. Jackson et al. (2010) identified TSS in the 11–14 mg/L range as being associated with high bluegill/largemouth bass catch rates and low common carp catch rates in 129 Iowa lakes. Conversely, TSS in the 25–30 mg/L range was associated with low bluegill/largemouth bass and high common carp catch rates. Growing season TSS of 15 mg/L has been identified as a tipping point for SAV establishment, waterfowl, fish and invertebrate populations on Chesapeake Bay (Kemp et al. 2004). Lougheed et al. (1998) observed dramatic shifts in Great Lake wetlands among fish and SAV communities as turbidity values shifted from 6 NTU (equivalent to 8 mg/L TSS using relationships in Giblin et al. 2010) to 20 NTU (equivalent to 30 mg/L). When considering public perception and the value of aquatic resources, Michigan (USA) residents identified 20 mg/L TSS as the point where water was perceived to be 'clear' (http://www.michigan.gov/documents/deq/wb-npdes-TotalSuspendedSolids_247238_7.pdf, accessed 12 May 2016).

Freshwater ecosystems are constantly undergoing changes of both natural and human-induced origins, and many changes over the past century have led to ecosystems locked in degraded ecological states (Scheffer 2004). The mechanisms leading to such shifts arise from varying processes, including compromised water quality (Hilton et al. 2006), establishment of invasive and competitively superior species (Zambrano et al. 2006) and land uses and ecosystem extractions that exceed the assimilative capacity of ecosystems (Parks et al. 2014). Such ecological shifts often come with notable social and economic costs, progressing from a diverse natural system with diverse ecosystem service benefits, toward simplified ecosystems with fewer and harder-to-manage ecosystem service benefits. Such transitions are not limited to freshwater ecosystems. Examples in terrestrial ecosystems include an irreversible shift from grasslands to desert where native grazers were (even temporarily) replaced with livestock in the Sahel (Van De Koppel et al. 1997). In marine ecology, coral bleaching (Hoegh-Guldberg 1999; Fitt et al. 2001) – the loss of dinoflagellate algal symbionts from coral hosts – is a threshold response to anthropogenic disturbances, leading to fundamental change in primary production, ecosystem simplification and a loss of ecosystem services. Understanding the thresholds where ecosystems begin to shift ecological states is critical for the applied management of ecosystems. While sometimes abrupt (e.g. Hilt et al. 2011), ecosystem state shifts are most commonly slow-moving, cumulative responses to a variety of ecosystem impairments. For this reason, long-term standardized observation is a key tool for documenting these shifts, and for identifying their proximate causes, so that management can be applied before important thresholds are crossed and undesirable ecological shifts occur. Here, I have used long-term and standardized observations to identify shifts in the functional attributes of a large river fish community, and to identify the environmental factors associated with this ecological shift. I have also proposed an ecological threshold in TSS and associated changes in aquatic plant and fish community attributes where an ecosystem shift occurred for the UMR. Science-informed management is frequently required to address ecosystem shifts, and because of the size and inter-jurisdictional nature of the UMR, management will require a plurality of stakeholders to actively engage in seeking and meeting threshold targets.

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Notes on contributor

Shawn Giblin is the Mississippi River water quality specialist for the Wisconsin Department of Natural Resources.

ORCID

Shawn M. Giblin http://orcid.org/0000-0002-8246-4049

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Appendix

Table A1. Native/non-native status, exploitation status, feeding guild, habitat guild, reproductive guild and trophic position by species among fishes in Navigation Pool 8 of the Upper Mississippi River (1993–2011).

