Fish-Assemblage Evaluation in the Lower Sandusky River, Ohio, Following Dam Removal

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Data Availability Statement

The data that support the findings of this study are publicly available at Schulz, K. A., Acre, M. R., Mueller, A. T., Wamboldt, J. J., Broaddus, D., Hessler, T. M., Wilson, T. M., Mapes, R. L., Amberg, J. J., Calfee, R. D., 2023, Fish Community and habitat assessment in the Sandusky River, OH, April 2021 through October 2021: U.S. Geological Survey data release, https://doi.org/10.5066/P9C7GF0L.

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Declaration of Conflicts of Interest

No conflicts of interest exist for all authors.

Disclaimer

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TABLE OF CONTENTS

ABSTRACT

The Sandusky River, Ohio, USA, has experienced more than a century of alterations, including dam implementation and removal, causing a cascade of habitat changes. The physical changes in the river led to establishment of several invasive species. Ten hoop-net sampling sites, spaced about 500 m apart were established in the river to monitor fish assemblage and their habitat preferences. Four 10-d sampling events were completed from April through October 2021. Ordination analyses were used to assess fish-assemblage structure seasonably, species-habitat relationships, and life-history strategies of 31 species. Generalized linear mixed-effects models were used to assess temporal factors that may drive diversity and community assemblage. Models indicated increased species richness after removal of the dam. Presence and proportion of catch data were compared to Ohio Environmental Protection Agency 2009 pre-dam-removal data to further assess changes in fish assemblage. Several species, especially catostomids, have begun to use the habitat downstream of the former dam, altering fish assemblage throughout the river. We expect shifts in assemblage structure to persist, making continued monitoring essential for understanding how non-native and recreationally important species continue to respond to dam removal.

INTRODUCTION

Tributary condition and functionality are vital to the success of resident species in the Laurentian Great Lakes. The Sandusky River, a tributary of Lake Erie, has functioned historically as a nursery (Becher and Gottgen 2012) and spawning ground for native fish, including White Bass *Morone chrysops* (Hayden et al. 2011) and Walleye *Sander vitreus* (Trautman 1981; DuFour et al. 2015; Zimmerman and Rice 2019; Myers et al. 2024). Creel records from the Sandusky River suggest the Walleye population has declined in recent years, which is hypothesized to be from a lack of quality spawning habitat in the river (Cheng et al. 2006). Cumulative impacts of dam construction and habitat degradation are also likely culprits for decreased sportfish abundance throughout the Great Lakes (Fielder et al. 2007).

Depending on a dam's function and location along a river course, a dam can have large effects on available habitat and flow regime (Ward and Stanford 1983). In addition to altering abiotic components of a river, dams can fragment river connectivity, block fish migrations, and limit spawning habitat, which can alter the composition of native fish communities (Catalano et al. 2007; Acre et al. 2021). Historically, four dams were placed across the Sandusky River. The largest of the dams, Ballville Dam, was located 29 river kilometers (rkm) upstream of the Lake Erie confluence (Figure 1); it was built in 1911 to provide hydroelectric power to the city of Fremont, Ohio (USFWS 2016). Ballville Dam's presence on the Sandusky River resulted in an increase in sedimentation, causing a shift from gravel to sand substrates in portions of the river (Sanderson 2009). Alterations in streamflow and sedimentation create ideal conditions for invasions by non-native species (Murphy et al. 2007) and often negatively affect native fish diversity and species richness (Sanderson 2009). For example, Ballville Dam restricted Walleye upstream passage, confining spawners downstream to one tenth of the suitable spawning habitat (Cheng et al. 2006).

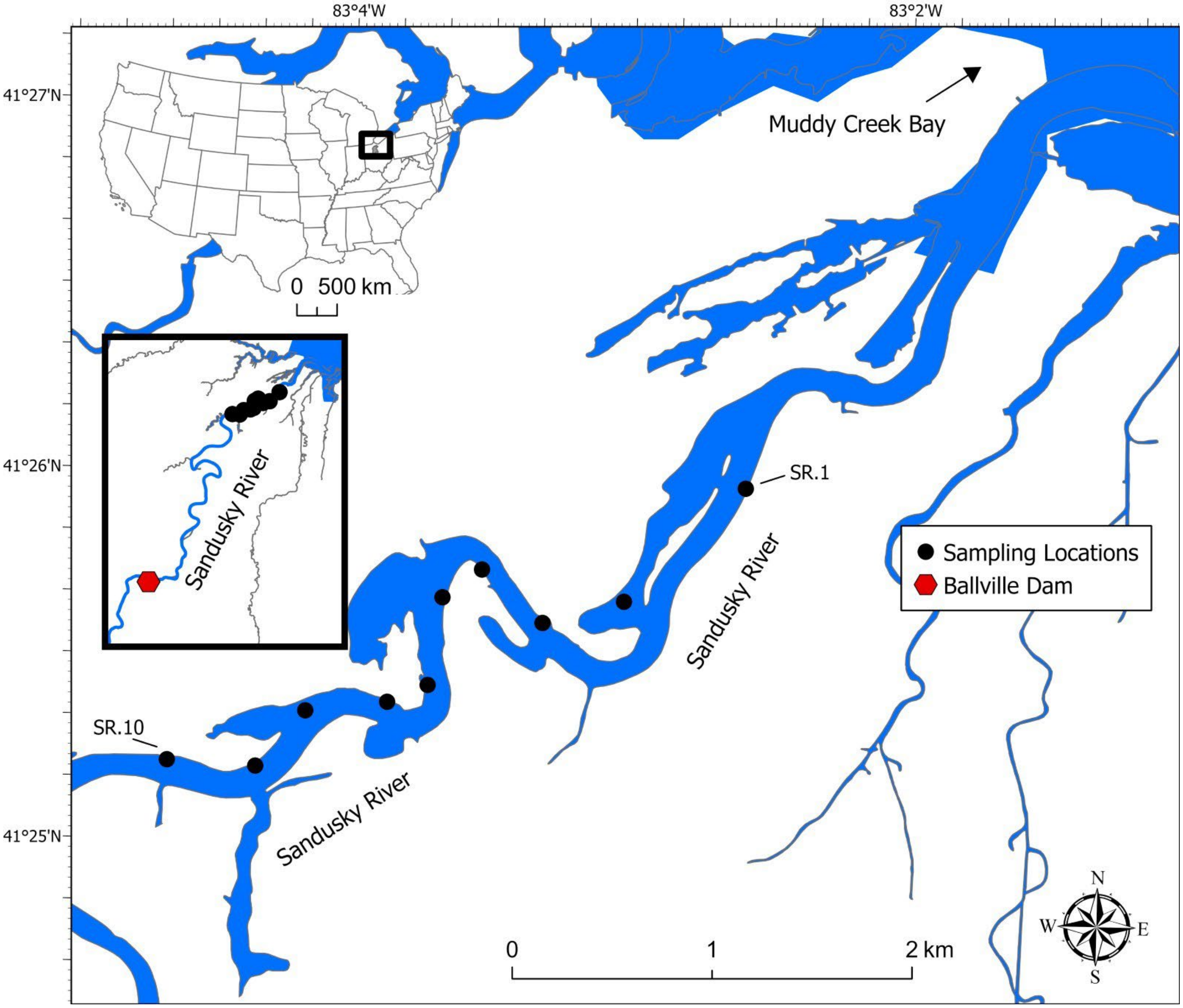

FIGURE 1. Location of hoop-net sampling sites in the Sandusky River, Ohio, in 2021. Sites were sequentially numbered from SR.1 to SR.10. At SR. 1, SR. 3–SR. 6, and SR. 8–S.R. 10, a hoop net was deployed on the upstream and downstream sides of a platform depicted together with dots, including in the legend. At control sites (SR. 2 and SR. 7), a platform was not present, and 2 hoop nets were placed on either side of a buoy.

