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FEATURED PAPER

Understanding Fish Assemblage Structure in Lentic Ecosystems: Relative Effects of Abiotic Factors and Management Legacies

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Abstract

We investigated associations of fish assemblages and habitat characteristics (e.g., morphology and water chemistry) from 45 natural lakes and reservoirs in Iowa to determine whether species or trophic guild composition and environmental correlations were concordant between waterbodies of different origins. Overall, fish assemblage composition between natural lakes and reservoirs was consistently dissimilar based on a permutational multivariate ANOVA. Species composition from nonmetric multidimensional scaling ordinations for reservoirs was correlated with a variety of limnological and physical characteristics, whereas species composition and trophic composition of natural lakes were weakly associated with habitat characteristics. Species richness was positively related to waterbody and watershed size for reservoirs but not for natural lakes. Conversely, species richness was negatively correlated with increasing eutrophic conditions in natural lakes but not in reservoirs. Overall, distinct differences in assemblage composition were observed between natural and artificial lentic ecosystems and may have resulted from underlying differences in limnological, physical, and anthropogenic influences between systems. Dissimilar management legacies between waterbody types, such as limited or no stocking of nonrecreationally important species and the use of piscicides, may have additionally had overriding effects on the observed assemblage-environmental relationships. For instance, lower trophic richness and species richness in reservoirs appeared to have resulted from replacement of a diversity of small-bodied native species by relatively few commonly stocked sport fishes. Our results emphasize the need to consider waterbody origin and the potential influence of historical or current management strategies on fish assemblage characterization and subsequent inferences made from environmental correlations.

Fish assemblage composition and structure in lentic ecosystems have long been of interest to community ecologists, largely because both natural and artificial lakes possess characteristics that are analogous to islands (e.g., discrete, isolated, repeated units; Barbour and Brown 1974; Brown 1981). Consequently, numerous studies have evaluated the influence of environmental characteristics on fish assemblage composition in natural lakes (e.g., Tonn and Magnuson 1982; Eadie et al. 1986; Jackson and Harvey 1993; Magnuson et al. 1998; Wehrly et al. 2012). Fish assemblages in artificial lentic habitats (i.e., reservoirs) have received considerably less attention (Irz et al. 2002, 2006; Miranda et al. 2008) beyond that focusing solely on recreationally valuable species. Although sport fish population information is undoubtedly important to understanding complex lacustrine ecosystems, evaluation of fish composition structure and potential influences of environmental conditions is necessary to inform

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monitoring, research, and management strategies in both natural and artificial systems (Guy and Willis 1995; Launois et al. 2011; Menezes et al. 2013).

Distinct differences between natural lakes and reservoirs present potential challenges to fisheries research and management but also provide an opportunity to understand how lentic fish assemblages are structured by widely varying physical and chemical characteristics. For instance, structurally complex habitats are often assumed to support a greater diversity of species and functional traits than simpler habitats (Klopfer and MacArthur 1960), and reservoirs provide an opportunity to understand whether patterns of assemblage structure in natural lakes are upheld in artificial ecosystems. Comparisons of lakes and reservoirs are also necessary to determine whether similar responses to anthropogenic factors or monitoring would be expected despite dissimilarity in origin and associated habitat characteristics. Reservoirs commonly exhibit characteristics of lacustrine and riverine ecosystems (Wetzel 2001) and often have potential for increased habitat complexity (e.g., shoreline development; Kalff 2002) as a result of impounding dendritic river valleys; therefore, they may have the potential to support a greater number of species than natural lakes. Miranda et al. (2008) observed that species richness generally increased as large-bodied riverine specialists were added to downstream reservoirs in a connected system. However, Gido et al. (2009) observed a reduced species pool in reservoirs relative to streams and rivers in similar geographic regions, suggesting limited persistence or contribution of lotic species to the fish assemblages of reservoirs. Despite the potential for similar environmental regulation of biotic communities between waterbody types, comparative ecological studies of lake and reservoir fish assemblage structure are uncommon (e.g., Irz et al. 2006, 2007) but can provide guidance for the conservation, management, and restoration of these similar systems (Irz et al. 2006, 2007; Launois et al. 2011).

Comparisons of reservoirs and natural lakes are primarily warranted because both ecosystems have the propensity to share comparable fish faunas-and thus may be managed similarly (Guy and Willis 1995)-as a result of the widespread introduction of lentic species for recreational purposes. Stocking of sport fishes to enhance and establish fisheries is common in reservoirs and natural lakes, and many sport fish species are widely distributed across North America. Stocking of sport fish or other recreationally associated species (e.g., prey species) can both directly and indirectly influence the occurrence of other fish species. For example, species richness in natural lakes was positively associated with sport fish stocking intensity and was attributed to unintentional introductions of nontarget species from anglers (i.e., bait bucket sources) and hatchery rearing ponds in Minnesota (Radomski and

Goeman 1995). Sport fish introductions in reservoirs may also directly decrease native fish biodiversity and increase biotic homogenization of connected lotic fish assemblages through competition, predation, and displacement (Clavero and Hermoso 2011). Therefore, an understanding of patterns in fish assemblage composition and abundance in lentic ecosystems requires an understanding of environmental relationships as well as historical management actions.

Because previous research on lentic fish assemblageenvironmental relationships has primarily focused either on reservoirs (e.g., Miranda et al. 2008) or on natural lakes (e.g., Tonn and Magnuson 1982), the goal of our study was to examine the influence of physicochemical characteristics on fish assemblage species and trophic structure in both of these lentic ecosystem types. We chose reservoirs and natural lakes within a spatially limited extent (i.e., Iowa) to increase the understanding of factors regulating fish assemblages in both ecosystems. We hypothesized that connectivity to lotic environments in reservoirs and the presence of riverine species would distinguish their fish assemblages and environmental relationships from those in natural lakes. However, ubiquitous and recreationally important species (i.e., stocked sport fish) would likely increase similarity of fish faunas between natural lakes and reservoirs despite any inherent differences in habitat characteristics. The specific objectives of our study were to (1) determine whether the relation between broad physical and chemical features and fish assemblage structure is consistent between natural lakes and reservoirs and (2) identify possible factors responsible for dissimilarities in fish assemblages between artificial and natural lentic ecosystems.

