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RESEARCH ARTICLE

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Characterization of fish assemblages in eleven multi-use reservoirs from North Carolina, USA

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ABSTRACT
Managing impounded river systems is a recurring challenge for aquatic resource professionals because reservoirs serve multiple functions with different ecological and socioeconomic outcomes. However, research on fishes in reservoirs has disproportionally focused on recreationally and economically important species, with less attention directed toward fish assemblages despite the potential for management at the assemblage level. As such, evaluation of relationships between reservoir fish assemblages and biotic and abiotic factors and testing whether assemblage structure is affected by changing environmental conditions may deepen ecological understanding and provide insights for reservoir fisheries management. Our overall objective was to assess these relationships in 11 reservoirs from North Carolina, USA. We sampled fish assemblages in the reservoirs, which spanned five river basins representing a range of habitat conditions, using experimental gillnets and pulsed DC nighttime electrofishing. Multivariate statistical analyses indicated that taxonomic differences in fish assemblage composition among river basins followed a gradient of productivity. The top contributing species to reservoir dissimilarity were bluegill (*Lepomis macrochirus*), gizzard shad (*Dorosoma cepedianum*), black crappie (*Pomoxis nigromaculatus*), and white perch (*Morone americana*). These four species were positively associated with factors that reflect increasing eutrophic conditions in the 11 reservoirs and could, therefore, serve as indicators of reservoir productivity, anthropogenic influence, and fish assemblage structure, in addition to their key role in reservoir fisheries management. Whereas fisheries research has historically focused on assessing fish populations, our results illustrate the ecological and management insights derived from simultaneously collecting assemblage- and population-level data. Research on reservoir fish assemblages in

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relation to biotic and abiotic conditions may help advance fish ecology and management alike.

KEY POLICY HIGHLIGHTS

- Reservoir research has disproportionally focused on individual species of recreational and socioeconomic importance, rather than fish assemblages.
- Simultaneous collection of assemblage- and population-level fisheries data may generate both ecological and management insights that species-specific sampling cannot.
- As anthropogenic influences on reservoirs continue to increase, integrating environmental (biotic and abiotic conditions) and fish-assemblage data may be helpful for advancing our understanding of fish ecology and management alike.

Introduction

Flow regulation in the form of dams, wing dikes, levees, and other structures is the most pervasive anthropogenic alteration to rivers worldwide (Nilsson et al. 2005). A global surge in dam construction between 1950 and 1986 caused a sevenfold increase in the number of large reservoirs (i.e. > 10,000 ha; Dynesius and Nilsson 1994). Managing impounded river systems to achieve ecological and socioeconomic goals is a recurring challenge for aquatic resource professionals because reservoirs serve multiple functions (e.g. flood control, irrigation, recreation; Erickson et al. 2008; Allen et al. 2008) and have been important to human civilizations for over 5,000 years (Schnitter 1994). However, despite their broad utility and presence in virtually every major river in North America (Benke 1990), reservoirs have received less research attention than other aquatic systems (Kubečka et al. 2009, Guo et al. 2021).

Relative to natural lakes, research on reservoir fishes has focused disproportionally on individual species of recreational and socioeconomic importance, rather than fish assemblages (Tonn and Magnuson 1982; Jackson et al. 2001; Irz et al. 2002; Miranda et al. 2008), despite the potential for management at the assemblage level (Fischer and Quist 2019). Reservoirs can have varying effects on the composition and distribution of aquatic organisms by altering the physical and chemical processes of lotic habitats (Baxter 1977; Chien 1985; Bonner and Wilde 2000), limiting passage of migratory freshwater and diadromous species (Shields et al. 2000; Hall et al. 2011), and reducing diversity by limiting lotic taxa (Gido et al. 2009; Freedman et al. 2014). Reservoirs are also commonly stocked with ubiquitous sportfish species that can provide recreational opportunities but are often non-native (Gozlan et al. 2010). Although introduction and management of non-native top predators can have deleterious effects on native taxa (Clarkson et al. 2005; Eby et al. 2006), reservoirs provide insight into the processes regulating assemblage composition because they represent novel habitats with established colonization inputs (e.g. connected systems, human introduction; Gido et al. 2009). Reservoir management often prioritizes recreational angling through fish manipulation such as stock enhancement, species-specific harvest regulations, and species introduction, providing an opportunity to characterize the factors that influence fish assemblage structure (Bonner and Wilde 2000, Carol et al. 2006, Fischer and Quist 2019). Investigation of fish assemblages may support better understanding of their ecological structure amid changing environmental conditions (e.g. land-use change, urbanization, water demands; Fischer and Quist 2019) and may allow optimization of management and conservation strategies for species or populations that reside in, or are influenced by, reservoirs.