Ballville Dam removal began in 2016 and was completed in 2018, opening 36 rkm of the upper Sandusky River for fish passage from Lake Erie to historically available habitat (Cheng et al. 2006; Gillenwater et al. 2006; USFWS 2016). The dam removal was hypothesized to spatially shift the availability of previously known spawning habitats, benefiting Lake Erie fish populations over time (Myers et al. 2024). A study by Sasak (2021) concluded removal of the Ballville Dam increased the amount of Walleye and White Bass preferred habitat by 21.9 hectares. Two years after dam removal, Walleye was found upstream of the old dam site; however, catch per unit effort of White Bass and Walleye was lower after dam removal than before (Sasak 2021). Further, removal of the dam increased river flow and exposed large amounts of sediment that likely increased spawning habitat for invasive species (Bellmore et al. 2017).

Since the 1950s, multiple invasive species have expanded their range into the Lake Erie basin and use the Sandusky River as spawning and feeding grounds. White Perch *Morone americana* was first reported in Lake Erie in 1953 (Larsen 1954) and has been collected consistently throughout the Sandusky River for decades (Schaeffer and Margraf 1987). Several invasive cyprinids and xenocyprinida are also present in the river, most notably a population of Grass Carp *Ctenopharyngodon idella* (DuFour et al. 2021). It was believed that no self-sustaining populations of Grass Carp had been found in a Lake Erie tributary (Kocovsky et al. 2012) until Embke et al. (2016) discovered evidence of its reproduction in the Sandusky River.

A self-sustaining population of Grass Carp in the Laurentian Great Lakes could reduce aquatic macrophytes, resulting in an ecological cascade of potentially deleterious effects (Cudmore et al. 2017; Gertzan et al. 2017). The primary effect of a decrease in macrophytes is changed water quality and deterioration of critical spawning and nursery habitat, causing a reduction in native fish recruitment (Chapman et al. 2013; Wilson et al. 2014). Reduced recruitment along along with egg predation by White Perch could reduce the recruitment of native sport fish to Lake Erie (Schaeffer and Margraf 1987; Fielder 2002). Therefore, detection and management of non-native species in the Lake Erie basin are necessary to mitigate alteration of native fish communities.

The proximity of our sampling locations to Lake Erie allowed us to observe fish movements into the Sandusky River and back into the lake. Most migratory species, such as Walleye, White Bass, and White Perch, move into the river in early April or when temperatures are typically between 15 and 18°C (Schaeffer and Margraf 1987). However, it is largely unknown how the introduction of other invasive species combined with the removal of the Ballville Dam have impacted fish migration.

The objectives of this study were to establish baseline fish-assemblage diversity metrics and distinguish how invasive species affect them; determine fish-assemblage shifts on a pre/post-dam-removal temporal scale; and compare presence of native and non-native species in relation to habitat characteristics. We hypothesized that transient species would increase diversity downstream near Lake Erie, but that increased diversity would be limited by the presence of invasive species. We further hypothesized an increase in species richness, influenced by non-native species following dam removal. The results of this study will serve as a reference for future fish-assemblage research in the Sandusky River and Lake Erie basin.

METHODS

Study Area

The Sandusky River is 207 rkm long with a drainage of approximately 4,700 kilometers^2 located in northwest Ohio, USA (Harris et al. 2021). The river flows through Muddy Creek Bay and Sandusky Bay before entering the western basin of Lake Erie (Figure 1). The lower Sandusky River watershed had good overall habitat quality. Historically, free-flowing portions of the river were predominated by limestone bedrock and gravel substrates, but most of the lotic sites over time were covered by fine sand and silt (OEPA 2011). Prior to 2018, the reach of the Sandusky River impounded by the Ballville Dam had bottom substrates predominated by muck and silt (OEPA 2011). Sandusky Bay is negatively influenced by the surrounding agricultural landscape and poor sewage treatment (OEPA 2010).

Study Design

Our study took place in the Sandusky River near its confluence with Muddy Creek Bay. Ten fixed sampling locations were distributed throughout the study area at a minimum of 500 meters (m) apart (Figure 1). Eight sites were marked with a platform (deployed as part of another project) to standardize hoop-net placement, and two sites were marked with a buoy to assess any bias the platform may have introduced to our fish catches. Four trials, each 10 days (d) in duration, were completed from April through October 2021.

Fish Collection

Two hoop nets were set daily at each of the ten sites. One hoop net was set immediately upstream of each platform or buoy, and one was set directly downstream, approximately 25 m apart. Landmarks were used to standardize the distance from the platform for each set. Each hoop net was 3.7 m long with an initial hoop diameter of 0.9 m and 3.8-cm square-mesh netting. A 3.1-m wing was attached to each side of a hoop net with a 7.6-m lead anchoring the net to the river bottom, like a traditional fyke net. The wings were set at an approximately 60° angle from the lead. Each net contained seven hoops and two throats attached to the second and fourth hoops. Nets were set perpendicular to the river flow, opening toward the shoreline. When appropriate, hoop nets were also secured with a safety rope connected to a tree on the bank. Nets were fished for approximately 24 hours (h). Catch rates for each site were defined as the number of fish caught in the two hoop nets per 24-h sampling period. Fish were identified to species, their total length was measured to the nearest millimeter, and they were then released.

Predictor Variables

Water-quality information was collected near the same time of day when hoop nets were monitored during each 10-d sampling period. A YSI Exo2 multiparameter sonde (Xylem®; Yellow Springs, Ohio) was used to measure dissolved oxygen (mg/L), specific conductivity (µS/cm), turbidity (FNU), pH, and chlorophyll (µg/L). Daily minimum and maximum depths (m) and water temperature (°C) were calculated from data recorded using an Onset HOBO® Water Level Data Logger (Onset Computer®; Borne, Massachusetts) that were attached to two of the floating platforms approximately 0.5 m above the bottom substrate, and recorded data at 15-minute intervals throughout each 10-d trial. Water temperature and mean depth were used as measures of the change in river depth, a proxy for river discharge, throughout the study and were linked to fish-capture data at the date and time hoop nets were lifted. The distance of each site from the confluence of Muddy Creek Bay (m) was estimated from the midpoint of a site using ArcGIS® Pro 2.7.1 (Esri®; Redlands, California).