METHODS

This study was conducted in Iowa within the agriculturally dominated Western Corn Belt Plains ecoregion of the Mississippi River basin. Standing waterbodies in Iowa are among the most eutrophic environments in the world due to the predominance of row-crop agriculture across the landscape (Arbuckle and Downing 2001). The presence of both natural (i.e., glacially formed lakes) and artificial (i.e., reservoirs) lentic ecosystems in Iowa provided an opportunity to understand fish assemblage structure dynamics from a limited geographic extent and similar source populations of native species. Overall, 45 lakes and reservoirs across Iowa were selected to represent the range of physical and water quality conditions present in Iowa's lentic ecosystems (Table 1). Furthermore, lakes and reservoirs were selected to encompass major drainage basins throughout Iowa and to limit the influence of zoogeography on assemblage comparisons. Natural lakes and reservoirs were selected from a subset of Iowa's approximately

		Natural		Reservoirs $(n = 31)$						
Variable	Mean	Median	SD	Min	Max	Mean	Median	SD	Min	Max
Surface area (ha)	664	402	683	47.8	2174	95.5	46.7	112	10.0	352
Watershed area (ha)	3,546	4,055	2,443	75.8	6,948	2,913	990	4,097	81.5	18,948
Watershed area : lake surface area ratio	9.1	4.6	10.4	0.8	39.9	32.9	25.3	30.0	4.9	139
Shoreline development index	2.2	1.8	1.4	1.4	6.7	3.4	2.8	1.9	1.6	9.2
Mean depth (m)	3.2	2.5	2.6	0.9	11.6	3.5	2.9	1.4	1.0	6.7
Maximum depth (m)	7.6	4.9	9.7	1.7	40.8	9.1	9.8	4.1	3.0	17.2
Secchi depth (m)	1.2	0.6	1.4	0.3	5.6	1.4	1.2	0.7	0.5	3.5
Chlorophyll a (µg/L)	38.0	32.1	30.6	3.6	132	34.0	29.1	23.1	5.2	105.6
Total phosphorus (µg/L)	108	106	44.5	36.3	192	95.6	74.3	77.7	33.0	412.5
Total nitrogen (µg/L)	1.6	1.4	0.7	0.7	3.4	2.8	1.5	2.8	0.7	10.6
Total suspended solids (mg/L)	24.1	27.9	12.6	3.4	46.2	13.4	10.1	10.8	5.7	57.7
Watershed soil loss $(T \cdot ha^{-1} \cdot year^{-1})$	6.0	6.7	1.6	0.3	11.3	16.9	15.0	4.9	1.6	45.8

TABLE 1. Physicochemical characteristics of 45 lentic waterbodies located in Iowa (Min = minimum; Max = maximum).

5,400 lentic waterbodies defined as significant publicly owned lakes (SPOLs) by the Iowa Department of Natural Resources (IADNR). The IADNR defined SPOLs identified in the Lake Restoration Program as waterbodies with the following characteristics: a surface area of at least 4 ha (10 acres); a watershed area : lake surface area ratio of less than 200:1; maintained principally for public use; capable of supporting viable sport fisheries and recreational opportunities; not a federal flood control impoundment; and not solely used as a water supply reservoir (IADNR 2011).

All 45 lentic ecosystems were sampled a total of three times annually (May 1-August 31 in 2000-2010) for measures of water clarity (i.e., Secchi depth [m] and total suspended solids [mg/L]), total nitrogen and total phosphorus $(\mu g/L)$, and chlorophyll *a* $(\mu g/L)$. Detailed methodology of the techniques used for the collection, processing, and analysis of water chemistry samples is described by Egertson and Downing (2004). Averages of mean annual values were estimated using all years prior to fish assemblage sampling for each waterbody to characterize individual lake and reservoir water chemistry. Additional physical covariates included mean depth (m), maximum depth (m), surface area (ha), watershed area (ha), watershed area : lake surface area ratio, and shoreline development index. Estimated watershed soil loss (metric tons [T]·ha⁻¹·year⁻¹) was estimated for each waterbody by using a geographical information system based on the Revised Universal Soil Loss Equation (Renard et al. 1997). Environmental covariates selected for analyses included those previously identified as important in structuring lentic fish assemblages (Jackson and Harvey 1993; Irz et al. 2007; Miranda et al. 2008).

We included environmental covariates that were highly correlated (e.g., Spearman's rank correlation coefficient $[r_s] \ge 0.70$; Table 2) because the ordination methods (see below) used to evaluate assemblage–environmental relations were robust to correlations between covariates. We also assumed that differences between lake and reservoir ecosystems may result in dissimilar regulation of assemblage structure despite high correlation. For example, Secchi depth and total phosphorus were highly correlated ($r_s = -0.74$, P < 0.0001), but both were retained in our analysis because they indicate features that likely regulate assemblage structure differently. Decreased water clarity or high total phosphorus can result because of system-specific mechanisms (i.e., internal versus external nutrient loading) that may differ between lentic waterbody types.

Quantification of fish assemblages in both natural and artificial lentic habitats is complex because multiple sampling methods are necessary to account for temporally dynamic selectivity of species and other important assemblage and population characteristics (e.g., size structure and trophic structure; Austen 1992; Jackson and Harvey 1997; Fischer and Quist 2014a, 2014b). Sampling biases in lentic ecosystems can often be the result of distinct zones (i.e., pelagic and littoral) and habitat characteristics (e.g., morphology and water chemistry), which can be exaggerated in reservoirs relative to natural lakes (Menezes et al. 2013). Therefore, fish assemblage sampling in our study used a variety of passive and active sampling methods that were selected to maximize the number of fish species and individuals sampled while reducing biases associated with waterbody type (Fischer and Quist 2014a).

Benthic trawling, boat electrofishing, and modified fyke-netting were used to characterize fish assemblage composition from all 45 waterbodies in 2008–2011. Sampling of an individual waterbody occurred between July and October to minimize temporal variation among individual waterbody fish samples, yet exploit known sampling biases in species representation among seasons (Fischer and Quist 2014a, 2014b). Juveniles and small-bodied

TABLE 2. Spearman's rank correlation coefficients for surface area (ha), watershed area (WS area; ha), watershed area : lake surface area ratio (W–L ratio), shoreline development index (DL), mean depth (m), maximum depth (max depth; m), Secchi depth (m), chlorophyll *a* (Chl *a*; $\mu g/L$), total phosphorus (TP; $\mu g/L$), total nitrogen (TN; $\mu g/L$), total suspended solids (TSS; $\mu g/L$), and estimated watershed soil loss (T·ha⁻¹·year⁻¹) of 45 lentic waterbodies located in Iowa. Correlation coefficients with $P \le 0.05$ are indicated in bold italics.