Fish code	Common name	Scientific name	Native or non-native[a]	Exploitation status	Feeding guild	Habitat guild	Reproductive guild	Trophic status
ABLP	American brook lamprey	*Lampetra appendix*	N	Non-game	No feed		Lithophil	
AMEL	American eel	*Anguilla rostrata*	N	Commercial	Invertivore/ carnivore	Rheo-limnophilic		4
BDDR	Banded darter	*Etheostoma zonale*	N	Non-game	Invertivore		Phytophil	3
BHMW	Bullhead minnow	*Pimephales vigilax*	N	Non-game	Invertivore/ herbivore	Rheo-limnophilic	Speleophil	3
BKBF	Black buffalo	*Ictiobus niger*	N	Commercial	Invertivore/ herbivore	Rheo-limnophilic	Lithopelagophil	3
BKBH	Black bullhead	*Ameiurus melas*	N	Commercial	Invertivore/ carnivore	Limnophilic	Speleophil	4
BKCP	Black crappie	*Pomoxis nigromaculatus*	N	Recreational	Invertivore/ carnivore	Limnophilic	Phytophil	4
BKSB	Brook stickleback	*Culaea inconstans*	N	Non-game	Planktivore/ invertivore		Ariadnophil	3
BKSS	Brook silverside	*Labidesthes sicculus*	N	Non-game	Planktivore/ invertivore	Rheo-limnophilic	Phytolithophil	3
BLGL	Bluegill	*Lepomis macrochirus*	N	Recreational	Invertivore	Limnophilic	Polyphil	3
BMBF	Bigmouth buffalo	*Ictiobus cyprinellus*	N	Commercial	Invertivore	Pelagic Limno-rheophilic	Lithopelagophil	3
BNMW	Bluntnose minnow	*Pimephales notatus*	N	Non-game	Detritivore		Speleophil	3
BNBH	Brown bullhead	*Ameiurus nebulosus*	N	Commercial	Invertivore/ carnivore		Speleophil	4
BNTT	Brown trout	*Salmo trutta*	NN	Recreational	Invertivore/ carnivore		Lithophil	4
BRBT	Burbot	*Lota lota*	N	Recreational	Invertivore/ carnivore		Lithopelagophil	4
BSDR	Blackside darter	*Percina maculata*	N	Non-game	Invertivore		Lithophil	3
BSMW	Brassy minnow	*Hybognathus hankinsoni*	N	Non-game	Planktivore/ detritivore		Phytophil	3
BUSK	Blue sucker	*Cycleptus elongatus*	N	Non-game	Invertivore/ herbivore		Lithopelagophil	3
BWFN	Bowfin	*Amia calva*	N	Commercial	Carnivore		Phytophil	4
CARP	Common carp	*Cyprinus carpio*	NN	Commercial	Invertivore/ detritivore	Limno-rheophilic	Phytolithophil	3
CKCB	Creek chub	*Semotilus atromaculatus*	N	Non-game	Invertivore/ carnivore		Lithophil	4
CLDR	Crystal darter	*Ammocrypta asprella*	N	Non-game	Invertivore	Rheophilic	Psammophil	3
CLSR	Central stoneroller	*Campostoma anomalum*	N	Non-game	Herbivore		Lithophil	3
CMMW	Central mudminnow	*Umbra limi*	N	Non-game	Invertivore	Limnophilic	Phytophil	3
CNCF	Channel catfish	*Ictalurus punctatus*	N	Commercial	Invertivore/ carnivore	Rheophilic	Speleophil	4
CNLP	Chestnut lamprey	*Ichthyomyzon castaneus*	N	Non-game	Carnivore	Rheo-limnophilic	Lithophil	4
ERSN	Emerald shiner	*Notropis atherinoides*	N	Non-game	Planktivore	Rheo-limnophilic	Pelagophil	3
FHCF	Flathead catfish	*Pylodictis olivaris*	N	Commercial	Invertivore/ carnivore	Rheo-limnophilic	Speleophil	4
FHMW	Fathead minnow	*Pimephales promelas*	N	Non-game	Detritivore/ invertivore		Speleophil	3

(*continued*)

Table A1. (*Continued*)