Physical-habitat data were recorded at the start of each of the four 10-d trials. Vegetation coverage was characterized by type of vegetation (submerged, emerged, or floating) and genus (Phragmites (*Phragmites* spp.), Duckweed (*Lemna* spp.), Lotus (*Nelumbo* spp.)). Large wood debris (trees, logs, branches, roots) and river-bottom substrate (silt, sand, clay, rock) were also categorized at each site. Physical habitat was defined and recorded as the percentage of area within 50 m of a platform having a habitat feature present. Physical-habitat features were considered variable, and coverage was estimated at time of data collection to account for temporal changes.

Data Analysis

Differences in fish assemblages among trials were visualized using nonmetric multidimensional scaling (NMDS; vegan package version 2.5.7; R Program© version 4.1.2; Oksanen et al. 2019). First, Bray-Curtis similarity coefficients were calculated based on joint occurrence and catch of fish species. Because our objective was to determine temporal shifts in fish assemblages, data were averaged per trial. These data were log(x + 1) transformed prior to calculating the similarity coefficient to reduce the weight of the dominant species. An analysis of similarity (ANOSIM) determined the statistical differences among trial groups (function 'anosim'; *vegan* package version 2.5.7; R Program© version 4.1.2). A similarity of percentage analysis (SIMPER) was then used to identify the fish species that drove dissimilarities among groups in trials, which helped to quantify how each species contributed to the assemblage differences among trial groups (function 'simper', *vegan* package version 2.5.7; R Program© version 4.1.2). Values from the analysis were generated per species. A significant *P*-value suggested a contribution of species to the dissimilarity of fish assemblage among trials.

Species-habitat and site-habitat associations were identified with a canonical correspondence analysis (CCA). The log-transformed fish abundance for all species (n = 31) was compared to the habitat data set across the ten sites (vegan package version 2.5.7; R Program© version 4.1.2). The habitat data set included environmental variables, physical habitat, and mean temperature and water depth. For visualization purposes, habitat variables with CCA1 or CCA2 absolute eigenvalues of 1.5 or less were removed from the plot (n = 11). A permutational analysis of variance (PERMANOVA) test (function anova.cca; vegan package version 2.5.7; R Program$^{©}$ version 4.1.2) verified the significance of the model. A Shannon-Wiener Diversity index (H') was calculated for fish capture data per day. A random forest analysis (Breiman 2001) was used to evaluate the relative influence of the predictor variables mentioned above, with site and trial as factor variables on H' (function randomForest; package randomForest version 4.6.14; R Program$^{©}$ version 4.1.2; Liaw and Wiener 2002).

Pearson correlation coefficients were calculated for the predictor variables ($n = 29$), and highly correlated (≥0.7; Härdle and Simar 2019) or confounded variables were removed to avoid false-positive influence (function cor; package stats version 4.1.2; R Program$^{©}$ version 4.1.2). RandomForest functions build a selected number of regression trees (*m*) from a bootstrap sample of the original data set to allow for non-linear relationships between predictors and a response variable without making any parametric assumptions about the distribution of the response variable (Breiman 2001). To stabilize the mean squared error (MSE), we used 500 trees that diagnostics showed were adequate (function tuneRF; package randomForest version 4.7-1.1; R Program$^{©}$ version 4.1.2). For each regression tree, a set of predictors (*mtry*) was randomly selected from the original predictors at a given node. Using function tuneRF from the randomForest package, the optimal value (with respect to out-of-bag error estimate) of *mtry* was found to be seven.

The percentage increase in the MSE (%IncMSE), when variables were randomly permuted, and the total decrease in node “impurity” from splitting on a given descriptor (IncNodePurity) were averaged over all generated trees to show the importance of variables in the randomForest analysis. The importance score reflects the loss of prediction accuracy associated with omitting, in turn, each predictor variable. We present the top ten variables through partial dependence plots (PDPs) that demonstrate the marginal effect of a selected variable on the response variable, in the order of importance, or greatest MSE. This provides insight to the directionality of the effect for a given predictor (function partial; package pdp version 0.7.0; R Program$^{©}$ version 4.1.2; Greenwell et al. 2018).

The fitdistrplus function (package MASS version 7.3-58.1; R Program$^{©}$ version 4.1.2; Delignette-Muller and Dutang 2015) determined a gamma error distribution provided the best fit of the model. We then fit a generalized linear mixed-effects model (GLMER) with life-history strategy (equilibrium, periodic, and opportunistic), as defined by Winemiller and Rose (1992) and Miyazono et al. (2010), time of year (Julian date), and distance to the bay (m) as predictor variables, with site as a random effect (function glmer; package *lme4* version 1.1-27.1; Bates et al. 2021). Candidate models were generated with combinations of fixed effects using the dredge function (package MuMIn version 1.46.0, R Program$^{©}$ version 4.1.2; Burnham and Anderson 2002), and Akaike’s information criterion (Akaike 1973) was used to determine the best-fit model. The predicted response values were plotted with ggpredict (package ggeffects version 1.1.1; R Program$^{©}$ version 4.1.2; Lüdecke 2018). Each variable was back transformed to make predictions at the population level.

The discussion of our results was aided by a comparison of fish-assemblage data collected throughout the Sandusky River (0.8 rkm to 29 rkm) by the Ohio Environmental Protection Agency (OEPA) in 2009 (OEPA 2010). The OEPA sampled fish using electrofishing from July through September 2009. It is widely accepted that electrofishing is more efficient at detecting fish species in comparison to hoop nets (Pugh and Schramm 1998; Smith et al. 2015). Therefore, only presence/absence data, species richness, and species proportion of catch were compared between the two data sets. For comparison, the OEPA data set was reduced to fish captured within our sampling area (with a degree of estimation). Additionally, small-bodied fish and hybrids, which could not be captured by our hoop nets, were removed from the OEPA data set prior to comparisons. The species removed included: Emerald Shiner *Notropis atherinoides*, Spottail Shiner *Notropis hudsonius*, Spotfin Shiner *Cyprinella spiloptera*, Fathead Minnow *Pimephales promelas*, Common Carp *Cyrpinus carpio* x Goldfish *Carassius auratus*, Blackstripe Topminnow *Fundulus notatus*, Brook Silverside *Labidesthes sicculus*, Logperch *Percina caprodes*, Mimic Shiner *Notropis volucellus*, Bluntnose Minnow *Pimephales notatus*, and Ghost Shiner *Notropis buchanani*. The OEPA identified bullheads *Ameiurus* spp. to species, whereas we identified them to genus. Therefore, all OEPA bullhead data were added together for consistency between the two data sets.