Variable	Surface area	WS area	W–L ratio	DL	Mean depth	Max depth	Secchi depth	Chl a	TP	TN	TSS
WS area	0.75										
W–L ratio	-0.37	0.27									
DL	0.03	0.30	0.48								
Mean depth	0.22	0.34	0.11	0.37							
Max depth	0.12	0.29	0.20	0.56	0.89						
Secchi depth	-0.12	0.10	0.22	0.28	0.77	0.69					
Chl a	-0.13	-0.25	-0.11	-0.17	-0.79	-0.67	-0.81				
ТР	-0.05	-0.17	-0.13	-0.35	-0.81	-0.78	-0.74	0.80			
TN	0.01	0.27	0.41	0.04	-0.21	-0.24	-0.28	0.40	0.51		
TSS	0.04	-0.13	-0.18	-0.40	-0.84	-0.78	<i>-0.94</i>	0.83	0.83	0.38	
Watershed soil loss	-0.20	0.13	0.48	0.32	0.21	0.24	0.14	-0.02	-0.08	0.13	-0.16

fish that were associated with benthic and littoral habitats were sampled with a benthic trawl. Trawl dimensions included a headrope length of 2.4 m, footrope length of 3.7 m, and upright height of 0.6 m. The body of the trawl consisted of two overlapping meshes. The small outer mesh (6.3-mm delta mesh) and larger inner mesh (34.9mm bar mesh of 1.0-mm multifilament nylon) provided protection to smaller individuals from injury and damage due to the separation of larger fish or debris (e.g., rocks) from the rest of the catch. Towlines used for the benthic trawl were 38.1 m in length to ensure a maximum effective depth of 5.4 m (assuming a 7:1 drop ratio). All trawls were conducted for 3 min at approximately 3.2 km/h perpendicular to the shores. Design, development, and further research using the benthic trawl used in our study (also referred to as the "mini-Missouri trawl") is detailed in Herzog et al. (2005), Guy et al. (2009), and Neebling and Quist (2011). Trawling occurred during the day from June 24 to July 13, when the species richness of trawl samples was found to be maximized in Iowa lakes and reservoirs (Fischer and Quist 2014a). Modified fyke nets with a $1-\times$ 2-m frame, 12.7-mm bar-measure mesh, and 15.2-m lead, as detailed by Miranda and Boxrucker (2009), were used to target and sample structure-oriented and mobile species, such as crappies *Pomoxis* spp. and sunfishes *Lepomis* spp. that often occupy littoral habitats (Hubert 1996). Modified fyke nets were set in the late afternoon prior to dusk and retrieved the following day after dawn. Boat electrofishing was used to target species that use littoral areas during the night (i.e., 30 min after sunset to 30 min before sunrise), as electrofishing catch rates have repeatedly been observed to be influenced by diel period (Sanders 1992; Reynolds 1996; McInerny and Cross 2004) and

our goal was to maximize the number of species and individuals encountered to best characterize assemblage composition (Fischer and Quist 2014a). All electrofishing was conducted parallel to the shoreline for 5 min, with two netters using dip nets with 6.3-mm delta mesh. Pulsed-DC electrofishing output was standardized between waterbodies following Burkhardt and Gutreuter (1995), Miranda and Boxrucker (2009), and Miranda (2009). Sampling using boat electrofishing and modified fyke nets was conducted between September 14 and November 3 in the same year as the benthic trawl. Fish were identified to species in the field and were released when possible. Unidentifiable specimens were preserved using a 10% formalin solution for later identification in the laboratory. The CPUE was estimated for all species individually for each waterbody as the mean number of individuals per haul for trawls, the mean number of individuals per net-night for modified fyke nets, and the mean number of individuals per hour of electrofishing.

The number of samples allocated to each waterbody was determined based on surface area, with larger systems receiving a greater number of samples. Natural lakes and reservoirs with surface areas of less than 101 ha received 10 samples, those with 102–202 ha received 12 samples, those with 203–405 ha received 15 samples, and those greater than 405 ha received 20 samples of each sampling method. To ensure that a diversity of habitats was represented and assemblage composition was representative of each system, a systematic random sampling design was used to allocate samples. Specifically, the shoreline length of each waterbody was divided into segments based on the number of samples (see above) that included at least one randomly located shoreline reach from each of the three sampling methods. Sampling reaches for different gears did not overlap and were a minimum of 200 m apart.

A permutational multivariate ANOVA (PERMA-NOVA) on the Bray-Curtis dissimilarity matrices of habitat covariates was used to test for differences in physical and limnological characteristics between natural lakes and reservoirs. The PERMANOVA is a nonparametric test that can directly partition variation from dissimilaritybased matrices; it does not rely on an assumption that the data are multivariate normal (Anderson 2001) and it is well suited for ecological assemblage data. Additionally, the PERMANOVA estimates a multivariate analogue to Fisher's *F*-ratio and permutational-derived *P*-value (Anderson 2001). Finally, if differences in habitat characteristics between natural lakes and reservoirs were observed (i.e., $P \le 0.05$), a Wilcoxon test was used to evaluate differences between waterbody types for individual environmental covariates.

Trophic categories were assigned to individual species and were based on those proposed by Goldstein and Simon (1999). Specific trophic categories used in our comparison included herbivores, detritivores, planktivores, invertivores, and carnivores. Trophic guilds were combined to account for species that belonged to more than one trophic category during different life history stages following Miranda et al. (2008). The combined classifications included invertivore-carnivore, invertivore-detritivore, invertivore-herbivore, planktivore-detritivore, and planktivore-invertivore. Differences in trophic richness and the relative abundance of trophic categories between waterbody types were evaluated with individual Wilcoxon rank-sum tests if differences in assemblage structure were observed (PERMANOVA: $P \le 0.05$). Species or guilds that were considered rare were defined as those occurring at less than 5% of the waterbodies and were subsequently excluded from analyses.

Nonmetric multidimensional scaling (NMDS) was used to identify patterns of fish assemblage structure in the study systems. Nonmetric multidimensional scaling is a nonparametric ordination method based on rank order distances and does not rely on assumptions of data distributions or the form of relationship (e.g., linear) among variables (McCune and Grace 2002). Because NMDS is an iterative ordination technique, goodness of fit is measured with a stress value represented as a percentage. Ordinations with stress greater than 0.20 are generally considered uninterpretable, while stress values less than 0.20 are increasingly considered to be representative of the data structure considered (Kruskal 1964; Clarke 1993; McCune and Grace 2002). All NMDS ordinations were performed with up to 10 dimensions, and individual scree plots of stress and dimensions were used to reduce and select the most appropriate number of dimensions for further interpretation (McCune and Grace 2002). Fish assemblage composition was evaluated separately for each of the sampling methods (i.e., trawl, modified fyke net, and electrofishing) to reduce the effect of sampling bias associated with using a single sampling gear and the inability to combine indices of relative abundance from multiple sampling methods. Fish composition data used in the NMDS analyses consisted of species CPUE and trophic guild CPUE. The NMDS ordinations were conducted using Bray–Curtis dissimilarity matrices of fish assemblage data.

Fish assemblage composition differences between natural lakes and reservoirs were tested using PERMANOVA. Similar to the NMDS analysis, the PERMANOVAs were conducted separately for each sampling method and each assemblage composition measure (i.e., species and trophic). If differences in fish assemblage composition between natural lakes and reservoirs were observed using the PERMANOVA (i.e., $P \le 0.05$), the similarity percentage (i.e., SIMPER) was estimated to evaluate the contributions of species or trophic guilds to the overall Bray-Curtis dissimilarity. Additionally, correlations between physicochemical and morphometric characteristics of lentic ecosystems and fish assemblage composition were evaluated using rotational vector fitting (Faith and Norris 1989). Vector fitting with NMDS ordinations was used to identify significantly correlated environmental vectors and to evaluate the direction of the maximum correlation. Environmental vector significance ($P \le 0.05$) was estimated using 999 random permutations of the data (Faith and Norris 1989). Rotational vector fitting analysis was conducted for combined assemblage data and ecosystemspecific (i.e., natural lake or reservoir) NMDS ordinations.