Longitudinal environmental gradients and local habitats affect reservoir fish assemblage structure (Matthews et al. 1989; Gido et al. 2002). Unlike rivers and streams that are often sampled with a single method (i.e. backpack or boat electrofishing), reservoirs contain multiple zones (e.g. littoral, limnetic) and characteristics of riverine and lacustrine habitats that require multiple methods to characterize fish assemblages (Fischer and Quist 2014a, 2014b). Previous studies of reservoir fish assemblages have investigated environmental gradients (Gido et al. 2002), habitat use (Werner et al. 1977), individual lake zones (Gido and Matthews 2000), or interspecific interactions (Garvey et al. 1998; Winters and Budy 2015) within one or several systems.

Comparisons of reservoir fish assemblages may be useful for testing whether and how biotic and abiotic factors influence fish assemblage structure. This information may be used to understand large-scale factors influencing the occurrence and distribution of fishes, monitor environmental changes, and improve management. Therefore, the objectives of this study were to (1) assess the relative importance of morphometric and physicochemical variables in structuring fish assemblages, (2) evaluate associations between fish assemblage structure (e.g. species abundances, diversity indices) and environmental gradients, and (3) characterize the relative contributions of individual species to taxonomic differences among river basins.

Methods

Study site

Eleven reservoirs from five river basins across North Carolina (Figure 1) were studied because they encompassed a wide range of morphometric and physicochemical conditions (Tables 1 and 2), yet were managed similarly for recreational angling opportunities. Morphometric and physiochemical variables were measured and calculated by the North Carolina Environmental Quality Water Sciences Section using standardized methods as part of the Ambient Lakes Monitoring Program Database (1981) (weblink in References and Data Deposition section). Reservoirs were characterized with measurements of morphometric and physiochemical

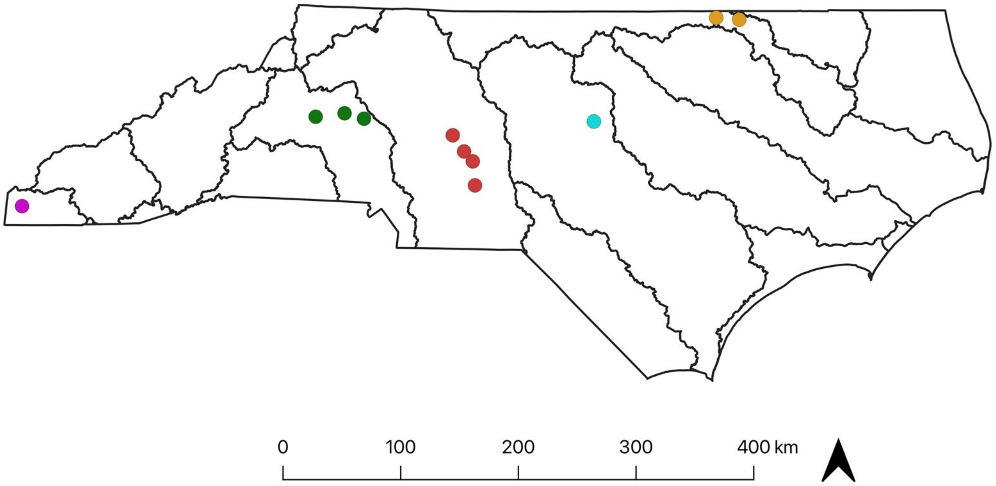

Figure 1. Map of 11 reservoirs (points) across 5 river basins in North Carolina, USA: Hiwassee basin in purple (Hiwassee Lake); catawba basin in green (east to west—Lake rhodhiss, Lake hickory, lookout shoals Lake); Yadkin-Pee dee river basin in red (North to South—high rock Lake, tuckertown reservoir, badin Lake, Lake tillery); cape fear river basin in blue (Jordan Lake); Roanoke river basin in gold (east to west—Lake gaston, Roanoke rapids Lake).