Results

Over four trials, 8,875 fish were captured in 880 hoop-net sets with approximately 21,013 h of soak time. The total catch comprised 31 species representing 11 families (Table 1). Non-native species (Grass Carp, Common Carp, Goldfish, White Perch) comprised 13% of the total catch. Twelve species were present in ≤5% of our daily catches (*n* = 440) and considered rare. Fish relative abundance and species richness decreased sequentially across trials (Table 2). Seventy-one percent of all fish were caught in Trial 1, 15% in Trial 2, and 7% in Trials 3 and 4. Eighty percent of non-native fishes and 87% of recreationally/commercially important species were captured between April and June 2021 (Trials 1 and 2). Important sportfish species, including Smallmouth Bass *Micropterus dolomieu*, Rock Bass *Ambloplites rupestris*, Walleye, and Yellow Perch *Perca flavescens*, were only captured in Trials 1 and 2.

Table 1. Total catch of each fish species in hoop nets from the Sandusky River, Ohio, during 2021. The corresponding ID number is used throughout the document to identify the species. Bold ID numbers represent non-native species.

ID	Family	Species	Common name	Life-history strategy	Catch
5	Amiidae	*Amia calva*	Bowfin	Equilibrium	123
1	Catostomidae	*Ictiobus cyprinellus*	Bigmouth Buffalo	Periodic	111
3	Catostomidae	*Moxostoma duquesnei*	Black Redhorse	Periodic	3
17	Catostomidae	*Carpiodes cyprinus*	Quillback	Periodic	243
19	Catostomidae	*Moxostoma carinatum*	River Redhorse	Periodic	5
21	Catostomidae	*Moxostoma macrolepidotum*	Shorthead Redhorse	Periodic	6
22	Catostomidae	*Moxostoma anisurum*	Silver Redhorse	Periodic	3
24	Catostomidae	*Ictiobus bubalus*	Smallmouth Buffalo	Periodic	900
25	Catostomidae	*Minytrema melanops*	Spotted Sucker	Periodic	24
30	Catostomidae	*Catostomus commersonii*	White Sucker	Periodic	8
2	Centrarchidae	*Pomoxis nigromaculatus*	Black Crappie	Equilibrium	277
4	Centrarchidae	*Lepomis macrochirus*	Bluegill	Equilibrium	1,019
14	Centrarchidae	*Micropterus salmoides*	Largemouth Bass	Equilibrium	130
18	Centrarchidae	*Lepomis humilis*	Orangespotted Sunfish	Equilibrium	1
20	Centrarchidae	*Ambloplites rupestris*	Rock Bass	Equilibrium	5
23	Centrarchidae	*Micropterus dolomieu*	Smallmouth Bass	Equilibrium	2
28	Centrarchidae	*Pomoxis annularis*	White Crappie	Equilibrium	233
11	Clupeidae	*Dorosoma cepedianum*	Gizzard Shad	Periodic	131
8	Cyprinidae	*Cyprinus carpio*	Common Carp	Periodic	444
12	Cyprinidae	*Carassius auratus*	Goldfish	Periodic	159
16	Esocidae	*Esox lucius*	Northern Pike	Equilibrium	114
6	Ictaluridae	*Ameiurus* spp.	Bullhead	Equilibrium	3,303
7	Ictaluridae	*Ictalurus punctatus*	Channel Catfish	Equilibrium	626
9	Ictaluridae	*Pylodictis olivaris*	Flathead Catfish	Equilibrium	183
15	Lepisosteidae	*Lepisosteus osseus*	Longnose Gar	Periodic	53
27	Moronidae	*Morone chrysops*	White Bass	Periodic	167
29	Moronidae	*Morone americana*	White Perch	Periodic	511
26	Percidae	*Sander vitreus*	Walleye	Periodic	3
31	Percidae	*Perca flavescens*	Yellow Perch	Periodic	1
10	Sciaenidae	*Aplodinotus grunniens*	Freshwater Drum	Periodic	83
13	Xenocyprididae	*Ctenopharyngodon idella*	Grass Carp	Periodic	4

Table 2.—Summary of sampling dates and fish catches made in hoop nets on the Sandusky River, Ohio, in 2021. Species captured are represented by their numeric ID.

Trial	Sampling dates	Total catch	Number of species	Species captured
1	April 29–May 9	6,322	28	1–12, 14–18, 20–30
2	July 1–July 11	1,347	26	1, 2, 4–17, 19, 21, 23–29, 31
3	August 19–August 29	626	22	1, 2, 4–10, 12–17, 21, 22, 24, 25, 27–29
4	October 6–October 16	580	21	1, 2, 4–10, 12, 14–17, 19, 22, 24, 25, 27–29

The NMDS analysis (stress = 0.15) revealed temporal changes in fish assemblages (ANOSIM, *r* = 0.70, *P* < 0.001; Figure 2). Trial 1was isolated in ordination space due to a unique composition characterized by a high catch of bullheads *Ameiurus* spp.(ID 6, numbers refer to species in Figures 1, 2), White Perch (ID 29), Quillback *Carpiodes cyprinus* (ID 17), White Bass (ID 27), Gizzard Shad *Dorosoma cepedianum* (ID 11), and rare species, such as Rock Bass (ID 20), White Sucker *Catostomus commersonii* (ID 30), Black Redhorse *Moxostoma duquesnei* (ID 4), and Orangespotted Sunfish *Lepomis humilis* (ID 18) (Figure 2). Trial 2 was isolated in ordination space due to a high abundance of Channel Catfish *Ictalurus punctatus* (ID 7), the presence of rarely caught Yellow Perch (ID 31), and the highest relative abundance of rarely captured River Redhorse *Moxostoma carinatum* (ID 19). Trial 2 was close in ordination space to Trial 3 due to a relatively equal and high catch of Flathead Catfish *Pylodictis olivaris* (ID 9) and rarely captured Grass Carp (ID 13). Trial 4 was primarily categorized by presence of Silver Redhorse *Moxostoma anisurum* (ID 22). A relatively high catch of Largemouth Bass *Micropterus salmoides* (ID 14) was made during Trials 1 and 4 compared to Trials 2 and 3 (Figure 2). Due to changes in fish assemblage among trials, the trials illustrated in Figure 2 occurred sequentially in ordination space in a counterclockwise pattern representing a distinct directional shift in fish assemblage over time.