Correlations between species richness observed from combining all sampling methods with physicochemical and morphometric characteristics of lentic ecosystems were evaluated using Spearman's rank correlation. Correlations were estimated for combined data and natural lakes and reservoirs separately for comparison to assemblage composition analyses. All statistical analyses were conducted using the program R (R Core Team 2016).

RESULTS

Physicochemical characteristics among waterbodies were highly variable but generally overlapped between natural lakes and reservoirs (Table 1). Overall, physicochemical characteristics differed between natural lakes and reservoirs (PERMANOVA: $F_{1, 43} = 3.57$, P = 0.026). Natural lakes tended to be larger (W = 49, P < 0.0001) and to have a smaller watershed area : lake surface area ratio (W = 381, P < 0.0001), lower shoreline development index values (W = 349, P = 0.001), shallower maximum depths (W = 327, P = 0.007), lower water clarity (W = 313, P =0.019), higher suspended solids (W = 121, P = 0.019), and

FISCHER AND QUIST

TABLE 3. Fishes sampled from 45 waterbodies across Iowa in 2008–2011. Species without abbreviated species codes occurred at fewer than 5% of the waterbodies sampled and were removed from taxonomic analyses. Trophic categories assigned to species were based on those proposed by Goldstein and Simon (1999) and were combined to account for species that belonged to more than one trophic category during different life history stages following Miranda et al. (2008).

Family and species	Code	Trophic category
Lepisosteidae		
Shortnose Gar Lepisosteus platostomus	SNGR	Carnivore
Clupeidae		
Gizzard Shad Dorosoma cepedianum	GZSD	Detritivore
Cyprinidae		
Spotfin Shiner Cyprinella spiloptera		Invertivore-detritivore
Golden Shiner Notemigonus crysoleucas	GLDS	Invertivore-herbivore
Emerald Shiner Notropis atherinoides		Planktivore
Spottail Shiner Notropis hudsonius	SPTS	Planktivore-invertivore
Sand Shiner Notropis stramineus		Planktivore-invertivore
Bluntnose Minnow Pimephales notatus	BNMW	Detritivore
Bullhead Minnow Pimephales vigilax	BHMW	Invertivore-herbivore
Fathead Minnow Pimephales promelas	FHMW	Invertivore-herbivore
Goldfish Carassius auratus		Invertivore-detritivore
Grass Carp Ctenopharyngodon idella	GCRP	Herbivore
Common Carp Cyprinus carpio	CCRP	Invertivore-detritivore
Catostomidae		
River Carpsucker Carpiodes carpio	RVCS	Planktivore-detritivore
Quillback Carpiodes cyprinus	QBCS	Invertivore-detritivore
White Sucker Catostomus commersonii	WHSK	Invertivore-detritivore
Smallmouth Buffalo Ictiobus bubalus	SMBF	Invertivore-detritivore
Bigmouth Buffalo Ictiobus cyprinellus	BMBF	Invertivore
Shorthead Redhorse Moxostoma macrolepidotum		Invertivore
Ictaluridae		
Black Bullhead Ameiurus melas	BLBH	Invertivore-carnivore
Yellow Bullhead Ameiurus natalis	YLBH	Invertivore-carnivore
Channel Catfish Ictalurus punctatus	CHCF	Invertivore-carnivore
Flathead Catfish Pylodictis olivaris	FHCF	Invertivore-carnivore
Tadpole Madtom Noturus gyrinus		Invertivore
Esocidae		
Northern Pike Esox lucius	NOPK	Carnivore
Muskellunge Esox masquinongy	MSKL	Carnivore
Salmonidae		
Rainbow Trout Oncorhynchus mykiss		Invertivore-carnivore
Percopsidae		
Trout-perch Percopsis omiscomaycus		Invertivore
Gasterosteidae		
Brook Stickleback Culaea inconstans		Planktivore-invertivore
Moronidae		
White Bass Morone chrysops	WHBS	Invertivore-carnivore
Yellow Bass Morone mississippiensis	YLBS	Invertivore–carnivore
White Bass × Striped Bass Morone saxatilis	HYSB	Invertivore–carnivore
Centrarchidae	a) 12-	
Green Suntish Lepomis cyanellus	GNSF	Invertivore–carnivore
Pumpkinseed Lepomis gibbosus	PMKS	Invertivore
Orangespotted Sunfish Lepomis humilis	OSSF	Invertivore
Warmouth Lepomis gulosus		Invertivore-carnivore

TABLE 3. Co	ontinued.
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Family and species	Code	Trophic category
Bluegill Lepomis macrochirus	BLGL	Invertivore
Redear Sunfish Lepomis microlophus	RESF	Invertivore
Smallmouth Bass Micropterus dolomieu	SMBS	Invertivore-carnivore
Spotted Bass Micropterus punctulatus		Invertivore-carnivore
Largemouth Bass Micropterus salmoides	LMBS	Invertivore-carnivore
White Crappie Pomoxis annularis	WHCP	Invertivore-carnivore
Black Crappie Pomoxis nigromaculatus	BLCP	Invertivore-carnivore
Percidae		
Iowa Darter Etheostoma exile	IADT	Invertivore
Johnny Darter Etheostoma nigrum	JNDT	Invertivore
Orangethroat Darter Etheostoma spectabile	OTDT	Invertivore
Northern Logperch Percina caprodes	LGPH	Invertivore
Yellow Perch Perca flavescens	YLPH	Invertivore-carnivore
Sauger Sander canadensis		Invertivore-carnivore
Walleye Sander vitreus	WLYE	Invertivore-carnivore
Sciaenidae		
Freshwater Drum Aplodinotus grunniens	FWDM	Invertivore-carnivore

lower estimated watershed soil loss (W = 375, P = 0.0001) than reservoirs. Watershed size, mean depth, total nitrogen, total phosphorus, and chlorophyll-*a* concentration were similar between waterbody types (P > 0.05).