Table 1. Morphometric and physicochemical variables of 11 reservoirs throughout North Carolina, USA.

Variable	Code	Mean	SE	Min	Max	Eigenvectors		
Surface area (km^2)	area	30.1	7.5	5.1	82.2	0.14	**0.41**	0.10
Drainage area (km^2)	drain	9,498	2,118	2,507	21,601	0.06	0.28	**−0.36**
Volume (km^3)	volume	0.2	0.05	0.01	0.6	−0.07	**0.45**	0.23
Shoreline Development Index	SDI	12.2	1.3	4.9	21.1	0.08	**0.25**	**0.42**
Elevation (m a.s.l.)	elevation	190	39	40	464	−0.20	−0.16	**0.38**
Depth (m)	depth	12.4	3.7	4.3	43.3	−0.22	0.18	**0.30**
Maximum depth (m)	depth_max	30.9	7.3	11.6	93.9	−0.23	0.19	**0.25**
Secchi depth (m)	Secchi	1.4	0.3	0.6	3.9	−0.28	0.19	0.16
Turbidity (NTU)	turbidity	6.7	1.2	1.8	14.8	**0.29**	−0.08	0.13
Temperature (°C)	temp	26.1	0.4	23.6	28.0	0.15	0.14	0.16
Maximum temperature (°C)	temp_max	30.1	0.4	27.9	32.3	**0.25**	−0.21	0.15
Dissolved oxygen (mg/L)	DO	8.4	0.3	6.3	9.8	−0.06	**−0.27**	0.20
Minimum dissolved oxygen (mg/L)	DO_min	5.9	0.5	3.3	7.9	−0.20	**−0.32**	0.16
Conductance (μmhos/cm)	conduct	83.7	11.2	29.2	169.2	**0.26**	0.19	−0.16
Chlorophyll *a* (μg/L)	Chla	19.9	3.6	4.7	42.1	**0.30**	−0.07	0.22
Maximum chlorophyll *a* (μg/L)	Chla_max	39.1	8.1	6.8	100.0	**0.30**	0.00	0.15
Total phosphorus (mg/L)	TP	0.04	0.01	0.02	0.08	**0.29**	−0.08	0.23
Ammonia (mg/L)	NH_3	0.03	0.01	0.02	0.05	0.24	0.19	−0.05
Nitrites and nitrates (mg/L)	NO_2+NO_3	0.2	0.04	0.02	0.4	0.22	−0.17	0.14
Total Kjeldahl nitrogen (mg/L)	TKN	0.5	0.06	0.2	0.9	**0.31**	0.02	0.10
	Eigenvalues					9.04	3.58	2.69
	Percent variance explained					45.2	17.9	13.5
	Cumulative percent variance explained					45.2	63.1	76.6

Physicochemical variables were estimated from monthly samples taken 1 m beneath the surface between may and September from 2014 to 2018 (Ambient Lakes Monitoring Program Database). means, standard errors (SE), minimums (Min), maximums (Max), eigenvalues for the first three principal components, and their associated eigenvectors are provided for each reservoir variable. Significant eigenvectors ($p \leq 0.05$) from the principal component analysis are indicated in bold.

Table 2. Mean and standard error (given in parentheses) of morphometric and physicochemical variables of five North Carolina, USA river basins (N represents reservoir sample size for each basin). physicochemical variables were sampled 1 m beneath the surface monthly (may through September) from 2014 to 2018 (Ambient Lakes Monitoring Program Database).