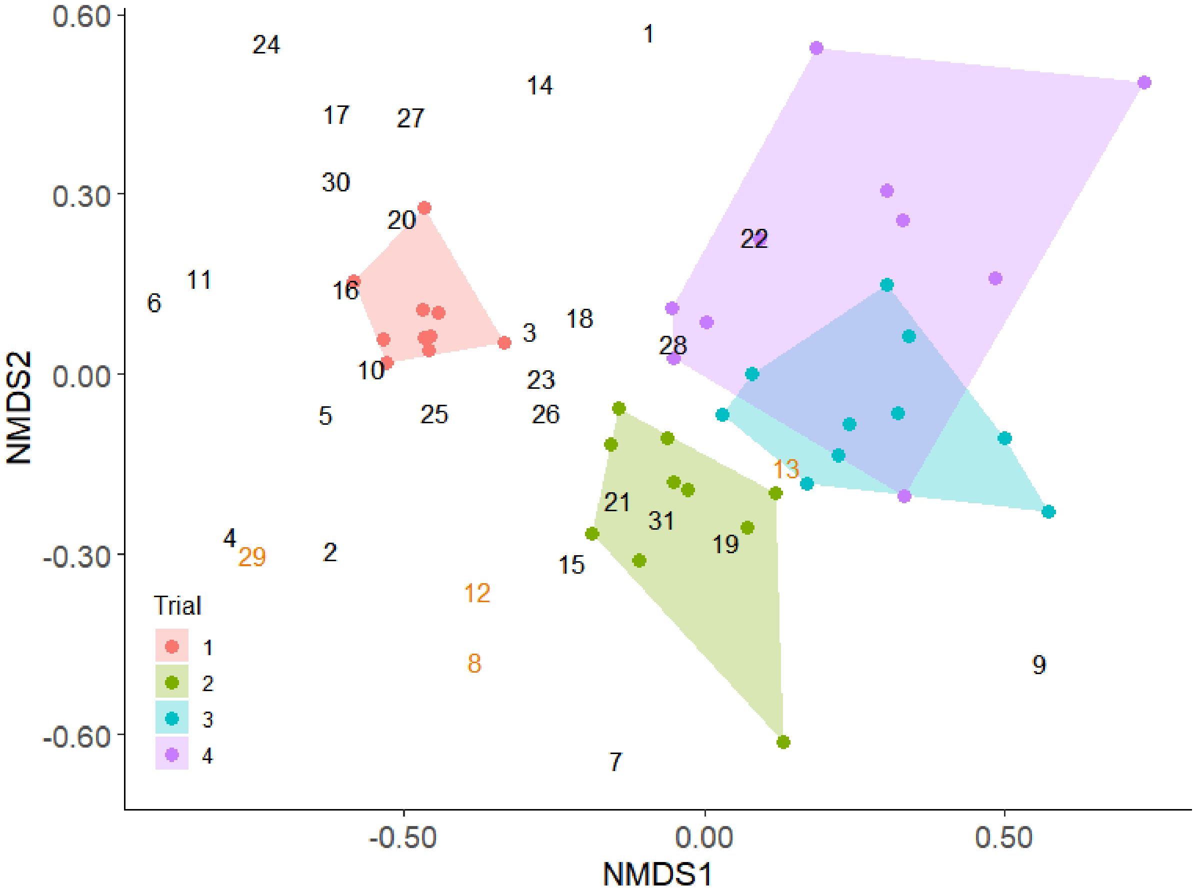

FIGURE 2.—Nonmetric multidimensional scaling (NMDS) ordination of fish species collected across four sampling trials in the Sandusky River, Ohio, in 2021. Species are plotted based on their scores for each axis. Stress = 0.15. Each point corresponds to a site and is colored by trial number. Convex hull polygons are colored similarly and represent the assemblage space across each site by trial. Numbers correspond to species ID (see Table 1) where black numbers are native species and orange are non-native species.

There was a significant association between habitat features and species' catches (PERMANOVA, $F = 2.975$, df = 31, $P = 0.001$; Figure 3). Temperature, specific conductivity, turbidity, and chlorophyll explained most of the variation in assemblage structure. Substrate influenced assemblage structure more than aquatic vegetation. Most species were associated with a silt substrate and greater point velocity, but several other species appear to have specific habitat requirements. Ictalurids were strongly connected to varying habitat features. Flathead Catfish (ID 9) were captured in areas with higher temperatures and vegetation (*Phragmites* sp.), while Channel Catfish (ID 7) were linked to sites with increased minimum depth and duckweed blooms. Bullhead species (ID 6) had an affinity for shorelines with high turbidity and silt. Notably, non-native Common Carp (ID 8), Goldfish (ID 12), and Grass Carp (ID 13) had habitat preferences similar to Channel Catfish, but they were more closely associated with sites characterized by shallow depths and sporadic duckweed blooms. Longnose Gar *Lepisosteus osseus* (ID15), Smallmouth Buffalo *Ictiobus bubalus* (ID 24), and White Sucker (ID 30) appeared at the center of the ordination indicating general habitat associations. When comparing community assemblage by trial (Figure 2) and species composition by habitat (Figure 3), the relationship suggests environmental and habitat features may influence when some species are present in a river and for how long. This theory is supported by data on White Sucker (ID 30), Quillback (ID 17), and Northern Pike *Esox lucius* (ID 16), habitat generalists that were not strongly associated with any trial in the NMDS.