Fish code	Common name	Scientific name	Native or non-native[a]	Exploitation status	Feeding guild	Habitat guild	Reproductive guild	Trophic status
FTDR	Fantail darter	*Etheostoma flabellare*	N	Non-game	Invertivore	Rheophilic	Speleophil	3
FWDM	Freshwater drum	*Aplodinotus grunniens*	N	Commercial	Invertivore/ carnivore		Pelagophil	4
GDEY	Goldeye	*Hiodon alosoides*	N	Commercial	Invertivore	Rheo-limnophilic	Lithopelagophil	3
GDRH	Golden redhorse	*Moxostoma erythrurum*	N	Commercial	Invertivore	Limno-rheophilic	Lithophil	3
GDSN	Golden shiner	*Notemigonus crysoleucas*	N	Non-game	Invertivore/ herbivore		Phytophil	3
GNSF	Green sunfish	*Lepomis cyanellus*	N	Recreational	Invertivore/ carnivore	Limnophilic	Polyphil	4
GZSD	Gizzard shad	*Dorosoma cepedianum*	N	Non-game	Herbivore	Limnophilic	Lithopelagophil	3
HFCS	Highfin carpsucker	*Carpiodes velifer*	N	Commercial	Detritivore	Limno-rheophilic	Lithopelagophil	3
IODR	Iowa darter	*Etheostoma exile*	N	Non-game	Invertivore		Phytophil	3
JYDR	Johnny darter	*Etheostoma nigrum*	N	Non-game	Invertivore	Limno-rheophilic	Speleophil	3
LGPH	Logperch	*Percina caprodes*	N	Non-game	Invertivore		Lithophil	3
LKSG	Lake sturgeon	*Acipenser fulvescens*	N	Recreational	Invertivore/ herbivore	Rheophilic	Lithopelagophil	3
LMBS	Largemouth bass	*Micropterus salmoides*	N	Recreational	Invertivore/ carnivore	Limnophilic	Polyphil	4
LNGR	Longnose gar	*Lepisosteus osseus*	N	Commercial	Carnivore	Rheo-limnophilic	Phytolithophil	4
MDDR	Mud darter	*Etheostoma asprigene*	N	Non-game	Invertivore	Limno-rheophilic	Phytophil	3
MMSN	Mimic shiner	*Notropis volucellus*	N	Non-game	Invertivore/ herbivore		Phytophil	3
MNEY	Mooneye	*Hiodon tergisus*	N	Commercial	Invertivore	Rheo-limnophilic	Lithopelagophil	3
NHSK	Northern hog sucker	*Hypentelium nigricans*	N	Commercial	Invertivore/ herbivore		Lithophil	3
NTPK	Northern pike	*Esox lucius*	N	Recreational	Carnivore	Limnophilic	Phytophil	4
OSSF	Orangespotted sunfish	*Lepomis humilis*	N	Recreational	Invertivore	Limnophilic	Lithophil	3
PDSN	Pallid shiner	*Notropis amnis*	N	Non-game				
PGMW	Pugnose minnow	*Opsopoeodus emiliae*	N	Non-game	Detritivore		Speleophil	3
PNSD	Pumpkinseed	*Lepomis gibbosus*	N	Recreational	Invertivore/ carnivore	Limnophilic	Polyphil	4
PRPH	Pirate perch	*Aphredoderus sayanus*	N	Non-game	Invertivore/ carnivore		Gill chamber brooder	4
QLBK	Quillback	*Carpiodes cyprinus*	N	Commercial	Invertivore/ detritivore	Limno-rheophilic	Lithopelagophil	3
RBST	Rainbow smelt	*Osmerus mordax*	NN	Non-game	Invertivore/ carnivore		Lithopelagophil	4
RKBS	Rock bass	*Ambloplites rupestris*	N	Recreational	Invertivore/ carnivore		Polyphil	4
RRDR	River darter	*Percina shumardi*	N	Non-game	Invertivore	Rheo-limnophilic	Lithophil	3
RVCS	River carpsucker	*Carpiodes carpio*	N	Commercial	Planktivore/ detritivore	Limno-rheophilic	Lithopelagophil	3
RVRH	River redhorse	*Moxostoma carinatum*	N	Commercial	Invertivore	Rheo-limnophilic	Lithophil	3
RVSN	River shiner	*Notropis blennius*	N	Non-game	Invertivore	Rheo-limnophilic		3
SFSN	Spotfin shiner	*Cyprinella spiloptera*	N	Non-game	Invertivore/ detritivore		Speleophil	3

(*continued*)

Table A1. (*Continued*)