In total, 51 species (including a Striped Bass Morone saxatilis hybrid) and 149,108 individuals were sampled from all waterbodies (combining all sampling methods; Table 3). Electrofishing sampled the greatest number of species (43) and sampled three species exclusively (Spotfin Shiner, Sand Shiner, and Goldfish). Modified fyke-netting sampled 38 species and was the only method to sample Shortnose Gar, River Carpsucker, and Shorthead Redhorse. Trawling sampled the fewest total species (34) but was the only method to sample Trout-perch and Brook Stickleback. Nine species were exclusive to natural lakes: Shortnose Gar, Spottail Shiner, River Carpsucker, Shorthead Redhorse, Tadpole Madtom, Trout-perch, Brook Stickleback, Iowa Darter, and Northern Logperch. In contrast, Sand Shiner, Goldfish, Rainbow Trout, Warmouth, and Spotted Bass were only sampled in reservoirs. Several species were ubiquitous (>80% of waterbodies sampled), particularly sport fishes (Channel Catfish: 37 of 45 waterbodies; Green Sunfish: 40 of 45; Largemouth Bass: 44 of 45; and Black Crappie: 44 of 45). Only Bluegill was sampled in every waterbody included in our study. Species richness varied from 10 to 30 (overall mean \pm SE = 20.6 \pm 1.5 species) for natural lakes and from 5 to 22 (10.7 \pm 0.7 species) for reservoirs and differed between waterbody types (W = 41, P < 0.0001).

Nearly all of the 10 trophic guilds used to characterize species sampled across waterbodies were present among sampling methods. Only the planktivore guild was absent from fyke nets, and night electrofishing sampled all trophic categories except planktivore–detritivore. Trawling samples lacked fish composing the herbivore and planktivore–detritivore guilds but sampled the other eight guilds evaluated. Waterbody-type-specific absences of trophic guilds were also common among sampling gears. Carnivores and planktivores were not present in trawl samples from natural lakes, whereas no planktivore–invertivores were sampled with trawling in reservoirs. Similarly, fyke nets did not sample planktivore–invertivores were the only trophic guild not sampled with fyke nets in natural lakes.

Trophic richness differed between waterbody types (W = 492, P < 0.0001) and varied from 3 to 8 guilds (mean \pm SE = 5.8 \pm 0.4 guilds) for natural lakes and from 2 to 6 guilds (3.5 ± 0.2 guilds) for reservoirs. Planktivore-invertivore catches were higher in natural lakes with the benthic trawl (W = 431, P < 0.0001), fyke nets (W = 415, P = 0.0001), and night electrofishing (W = 426, P = 0.0001), whereas invertivore catch was higher in reservoirs for fyke nets (W = 187, P = 0.001) and night electrofishing (W = 162, P < 0.0001). Natural lakes also exhibited higher catches of the invertivore-detritivore (trawling: W = 432, P = 0.0017; fyke nets: W = 437, P = 0.0037), planktivore-detritivore (fyke nets: W = 384, P < 0.0023), and carnivore (fyke nets: W = 456, P = 0.0011) guilds.

The NMDS ordinations of species composition data from reservoirs and natural lakes produced stable solutions for samples from the benthic trawl (2 axes; stress = 0.16; Figure 1), modified fyke nets (2 axes; stress = 0.14; Figure 2), and night electrofishing (2 axes; stress = 0.14; Figure 3). Results from the PERMANOVA indicated that fish species assemblage composition differed between natural lakes and reservoirs for sampling with the benthic

trawl ($F_{1, 43} = 2.38$, P = 0.005), modified fyke nets ($F_{1, 43} = 6.80$, P = 0.001), and night electrofishing ($F_{1, 43} = 12.5$, P < 0.001). Species that contributed to the overall dissimilarity between natural lakes and reservoirs included



FIGURE 1. Nonmetric multidimensional scaling (NMDS) ordinations of species composition (upper panels) and trophic composition (lower panels) for natural lakes (open circles) and reservoirs (solid circles), with 90% confidence ellipses, for summer benthic trawling fish assemblage data collected from 45 waterbodies in Iowa, 2008–2011. Environmental vectors indicate the direction and strength of significant ($P \le 0.05$) correlations within the NMDS ordination for lake surface area (L_Size; ha) and watershed area (WS_Size; ha). Species codes are defined in Table 3.



FIGURE 2. Nonmetric multidimensional scaling (NMDS) ordinations of species composition (upper panels) and trophic composition (lower panels) for natural lakes (open circles) and reservoirs (solid circles), with 90% confidence ellipses, for fall modified fyke-netting fish assemblage data collected from 45 waterbodies in Iowa, 2008–2011. Environmental vectors indicate the direction and strength of significant ($P \le 0.05$) correlations within the NMDS ordination for chlorophyll-*a* concentration (Chla; μ g/L), lake surface area (L_Size; ha), mean waterbody depth (Mn_Depth; m), maximum waterbody depth (Mx_Depth; m), Secchi disc depth (Secchi; m), total nitrogen concentration (TN; μ g/L), total phosphorus concentration (TP; μ g/L), total suspended solids concentration (TSS; mg/L), watershed area (WS_Size; ha), and watershed area : lake surface area ratio (WS_Ratio). Species codes are defined in Table 3.

invertivore–carnivore (58.1% contribution) and invertivore (38.1%) for modified fyke nets and invertivore (58.1%) and invertivore–carnivore (32.6%) for night electrofishing.

Similar to species composition, NMDS ordinations of trophic composition produced stable solutions for the benthic trawl (2 axes; stress = 0.07; Figure 1), modified fyke



FIGURE 3. Nonmetric multidimensional scaling (NMDS) ordinations of species composition (upper panels) and trophic composition (lower panels) for natural lakes (open circles) and reservoirs (solid circles), with 90% confidence ellipses, for fall night electrofishing fish assemblage data collected from 45 waterbodies in Iowa, 2008–2011. Environmental vectors indicate the direction and strength of significant ($P \le 0.05$) correlations within the NMDS ordination for lake surface area (L_Size; ha), Secchi disc depth (Secchi; m), watershed area : lake surface area ratio (WS_Ratio), and watershed area (WS_Size; ha). Species codes are defined in Table 3.

nets (2 axes; stress = 0.09; Figure 2), and night electrofishing (2 axes; stress = 0.11; Figure 3). Trophic guild assemblage composition between reservoirs and natural lakes was similar when using data from the benthic trawl $(F_{1, 43} = 0.99, P = 0.388)$ but differed for modified fyke nets $(F_{1, 43} = 9.39, P < 0.001)$ and night electrofishing $(F_{1, 43} = 7.26, P < 0.001)$. Trophic groups that contributed to the overall dissimilarity between natural lakes and

reservoirs included Black Crappie (21.6% contribution), Bluegill (19.1%), and Yellow Perch (11.6%) for the benthic trawl; Bluegill (28.1%), Black Crappie (16.9%), Black Bullhead (12.6%), and Freshwater Drum (11.0%) for modified fyke nets; and Bluegill (38.6%) and Yellow Bass (17.8%) for night electrofishing.