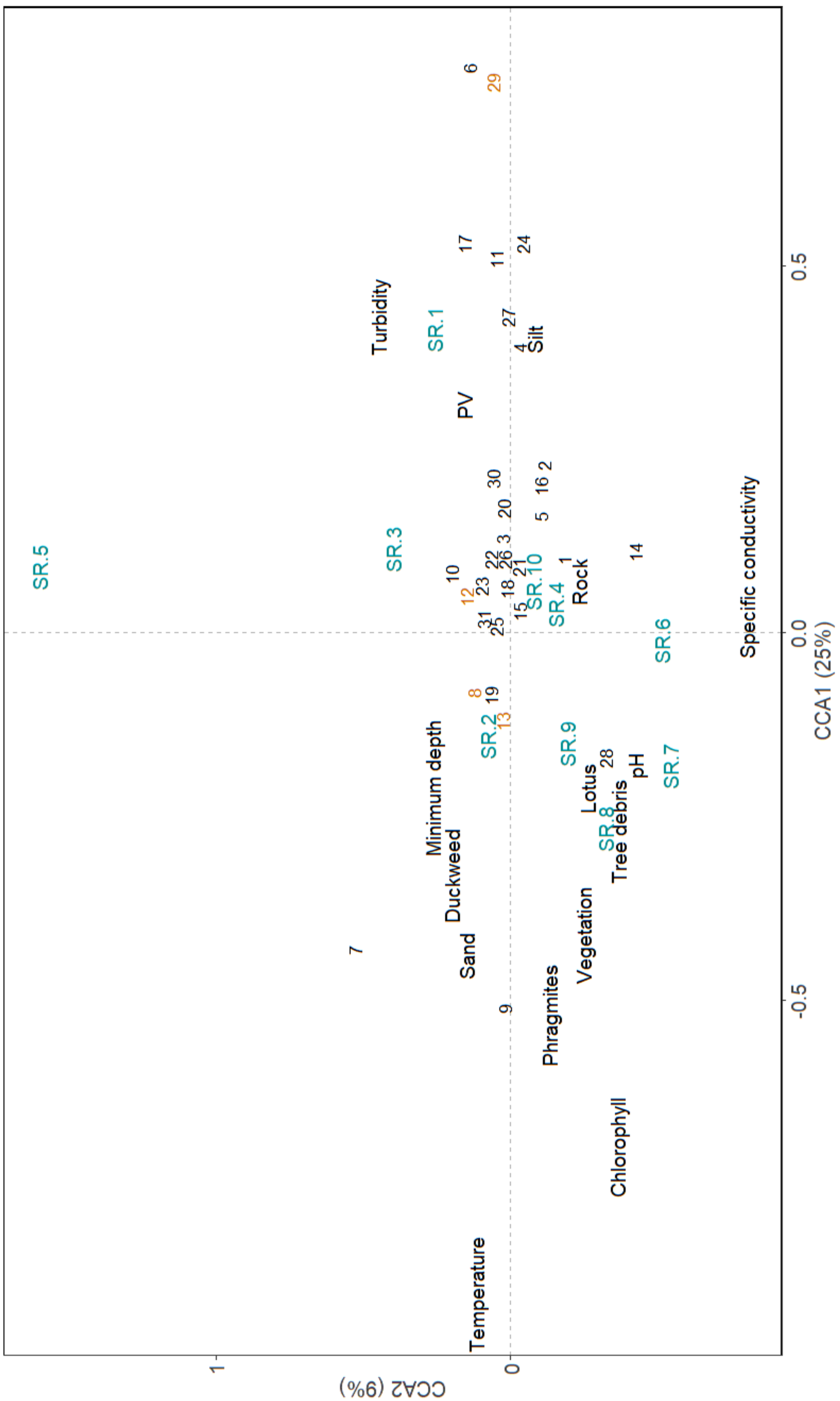

FIGURE 3. Canonical correspondence analysis (CCA) diagram representing the relationship of $\log_{10}$ transformed fish catch (n = 31) to habitat variables for eigenvalues greater than 1.5 in the lower Sandusky River, Ohio, in 2021. Sites are represented by green text, and species are separated into native (black) and non-native species (orange). PV = point velocity.

The random forest model, which included nine water-quality variables, 11 physical-habitat features, and three sampling specific factors, accurately classified 49% of the variation in daily fish diversity (*n* = 440). Variables with a %MSE of 10% or higher were considered important and interpreted further (Figure 4). Site, trial, and distance to bay contributed strongly to the model (Figure 5). Low fish diversity at site SR.2 can likely be attributed to its location. It was the only site located mid-channel away from either bank and near a shoal. Shoreline species diversity is known to be higher than mid-channel diversity (Wolter and Bischoff 2001). As with our catch, diversity was primarily affected by water-quality variables. Wood debris and log debris were the only physical-habitat features that significantly influenced the model and, therefore, fish diversity. Fish diversity was inversely related to temperature, pH, specific conductivity, water depth, log debris, and distance from the bay (Figure 5 A, B, C, E, F, H), while it was positively related to % wood debris (Figure 5 D).

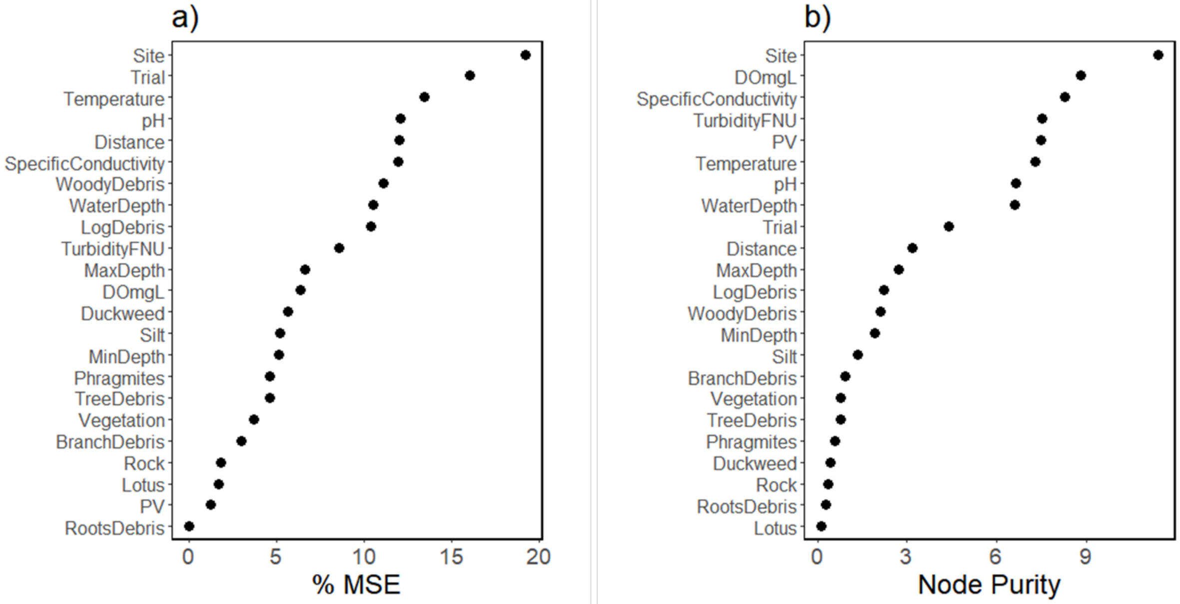

FIGURE 4.—The % mean squared error (MSE) and node purity of the Random Forest model for predicting habitat variables most important to fish assemblage in the Sandusky River during 2021. The % MSE helped determine which habitat features contributed most to the model. PV = point velocity; DO = dissolved oxygen; FNU = Formazin Nephelometric Units.