	Hiwassee	Catawba	Yadkin	Cape Fear	Roanoke
Variable	$N = 1$	$N = 3$	$N = 4$	$N = 1$	$N = 2$
Surface area (km^2)	23.7	12.0 (3.5)	28.7 (11.2)	56.4	50.4 (31.8)
Drainage area (km^2)	2,507	3,323 (270.7)	11,135 (48,141)	4,377	21,541 (59.6)
Volume (km^3)	0.5	0.1 (0.04)	0.2 (0.06)	0.3	0.3 (0.2)
Shoreline Development Index	15.2	10.1 (1.2)	13.6 (2.5)	12.1	11.2 (6.3)
Elevation (m a.s.l.)	464	281 (14.2)	153 (24.4)	66	51 (10.4)
Mean depth (m)	43.3	8.4 (1.2)	11.7 (5.4)	4.3	8.5 (3.7)
Maximum depth (m)	93.9	20.9 (2.9)	28.1 (10.0)	11.6	29.6 (0.6)
Secchi depth (m)	3.9	1.3 (0.07)	1.0 (0.2)	0.7	1.71 (0.01)
Turbidity (NTU)	1.9	5.6 (1.5)	8.7 (2.6)	10.8	5.02 (0.3)
Temperature (°C)	25.9	24.6 (0.5)	27.1 (0.5)	27.2	25.8 (0.6)
Maximum temperature (°C)	27.9	29.7 (0.5)	31.4 (0.4)	30.6	28.8 (0.4)
Dissolved oxygen (mg/L)	8.2	9.2 (0.1)	8.4 (0.8)	8.0	7.6 (0.4)
Minimum dissolved oxygen (mg/L)	7.5	7.5 (0.3)	5.3 (0.6)	4.6	4.7 (1.4)
Conductance (μmhos/cm)	29.2	54.0 (1.0)	89.5 (1.1)	169.2	101.5 (0.1)
Chlorophyll *a* (μg/L)	4.7	14.1 (1.2)	29.8 (4.2)	35.7	8.7 (0.5)
Maximum chlorophyll *a* (μg/L)	6.8	26.3 (0.9)	50.5 (8.2)	100.0	21.0 (1.0)
Total phosphorus (mg/L)	0.02	0.03 (0.01)	0.05 (0.02)	0.06	0.02 (<0.01)
Ammonia (mg/L)	0.02	0.02 (<0.01)	0.03 (<0.01)	0.05	0.03 (0.01)
Nitrites and nitrates (mg/L)	0.02	0.1 (0.02)	0.3 (0.06)	0.09	0.05 (0.01)
Total Kjeldahl nitrogen (mg/L)	0.2	0.4 (0.01)	0.6 (0.05)	0.9	0.4 (0.01)

variables previously recognized as important in structuring lentic fish assemblages (Jackson and Harvey 1993; Irz et al. 2007; Miranda et al. 2008; Fischer and Quist 2019).

Sample design and data collection

Fish assemblage

Fish sampling was conducted to ensure that samples were spatially allocated throughout each reservoir to sufficiently characterize fish assemblages. A geographic information system was used to generate 20 sample reaches that were evenly spaced based on the unique shoreline length of each reservoir. At each of the 20 sample reaches, a combination of passive and active sampling methods was used to characterize fish assemblage composition. For this study, each reservoir was sampled once actively (December 2018) and once passively (either December 2017–March 2018 or December 2018–March 2019). Sampling occurred during the same months to minimize temporal variation among fish samples and limit potential sampling biases in species representation among seasons.

Boat electrofishing and gillnets were used to sample fish assemblages to maximize the number of fish species, individuals, and length classes sampled, thereby reducing sampling gear bias (Fischer and Quist 2014a). Littoral species were targeted using pulsed DC nighttime boat electrofishing (beginning 30 min after sunset) to account for effects of diel period on electrofishing catch rates (Sanders 1992; Schael et al. 1995; Reynolds 1996; Pierce et al. 2001; McInerny and Cross 2005) and to maximize the number of species and individuals sampled for characterizing assemblage composition (Fischer and Quist 2014a). Twenty electrofishing samples in each reservoir were conducted along the shoreline in a randomly selected direction for 5 min at approximately 3.2 km/h with two netters using 6.3-mm delta mesh dipnets. Pulsed DC electrofishing output was standardized to 3000 W for all water bodies following Burkhardt and Gutreuter (1995), Miranda and Boxrucker (2009), and Miranda (2009).