Separate NMDS ordinations of fish species composition from the benthic trawl data resulted in stable ordinations for natural lakes (2 axes; stress = 0.13; Table 4; figure not shown) and reservoirs (4 axes; stress = 0.07; Table 4; figure not shown). Modified fyke net species assemblage NMDS resulted in stable ordinations for natural lakes (2 axes; stress = 0.15) and reservoirs (2 axes; stress = 0.10). Stable NMDS ordinations for species composition using night electrofishing were obtained for natural lakes (3 axes; stress = 0.08) and reservoirs (2 axes; stress = 0.10). Similar to species composition, stable NMDS ordinations were obtained for trophic composition data from natural lakes for sampling with the benthic trawl (2 axes: stress = 0.12). modified fyke nets (2 axes; stress = 0.05), and night electrofishing (2 axes; stress = 0.08). Reservoir NMDS ordinations for trophic assemblage data from benthic trawl sampling (2 axes; stress = 0.07), modified fyke nets (2 axes; stress = 0.07), and night electrofishing (2 axes; stress = 0.07) resulted in stable ordinations.

Environmental vector fitting for combined NMDS ordinations of species composition data revealed substantial differentiation of reservoir and natural lake assemblage composition along a gradient of waterbody size for all three sampling gears (Figures 1-3). Other significantly correlated physicochemical variables were primarily associated with NMDS axis 2 (modified fyke net: Figure 2; night electrofishing: Figure 3), suggesting limited influence on the separation of species composition between reservoirs and natural lakes. Environmental vector fitting for individual NMDS ordinations illustrated inconsistent patterns of habitat relationships between waterbody types. For instance, the combined NMDS ordination of fish species sampled with modified fyke nets illustrated significant correlations for all of the physicochemical variables included in our evaluation except the shoreline development index, maximum depth, and watershed soil loss (Figure 2), similar to the reservoir-only analysis (Table 4). However, total nitrogen was the only factor related to natural lake species composition from modified fyke net data (Table 4).

Similar to species composition, the environmental vector fitting for combined NMDS ordinations of trophic assemblage composition indicated that waterbody size differentiated reservoirs and natural lakes based on modified fyke net and electrofishing data (Table 4; Figures 2, 3). However, inconsistent patterns of correlated environmental variables were observed between individual NMDS ordinations for separate waterbody types (i.e., natural lakes and reservoirs; Table 4) among gears used to characterize trophic composition. Within waterbody types, similar environmental variables were consistently correlated for both species and trophic composition ordinations (Table 4).

Relationships between species richness and environmental variables demonstrated inconsistent patterns between natural lakes and reservoirs. Greater species richness was observed in larger waterbodies ($r_s = 0.77$, P < 0.0001; Table 5; Figure 4) with larger watersheds ($r_s = 0.61$, P =0.003) and less watershed soil loss ($r_s = -0.33$, P = 0.026) when waterbody type was ignored. Similarly, positive correlations between reservoir surface area ($r_s = 0.69$, P <0.0001) and watershed area $(r_s = 0.73, P < 0.0001)$ were observed. Reservoir species richness also increased with mean depth ($r_s = 0.45$, P = 0.01), maximum depth ($r_s =$ 0.48, P = 0.006), watershed area ($r_s = 0.73$, P < 0.0001), and shoreline development index ($r_s = 0.51$, P = 0.003; Figure 4). In contrast, fewer species were observed in natural lakes having low Secchi depth ($r_s = 0.61$, P = 0.022) and high total suspended solids ($r_s = -0.65$, P = 0.013; Figure 5). Overall, fish species richness in natural lakes was generally associated with limnological variables, whereas reservoirs appeared to be more highly influenced by morphometric characteristics.

DISCUSSION

Lentic fish assemblages are commonly shaped by a multitude of factors simultaneously acting at different scales (Eadie et al. 1986; Jackson et al. 1992, 2001; Irz et al. 2007). Overall, we consistently observed dissimilar relationships between waterbody types for the environmental variables evaluated, but we found consistent patterns of trophic and species assemblage structure within each ecosystem type. For example, the number of fish species observed from all sampling methods was related to differing habitat variables for each waterbody type. Species richness in reservoirs was highly correlated with waterbody size and habitat complexity. However, unlike Eadie et al. (1986), Irz et al. (2007), and Miranda et al. (2008), we did not observe a similar relationship between surface area and species richness in natural lakes. The lack of a relation between surface area and species richness in natural lakes may suggest that habitat diversity-the primary variable associated with species diversity as area increases (Williams 1964)-may not have been a function of surface area. Species richness in natural lakes was positively associated with water clarity and may have been indirectly associated with habitat complexity (e.g., biomass and richness of vegetation). For example, Tonn and Magnuson (1982) observed increased fish species richness in Wisconsin lakes with greater vegetation diversity. However, natural lakes can also be highly turbid systems, and