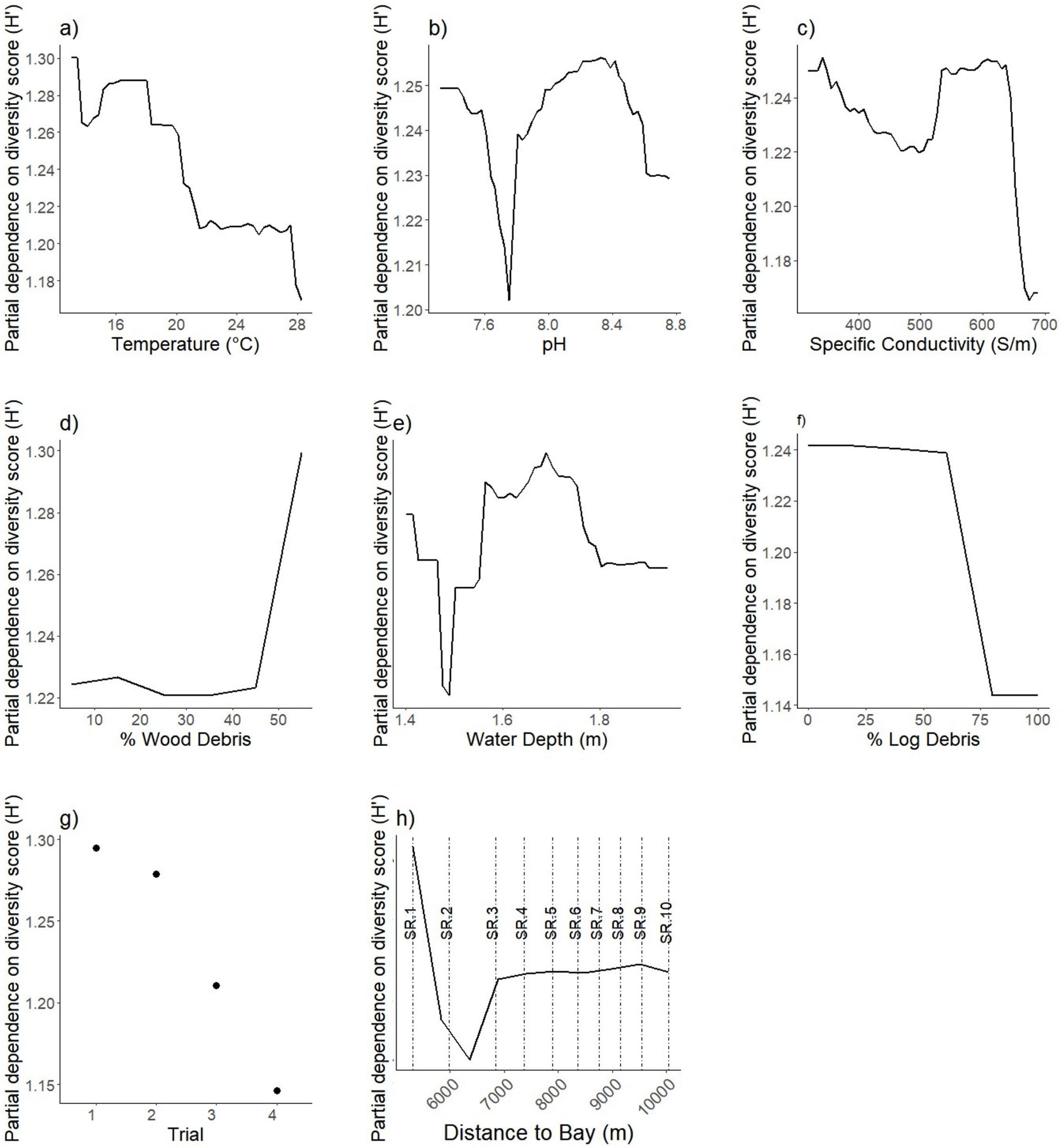

FIGURE 5.—Partial dependence plots for eight habitat- and site-specific metrics: (A) temperature (°C), (B) pH, (C) specific conductivity (S/m), (D) percent of site covered in wood debris (%), (E) water depth (m), (F) percent of site covered in log debris (%), (G) sampling trial, (H) distance of a site to Sandusky Bay (m). The y-axis is fish diversity (H') per catch data per day. Only metrics with ≥10% mean square error (MSE) were included in the figure. Vertical lines on (H) were added manually to illustrate distance to Muddy Creek Bay.

We hypothesized that our data would characterize fish-assemblage shifts as fish moved upriver for spawning or for feeding in the warmer months or large-scale downstream movements to the bay in accordance with overwintering behaviors (Hayden et al. 2014; Childress and McIntyre 2015). The GLMER revealed significant associations between the predictor variables and fish catch (intercept coefficient = 5.02, SE = 0.25, $P < 0.00$). Diversity was higher closest to the bay; decreased and remained relatively constant after site SR.1 (Figure 5h). This pattern indicates a community-wide preference to remain near the bay. However, as a main effect in the GLMER analysis, distance to bay was not a significant predictor of fish catch (coefficient = 0.18, SE = 0.24, $P = 0.46$). Distance to bay and sampling date interacted significantly to create temporal-specific patterns in fish catch within the sampled area (coefficient = 0.26, SE = 0.07, $P < 0.01$). Our fish catch was higher in the spring throughout the sampling area, but particularly higher further from the bay. Sampling date (coefficient = 0.18, SE = 0.24, $P < 0.01$) and life-history strategy were also significant to the model (coefficient = 0.26, SE = 0.07, $P < 0.01$), as fish with an equilibrium life-history strategy accounted for much of the catch.

Species richness was high in 2021 compared to 2009 (Table 3). Catostomids made up a higher percent of total catch in 2021 than in 2009, and two new sucker species were present in 2021—Black Redhorse and White Sucker. Differences in the catch of important sportfish varied between the OEPA and our data set, with the most intriguing result being the presence of Walleye and Northern Pike in 2021, as both species were absent in 2009. We also saw an increase in percentages for Black Crappie *Pomoxis nigromaculatus*, White Crappie *Pomoxis annularis*, and Channel Catfish (Table 3) and a decrease in sunfish species between 2009 and 2021. Changes in invasive-species presence and occurrence were variable as Common Carp and Goldfish were a higher percentage of total catch in 2009 than in 2021, but White Perch was much lower in 2021. Grass Carp was not caught in 2009 but was a small percentage of the total catch in 2021 (Table 3).

Table 3. A comparison of Ohio Environmental Protection Agency (OEPA) electrofishing catches in 2009 with the present study in a similar section of the Sandusky River (rkm 1 to rkm 8). Small-bodied fish were removed from the OEPA data set.

	OEPA study (2009)		**This study (2021)**	
Species	**Catch**	**%**	**Catch**	**%**
Bigmouth Buffalo	7	0.66	111	1.27
Black Crappie	1	0.09	277	3.18
Black Redhorse	0	0.00	3	0.03
Bluegill	47	4.43	1,019	11.69
Bowfin	0	0.00	123	1.41
Bullhead spp.	3	0.28	3,303	37.90
Channel Catfish	8	0.75	626	7.18
Common Carp	93	8.77	444	5.09
Flathead Catfish	1	0.09	183	2.10
Freshwater Drum	21	1.98	83	0.95
Gizzard Shad	651	61.36	131	1.50
Golden Redhorse *Moxostoma erythrurum*	32	3.02	0	0.00
Goldfish	41	3.86	159	1.82
Grass Carp	0	0.00	4	0.05
Green Sunfish	6	0.57	0	0.00
Largemouth Bass	17	1.60	130	1.49
Longnose Gar	3	0.28	53	0.61
Northern Pike	0	0.00	114	1.31
Orangespotted Sunfish	8	0.75	1	0.01
Pumpkinseed *Lepomis gibbosus*	17	1.60	0	0.00
Quillback	0	0.00	243	2.79
River Redhorse	0	0.00	5	0.06
Rock Bass	1	0.09	5	0.06
Shorthead Redhorse	9	0.85	6	0.07
Silver Redhorse	0	0.00	3	0.03
Smallmouth Bass	1	0.09	2	0.02
Smallmouth Buffalo	41	3.86	900	10.33
Spotted Sucker	4	0.38	24	0.28
Walleye	0	0.00	3	0.03
White Bass	14	1.32	167	1.92
White Crappie	5	0.47	233	2.67
White Perch	7	0.66	352	4.04
White Sucker		0.00	8	0.09
Yellow Perch	23	2.17	1	0.01