Gillnets were 61 m long and consisted of four 15.2-m sections (2.4 m in height) and four bar-mesh sizes arranged in a random order: 38 mm, 64 mm, 76 mm, 51 mm. In each reservoir, 20 gillnets were set at least an hour before sunset, bottom-deployed perpendicular to shore in at least 3 m depth, and retrieved an hour after sunrise the following day. The first deployed mesh (i.e. 38 mm or 51 mm) was randomized at each location and recorded.

Fish total length (TL) and weight were measured to the nearest millimeter and gram, respectively. Fish were identified to species in the field and released. Catch-per-unit-effort (CPUE) was estimated on a species-specific basis as the mean number of individuals per hour of electrofishing and the mean number of individuals per net-night (NN) for gillnets. Species represented by fewer than 10 individuals for a sampling method were removed from gear-specific taxonomic analyses (see below).

Statistical analyses

Group comparisons of reservoir environmental variables

Statistical analyses were performed using Program R version 3.6.1 (R Core Team 2019). An alpha value of 0.05 was used for detection of statistically significant differences. All environmental variables were treated as independent, allowing the exploration of all possible relationships in all analyses motivated by the objectives. A permutational multivariate analysis of variance (PERMANOVA) on the Bray-Curtis dissimilarity matrices of habitat variables was used to test for differences among morphometric and physicochemical variables of reservoirs and river basins. The PERMANOVA is a non-parametric test that partitions variation from dissimilarity-based matrices and estimates an analog to Fisher's F-ratio (Anderson 2001). Differences in environmental variables among river basins were evaluated using analysis of variance (ANOVA). Principal component analysis (PCA) was used to reduce the dimensionality of reservoir habitat variables and test for potential patterns in environmental variables that might otherwise be undetected. Eigenvectors from the PCA represent the magnitude or importance of, and tests for patterns among, the environmental variables (Table 1).

Catch summary

To summarize catches, differences in species, family, and trophic (following trophic classification from Miranda et al. 2008) richness among river basins were evaluated with individual tests based on the distribution of the data (ANOVA or Kruskal-Wallis) for overall differences in assemblage structure. Richness was defined as the total count of species. To further assess catches, nonmetric multidimensional scaling (NMDS) was used to ordinate the Bray-Curtis dissimilarity of reservoir fish assemblage composition using taxonomic CPUE. To minimize gear bias and prevent mixing of relative abundances from multiple sampling gears, fish assemblage composition (i.e. abundance and diversity) was evaluated separately for electrofishing and gillnet samples. Differences in fish assemblage composition among reservoirs were tested using PERMANOVA. Like the NMDS analysis, PERMANOVAs were conducted separately for each sampling method (i.e. electrofishing, gillnet) and assemblage composition measure. If statistically significant differences in fish assemblage composition among reservoirs were observed using PERMANOVA, similarity percentage (SIMPER; Clarke 1993) was estimated to determine the contributions of species to the overall Bray-Curtis dissimilarity. The Shannon diversity (Shannon 1948) and Pielou evenness (Pielou 1966) indices were used to compare the river-basin diversity among electrofishing and gillnet sampling methods.

Fish assemblage comparisons

Correlations between fish assemblage structure and morphometric and physicochemical reservoir variables were evaluated using rotational environmental vector fitting with NMDS ordinations to test for significantly correlated environmental vectors and evaluate the direction of the maximum correlation using 999 random permutations of the data (Faith and Norris 1989). Rotational vector fitting was conducted using taxonomic fish assemblage data for sampling-gear-specific NMDS ordinations to test for potential relationships between fish assemblage structure and habitat variables.

Analysis of similarities (ANOSIM; Clarke 1993) was performed on sampling-method-specific catch rate data to test for significant differences in river basin fish assemblages using Bray-Curtis dissimilarity and 999 random permutations of the data. A Bray-Curtis dissimilarity matrix was then used to generate pairwise comparisons of river-basin taxonomic structure to quantify differences in fish assemblages for each sampling method. Similarity percentages were subsequently calculated for each sampling method to identify species that disproportionally contributed to overall Bray-Curtis dissimilarity among river basins. Spearman's rank correlation was calculated to evaluate relationships among the catch rates of the top contributing species, reservoir habitat variables, and diversity indices.