	Natural lakes				Reservoirs				Combined			
Variable	Sp	ecies	Tro	ophic	Sp	ecies	Tro	ophic	Species		Trophic	
	r^2	Р	r^2	Р	r^2	Р	r^2	Р	r^2	Р	r^2	P
				Benthic	e trawl							
Surface area	0.39	0.054	0.15	0.408	0.19	0.047	0.11	0.189	0.43	0.001	0.05	0.369
Watershed area	0.23	0.223	0.12	0.514	0.39	0.001	0.16	0.085	0.13	0.049	0.04	0.414
Watershed area : lake surface area ratio	0.35	0.114	0.03	0.832	0.31	0.007	0.13	0.140	0.06	0.278	0.07	0.205
Shoreline development index	0.01	0.942	0.02	0.884	0.09	0.248	0.06	0.442	0.10	0.096	0.03	0.569
Mean depth	0.49	0.029	0.34	0.123	0.31	0.010	0.00	0.967	0.01	0.950	0.13	0.064
Maximum depth	0.38	0.112	0.41	0.056	0.25	0.017	0.05	0.531	0.01	0.724	0.09	0.134
Secchi depth	0.33	0.135	0.32	0.138	0.33	0.006	0.02	0.736	0.02	0.701	0.07	0.207
Chlorophyll <i>a</i>	0.08	0.593	0.05	0.717	0.34	0.004	0.00	0.975	0.03	0.555	0.03	0.514
Total phosphorus	0.31	0.124	0.09	0.594	0.27	0.021	0.01	0.915	0.01	0.790	0.02	0.624
Total nitrogen	0.22	0.277	0.26	0.172	0.34	0.006	0.17	0.077	0.04	0.455	0.10	0.099
Total suspended solids	0.08	0.631	0.17	0.375	0.33	0.010	0.01	0.851	0.00	0.985	0.02	0.664
Watershed soil loss	0.12	0.503	0.04	0.810	0.09	0.313	0.33	0.003	0.12	0.070	0.11	0.080
			Γ	Modified	fvke no	et						
Surface area	0.08	0.649	0.39	0.067	0.23	0.040	0.19	0.60	0.22	0.009	0.19	0.012
Watershed area	0.38	0.074	0.23	0.238	0.43	0.001	0.39	0.002	0.30	0.003	0.37	0.001
Watershed area : lake surface area ratio	0.13	0.481	0.35	0.120	0.29	0.009	0.31	0.005	0.12	0.048	0.20	0.006
Shoreline development index	0.04	0.857	0.01	0.937	0.11	0.202	0.09	0.266	0.06	0.239	0.11	0.800
Mean depth	0.03	0.863	0.49	0.032	0.30	0.008	0.31	0.002	0.23	0.006	0.33	0.001
Maximum depth	0.35	0.864	0.38	0.111	0.22	0.036	0.25	0.015	0.16	0.034	0.25	0.001
Secchi depth	0.10	0.579	0.33	0.126	0.28	0.010	0.33	0.002	0.24	0.004	0.26	0.003
Chlorophyll <i>a</i>	0.30	0.156	0.08	0.570	0.32	0.004	0.34	0.006	0.32	0.004	0.21	0.011
Total phosphorus	0.36	0.078	0.31	0.139	0.26	0.013	0.27	0.013	0.29	0.005	0.25	0.001
Total nitrogen	0.50	0.025	0.22	0.266	0.31	0.006	0.34	0.007	0.10	0.096	0.22	0.005
Total suspended solids	0.08	0.636	0.08	0.593	0.30	0.012	0.32	0.005	0.29	0.001	0.34	0.001
Watershed soil loss	0.24	0.228	0.12	0.518	0.09	0.262	0.09	0.305	0.06	0.277	0.05	0.331
			N	ight elec	trofishi	ng						
Surface area	0.38	0.069	0.37	0.068	0.22	0.043	0.12	0.156	0.53	0.001	0.42	0.001
Watershed area	0.78	0.001	0.65	0.006	0.35	0.010	0.22	0.032	0.30	0.003	0.26	0.001
Watershed area : lake surface area ratio	0.18	0.353	0.20	0.296	0.24	0.046	0.27	0.026	0.20	0.014	0.20	0.021
Shoreline development index	0.15	0.444	0.22	0.221	0.04	0.492	0.01	0.824	0.09	0.136	0.13	0.052
Mean depth	0.16	0.425	0.08	0.708	0.21	0.036	0.15	0.095	0.11	0.95	0.07	0.207
Maximum depth	0.19	0.303	0.07	0.783	0.27	0.013	0.25	0.019	0.14	0.062	0.11	0.085
Secchi depth	0.25	0.195	0.10	0.581	0.28	0.012	0.21	0.037	0.15	0.038	0.07	0.174
Chlorophyll <i>a</i>	0.28	0.160	0.32	0.104	0.15	0.117	0.11	0.185	0.10	0.108	0.09	0.149
Total phosphorus	0.05	0.781	0.18	0.304	0.09	0.251	0.06	0.366	0.03	0.564	0.02	0.665
Total nitrogen	0.04	0.833	0.01	0.992	0.13	0.145	0.13	0.162	0.09	0.109	0.06	0.292
Total suspended solids	0.17	0.34	0.18	0.328	0.05	0.455	0.02	0.675	0.08	0.157	0.01	0.723
Watershed soil loss	0.49	0.021	0.45	0.032	0.10	0.213	0.13	0.141	0.12	0.085	0.07	0.244

TABLE 4. Physicochemical correlations for nonmetric multidimensional scaling ordinations of fish species and trophic composition for natural lakes, reservoirs, and combined fish assemblage data collected using summer benthic trawling, fall modified fyke nets, and fall night electrofishing from 2008 to 2011 in Iowa. Units for physicochemical variables are shown in Table 1. Correlation coefficients with $P \le 0.05$ are indicated in bold italics.

	Natura	al lakes	Res	ervoirs	Combined		
Variable	r _s	Р	r _s	Р	r _s	Р	
Surface area	0.17	0.551	0.69	<0.0001	0.77	<0.0001	
Watershed area	0.13	0.646	0.73	<0.0001	0.61	<0.0001	
Watershed area : lake surface area ratio	-0.17	0.571	0.33	0.068	-0.28	0.066	
Shoreline development index	0.30	0.292	0.51	0.003	-0.06	0.700	
Mean depth	0.39	0.172	0.45	0.010	0.18	0.244	
Maximum depth	0.21	0.476	0.48	0.006	0.02	0.913	
Secchi depth	0.61	0.022	0.14	0.437	-0.03	0.845	
Chlorophyll a	-0.43	0.128	-0.26	0.156	-0.18	0.247	
Total phosphorus	-0.35	0.221	-0.28	0.121	-0.04	0.815	
Total nitrogen	-0.43	0.126	0.13	0.478	-0.02	0.883	
Total suspended solids	-0.65	0.013	-0.23	0.217	-0.02	0.895	
Watershed soil loss	0.00	0.988	0.00	0.989	-0.33	0.026	

TABLE 5. Spearman's rank correlation coefficients (r_s) between selected physicochemical characteristics and species richness from natural lakes, reservoirs, and combined fish assemblage data collected using summer benthic trawling, fall modified fyke nets, and fall night electrofishing from 2008 to 2011 in Iowa. Units for physicochemical variables are shown in Table 1. Correlation coefficients with $P \le 0.05$ are indicated in bold italics.

it should be noted that our study area included some of the most eutrophic lentic environments in the world (Arbuckle and Downing 2001). Shallow, natural lakes are highly susceptible to resuspension of sediments and associated nutrients by abiotic (e.g., wind) and biotic (e.g., bioturbation) processes (Scheffer et al. 1993). Although larger lakes are more susceptible to sediment resuspension from winds and associated waves, smaller systems may be turbid for other reasons, such as bioturbation from invasive Common Carp or more erodible watersheds. Unlike natural lakes, water clarity did not appear to be strongly associated with species richness in reservoirs. Therefore, the lack of a correlation between species richness and surface area in natural lakes was likely due to the overriding influence of water clarity on assemblage composition. In contrast, the greater number of species observed in larger reservoirs was likely due to larger littoral areas and an increased capacity to support more species.

Lack of similar environmental associations observed between natural lakes and reservoirs may have resulted from differences in physical and limnological characteristics that existed between waterbody types in our selected study systems. Specifically, reservoirs were generally smaller and deeper, with greater watershed area : lake surface area ratios, greater shoreline complexity, lower suspended solids, and greater estimated watershed soil loss than natural lakes. Reduced variation within waterbody type for environmental characteristics may have limited the potential to observe environmental relationships similar to those of reservoirs. Connectivity and watershed size may have also resulted in the reduced number of species observed in reservoirs as opposed to natural lakes. Specifically, watersheds of reservoirs were smaller than those of natural lakes and indicated that streams feeding reservoirs in our study were mostly small and may not have contributed a diverse lotic fish assemblage. Connectivity to downstream habitats and lotic species was also likely reduced in reservoirs compared to natural lakes due to differences in design and construction of water-level-controlling structures. However, the observation of fewer riverine species in reservoirs relative to the available riverine species pool may have also resulted from unsuitable habitat characteristics, negative biotic interactions with the established fish fauna, or both factors. For example, the biotic structuring of natural lotic and lentic fish assemblages has developed over much longer temporal periods (i.e., thousands of years) than reservoirs constructed in the last century. Although natural lakes have undoubtedly been altered by humans, natural systems may maintain more complex ecological interactions than reservoirs (Noble 1986). We observed several ubiquitous, abundant, and commonly stocked sport fish species among both waterbody types. Concordance among multiple sampling methods suggested that juvenile and adult life stages of relatively few species (i.e., Bluegill, Black Crappie, and Largemouth Bass) largely contributed to dissimilarities between reservoirs and natural lakes. However, species richness and trophic richness were also consistently lower in reservoirs, and several species (e.g., Spottail Shiner, Iowa Darter, and Northern Logperch) occurred in almost every natural lake but were absent from reservoirs. Low diversity coupled with assemblages dominated by cosmopolitan sport fishes may have resulted in fewer habitat-fish assemblage associations observed for reservoirs compared with more speciose natural lakes.