Total catch	1,061	8,716
Total number of species	25	31

DISCUSSION

Often, large-scale anthropogenic disruptions to river systems alter natural patterns of flow (Poff and Hart 2002) and reduce available native fish habitat (Nunes et al. 2015). After decades of declining water quality and reduced habitat connectivity, the Ballville Dam was removed from the Sandusky River in 2018 (USFWS 2016). The dam removal caused a temporary influx of fine sediment downstream of the dam, covering coarse substrates and filling deep pools (Evans et al. 2007; Murphy et al. 2007) that native species, such as Walleye (Thompson 2009) and several catostomids (Bowman 1970; Jenkins 1980; Reid 2006), require for spawning habitat (Thompson 2009). The effect correlates with the serial discontinuity concept, which predicts that natural and anthropogenic disruptions will lead to downstream altered states at the population, community, and even ecosystem level (Ward and Stanford 1983, 1995). As the quality of fish habitat often declines in the immediate years after dam removal because large amounts of fine sediments are exposed (Bellmore et al., 2017), the resident fish community may change and decrease in species richness (Poff et al. 2007; Kornis et al. 2015; Sasak 2021). It can take years for rivers to recover from impoundment effects as the physical habitat stabilizes and native species begin to disperse into newly restored segments of the river (Sasak 2021).

Important native sportfish like Walleye and White Bass have not yet been reported in the restored upstream spawning habitat (Sasak 2021), but we documented that the spatial organization of the Sandusky River fish community has started to change downstream. All catostomids besides Shorthead Redhorse *Moxostoma macrolepidotum* had an increased presence in the Sandusky River since the collection of the OEPA 2009 data. *Moxostoma* species, Smallmouth Buffalo and Spotted Sucker *Minytrema melanops* were present upstream of the dam site in 2020 (Sasak 2021). These suckers prefer riffle/run habitat with deeper pools nearby, habitat features often found near dams (Reid 2006, 2008). Therefore, dam removal likely reconnected ideal spawning and feeding habitat for catostomids to the downstream section of the river, contributing to the increase in their presence and to species richness. This theory is further supported by the presence of White Sucker in 2021, which was not caught in the main stem of the Sandusky River in 2009 (OEPA 2010) or upstream of the dam site in 2020 (Sasak 2021). Common Carp, Goldfish, and White Perch are also utilizing the restored habitat upstream of the former dam site, but how they alter the fish assemblage in that section of the river is unknown (Sasak 2021). We found that Common Carp, Grass Carp, and Goldfish were most often captured in deep water with submerged or floating vegetation and/or wood debris, whereas White Perch were caught in silt substrates and relatively faster-moving water. These habitat features increased downstream post dam removal (Lisius et al. 2018), which could, in part, have contributed to the introduction of Grass Carp to the Sandusky River. However, as invasive species continue to establish in the restored upstream portion of the river, they may compete with native fish for complex habitats, such as the riffle/pool sections preferred by *Moxostoma*.

The presence of some fish species in the lower Sandusky River was not affected by the removal of Ballville Dam. Instead, other habitat features were the primary drivers of their presence. There is not a lot of information on how the Sandusky River has changed since 2018, which makes it difficult to discern what changes in the community assemblage between 2009 and 2021 are a direct result of dam removal. However, our CCA analysis showed several species grouping closely in ordination space, suggesting similar habitat usage. Those same species were also often collected during the same trial. This indicates that, for species such as Channel and Flathead Catfish (ID 7, 9), Bullhead (ID 6), Gizzard Shad (ID 11), Bigmouth Buffalo *Ictiobus cyprinellus* (ID 1), and Largemouth Bass (ID 14), habitat and environmental variables may strongly influence fish presence and temporal migrations in the Sandusky River, regardless of changes from dam removal.

Life-history strategy may also affect fish movements and drive assemblage distribution in the river. For example, several of the rarely captured catostomids and moronids with a periodic life-history strategy were nearly exclusive to the spring sampling event, consistent with their spawning behavior (Winemiller and Rose 1992; Miyazono et al. 2010). Reid (2006) documented spawning for six redhorse species occurring between May and June, but individuals were captured at spawning habitats several weeks prior to spawning, which correlates to our findings. If fish were actively migrating downstream to the bay following spring and early-summer spawning, we would expect to see an increase in catches closer to the bay in mid to late summer, which was not the case for our study. This observation, as well as what we know about migratory behavior in freshwater fish, suggests that these species are remaining upstream instead of returning to the bay, but continued surveys further upstream of our sampling sites would be needed to confirm this hypothesis.

CCA results suggest most species prefer shallow depths and habitat complexity, such as branch debris, rock substrate, or submerged aquatic vegetation, a finding supported by the PDP. Downstream habitat alteration in the Sandusky River resulting from the removal of the Ballville Dam may have increased suitable habitat for several species that were not previously present in the river. Northern Pike, a species that prefers shallow depths and emergent and submergent vegetation (Diana et al. 1977), and Bowfin *Amia calva*, a species that resides in shallow, nearshore areas often with structural complexity (Patterson and Longbottom 1989; Midwood et al. 2016), were not present in the OEPA 2009 catch but were present in our 2021 catches. However, neither species was present upstream of the former dam in 2020 (Sasak 2021). In this instance, the often temporary but negative changes downstream of dam removal provided suitable habitat for some species, which increased species richness in the river. Despite the evident changes in habitat, it is not clear what specific changes in the Sandusky River promoted the establishment of Bowfin and Northern Pike.

Catostomids appear to have benefited most from dam removal, but sportfish, such as Walleye and Northern Pike, are beginning to migrate into the Sandusky River. The fish assemblage is expected to continue to change in the upcoming years. Short-term changes are detectable within five years, but it can take decades for a system to reach equilibrium after a large disturbance (Shafroth et al. 2002). The intermediate disturbance hypothesis suggests that the fish community may never reach equilibrium depending on the type and intensity of the disturbance (Connell 1978). Therefore, future studies should continue to assess diversity metrics and fish community dynamics upstream and downstream of the former dam. Although we were not able to compare habitat and environmental features pre- and post-dam removal, our results can be used to access changes in habitat throughout the system. Continued monitoring is particularly important in the Sandusky River, as removal of the dam could increase the abundance of recreationally and economically important species in Lake Erie as well as influence the spread of non-native species in the Great Lakes.

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