Fish code	Common name	Scientific name	Native or non-native[a]	Exploitation status	Feeding guild	Habitat guild	Reproductive guild	Trophic status
SGER	Sauger	*Sander canadense*	N	Recreational	Invertivore/ carnivore	Rheo-limnophilic	Lithopelagophil	4
SHDR	Slenderhead darter	*Percina phoxocephala*	N	Non-game	Invertivore		Lithophil	3
SHRH	Shorthead redhorse	*Moxostoma macrolepidotum*	N	Commercial	Invertivore	Rheo-limnophilic	Lithophil	3
SJHR	Skipjack herring	*Alosa chrysochloris*	N	Recreational	Planktivore	Rheo-limnophilic	Phytolithophil	3
SKCB	Speckled chub	*Macrhybopsis aestivalis*	N	Non-game	Invertivore	Rheophilic	Lithopelagophil	3
SMBF	Smallmouth buffalo	*Ictiobus bubalus*	N	Commercial	Invertivore/ herbivore	Pelagic Limno-rheophilic	Lithopelagophil	3
SMBS	Smallmouth bass	*Micropterus dolomieu*	N	Recreational	Invertivore/ carnivore	Limno-rheophilic	Polyphil	4
SNGR	Shortnose gar	*Lepisosteus platostomus*	N	Commercial	Carnivore	Rheo-limnophilic	Phytophil	4
SNSG	Shovelnose sturgeon	*Scaphirhynchus platorynchus*	N	Commercial	Invertivore	Rheophilic	Lithopelagophil	3
SNSN	Sand shiner	*Notropis stramineus*	N	Non-game	Invertivore/ detritivore	Rheo-limnophilic		3
SPSK	Spotted sucker	*Minytrema melanops*	N	Commercial	Invertivore	Limno-rheophilic	Lithopelagophil	3
STCT	Stonecat	*Noturus flavus*	N	Non-game	Invertivore/ carnivore	Rheophilic	Speleophil	4
STSN	Spottail shiner	*Notropis hudsonius*	N	Non-game	Invertivore/ planktivore	Limno-rheophilic	Lithopelagophil	3
SVCB	Silver chub	*Macrhybopsis storeriana*	N	Non-game	Planktivore/ invertivore	Rheophilic	Lithopelagophil	3
SVLP	Silver lamprey	*Ichthyomyzon unicuspis*	N	Non-game	Carnivore		Lithophil	4
SVMW	Mississippi silvery minnow	*Hybognathus nuchalis*	N	Non-game	Detritivore	Rheo-limnophilic	Lithopelagophil	3
SVRH	Silver redhorse	*Moxostoma anisurum*	N	Commercial	Invertivore	Limno-rheophilic	Lithophil	3
TPMT	Tadpole madtom	*Noturus gyrinus*	N	Non-game	Invertivore/ planktivore	Limnophilic	Speleophil	3
TTPH	Trout perch	*Percopsis omiscomaycus*	N	Non-game	Invertivore/ carnivore		Lithophil	4
WDSN	Weed shiner	*Notropis texanus*	N	Non-game	Detritivore	Limno-rheophilic		3
WLYE	Walleye	*Sander vitreum*	N	Recreational	Invertivore/ carnivore	Limno-rheophilic	Lithopelagophil	4
WRMH	Warmouth	*Lepomis gulosus*	N	Recreational	Invertivore/ carnivore	Limnophilic	Lithophil	4
WSDR	Western sand darter	*Ammocrypta clara*	N	Non-game	Invertivore	Rheophilic	Psammophil	3
WTBS	White bass	*Morone chrysops*	N	Recreational	Invertivore/ carnivore	Pelagic rheo-limnophilic	Phytolithophil	4
WTCP	White crappie	*Pomoxis annularis*	N	Recreational	Invertivore/ carnivore	Limnophilic	Phytophil	4
WTSK	White sucker	*Catostomus commersoni*	N	Commercial	Invertivore/ detritivore		Lithopelagophil	3
YLBH	Yellow bullhead	*Ameiurus natalis*	N	Commercial	Invertivore/ carnivore	Limnophilic	Speleophil	4
YWBS	Yellow bass	*Morone mississippiensis*	N	Recreational	Invertivore/ carnivore	Pelagic rheo-limnophilic	Phytolithophil	4
YWPH	Yellow perch	*Perca flavescens*	N	Recreational	Invertivore/ carnivore	Limno-rheophilic	Phytolithophil	4

[a]Native, N; non-native, NN.