FIGURE 4. Physical characteristics of natural lakes and reservoirs in relation to species richness for 45 waterbodies in Iowa, 2008–2011.

Legacy effects, such as historical land use (Harding et al. 1998; Maret and MacCoy 2002) and water development (Walter and Merritts 2008), often have persistent and overriding influences on fish assemblages despite improvements in contemporary water quality and terrestrial habitat quality (e.g., Clean Water Act, reforestation, and best management practices). Despite the long-lasting and substantial disruptions that historical land and water use can have on aquatic organisms, research focused on legacy effects has primarily been concentrated in lotic ecosystems (Kwak and Freeman 2010). Nevertheless, management legacies likely play a major role in structuring fish assemblages in Iowa lakes and help to explain many of our findings. Differentiation in assemblage composition



FIGURE 5. Water quality characteristics of natural lakes and reservoirs in relation to species richness for 45 waterbodies in Iowa, 2008–2011.

between natural lakes and reservoirs was likely influenced by systematic differences in patterns of sport fish stocking between waterbody types. First, natural lakes generally have a much longer management history than reservoirs, which were primarily constructed in the last 75 years. Redear Sunfish is not native to Iowa (Lee et al. 1980) but has been propagated and stocked in Iowa's reservoirs since the 1960s (Harlan et al. 1987); this species was sampled in 38% of reservoirs but only one natural lake. In contrast, Walleyes were encountered more frequently in natural lakes, where stocking regularly occurs to supplement wild populations in Iowa (Harlan et al. 1987). Although Walleyes are also stocked in larger reservoirs throughout Iowa, abundance was generally lower in reservoirs than in natural lakes (Fischer 2012). Largemouth Bass and Channel Catfish were also more abundant in reservoirs despite being stocked into most lentic waterbodies throughout Iowa (Harlan et al. 1987). Despite these minor differences in top-level predators, the remaining sport fish assemblage was generally ubiquitous among waterbodies (e.g., Bluegill and Black Crappie). Therefore, the increased diversity in natural lakes was generally attributable to small-bodied fishes (e.g., Spottail Shiner, Iowa Darter, and Northern Logperch) that are neither propagated nor stocked in reservoirs.

In addition to differences in stocking between natural and artificial lentic ecosystems, fish diversity in reservoirs was also likely influenced by management activities associated with sport fish enhancement and renovation efforts. Specifically, rotenone has been widely used to eliminate invasive and undesirable native species, with the goal of enhancing recreational fisheries in Iowa (Lennon et al. 1970) and across the United States (Flick and Webster 1992; Bettoli and Maceina 1996; Wydoski and Wiley 1999). The use of rotenone in the watershed during reservoir construction (a common practice in Iowa) likely eliminated source populations of small-bodied native species (e.g., cyprinids and darters). Quist and Schultz (2014) failed to find intolerant fish species despite the presence of sensitive macroinvertebrates in lotic systems upstream of a reservoir in southern Iowa after improvements to water quality and habitat throughout the watershed. Therefore, elimination of source populations through use of rotenone and upstream migration barriers—coupled with the widespread stocking of piscivorous sport fishes-may have resulted in the less diverse reservoir assemblages observed in our study despite the potential for greater habitat complexity.

The overriding influence of past management activities on fish composition in reservoirs is particularly evident when reservoirs undergo restoration practices to improve water quality. For example, Lake Ahquabi was constructed in 1935 and "restored" in the mid-1990s (Schultz et al. 2007). Several lake restoration projects were implemented, including the targeted removal of invasive and undesirable fishes (i.e., Gizzard Shad and Common Carp) with rotenone and the subsequent restocking of recreationally important species. The complete renovation of Lake Ahquabi resulted in increased water clarity, reduced total phosphorus and chlorophyll-a concentrations, increased reservoir visitor use, and increased angler catch rates (Schultz et al. 2007). However, the influence of management activities, such as the Lake Ahquabi restoration example, may suggest that the ability to understand fish assemblage composition in these reservoirs could be biased due to an overrepresentation of sport fishes in reservoirs. When Lake Ahquabi was sampled in 2011 as part of this

project, the fish assemblage included only 10 species and was dominated by a sport fish assemblage consisting of centrarchids (i.e., Bluegill, Redear Sunfish, Largemouth Bass, White Crappie, Black Crappie, and Green Sunfish) and ictalurids (Channel Catfish and Black Bullhead) that are common throughout all of the waterbodies in Iowa. Therefore, despite changes in habitat conditions and expected shifts in assemblage composition associated with improved water quality, the fish assemblage is largely similar to that occurring prior to the restoration, with the exception of Gizzard Shad and Common Carp losses to the species pool. As such, management legacies resulting from renovations or construction of reservoirs likely had overriding effects that resulted in dissimilar patterns of assemblage composition between natural lakes and reservoirs.

Distinct differences between natural lake and reservoir assemblage composition observed in our study provide guidance on the management of both aquatic ecosystem types. Specifically, numerous relationships between environmental characteristics and species composition in reservoirs imply that management activities (e.g., habitat restoration and nutrient reduction) could increase benefits over similar actions in natural lentic ecosystems despite the consistently lower diversity in constructed lakes. However, inconsistencies in assemblage-environment relationships between sampling methods suggest that reservoir fish assemblage composition may be more complex than we originally hypothesized, and additional research is needed to identify the relative importance of habitat characteristics for individual species or taxonomic groups. We did not find strong relationships between physicochemical conditions and fish assemblages in natural lakes, suggesting that further evaluation of biotic regulation and additional abiotic factors may be necessary to effectively manage fish and their habitat. Additionally, our finding of a correlation between species richness and surface area in reservoirs and a lack thereof for natural lakes is important for the classification, monitoring, and management of lentic fish assemblages. Although much remains to be learned about the mechanisms responsible for structuring reservoir and natural lake fish assemblages (e.g., Launois et al. 2011) and population characteristics (e.g., Guy and Willis 1995), our study suggests that the differences between these two types of system may be critical to development of ecological monitoring programs for lentic ecosystems and to understanding the factors that threaten aquatic ecological integrity.

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