Results

Group comparisons of reservoir environmental variables

The reservoirs in this study represented a wide range of surface areas, elevations, and depths, but collectively, morphometric variables did not differ among reservoirs ($F_{1,10}$ =

0.21; $p = 0.91$) or river basins ($F_{4,6} = 0.72$; $p = 0.69$). However, physicochemical variables differed among reservoirs ($F_{1,10} = 4.92$; $p = 0.03$) and river basins ($F_{4,6} = 26.61$; $p \leq 0.001$). Specifically, river basins differed in elevation ($F_{4,6} = 27.8$; $p \leq 0.001$), water temperature ($F_{4,6} = 5.96$; $p = 0.03$), chlorophyll *a* ($F_{4,6} = 8.21$; $p = 0.01$), conductance ($F_{4,6} = 1081$; $p \leq 0.001$), and total Kjeldahl nitrogen ($F_{4,6} = 21.49$; $p = 0.001$; Table 2).

Three principal component axes explained 76.6% of the variation in environmental variables, with 45.2% of the overall variation explained by the first principal component. The first principal component represented a gradient between increased nutrient availability (e.g. nitrogen and phosphorus) and greater water depth and clarity (Table 1). The second principal component denoted a gradient between larger reservoir size (i.e. volume, surface area) and lower dissolved oxygen (DO). Finally, the third principal component represented a gradient between (1) greater shoreline development and elevation and (2) smaller drainage area.

Catch summary

Collectively, 20,383 fish representing 52 species (Table 3) were sampled across all reservoirs using electrofishing ($N = 9{,}095$) and gillnets ($N = 11{,}288$). Electrofishing produced 43 species (12 exclusively), whereas gillnet sampling produced 40 species (9 exclusively; Figure 2). Fourteen species were detected in all reservoirs using at least one sampling

Table 3. Fishes sampled from 11 reservoirs across North Carolina, USA.

Common name	Scientific name	Code
Alewife[a]	*Alosa pseudoharengus*	ALWF
Black Crappie[c]	*Pomoxis nigromaculatus*	BLCR
Blue Catfish[b]	*Ictalurus furcatus*	BLCF
Blueback Herring[a,c]	*Alosa aestivalis*	BBHR
Bluegill[c]	*Lepomis macrochirus*	BLGL
Brown Bullhead	*Ameiurus nebulosus*	BRBH
Chain Pickerel[b]	*Esox niger*	CPIC
Channel Catfish[c]	*Ictalurus punctatus*	CHCF
Common Carp[c]	*Cyprinus carpio*	CCRP
Flathead Catfish[b,c]	*Pylodictis olivaris*	FHCF
Gizzard Shad[c]	*Dorosoma cepedianum*	GZSD
Green Sunfish[a]	*Lepomis cyanellus*	GNSF
Largemouth Bass[c]	*Micropterus salmoides*	LMBS
Longnose Gar[b]	*Lepisosteus osseus*	LNGR
Notchlip Redhorse[b]	*Moxostoma collapsum*	NLRH
Pumpkinseed[a,c]	*Lepomis gibbosus*	PUMP
Quillback[b]	*Carpiodes cyprinus*	QBCK
Redbreast Sunfish[a,c]	*Lepomis auritus*	RBSF
Redear Sunfish[c]	*Lepomis microlophus*	RESF
Silver Redhorse[b]	*Moxostoma anisurum*	SVRH
Smallmouth Bass[b]	*Micropterus dolomieu*	SMBS
Spotted Bass	*Micropterus punctulatus*	SPBS
Striped Bass[c]	*Morone saxatilis*	STBS
Threadfin Shad[a]	*Dorosoma petenense*	THSD
Walleye[b]	*Sander vitreus*	WLYE
Warmouth[a]	*Lepomis gulosus*	WMTH
White Bass[b]	*Morone chrysops*	WHBS
White Catfish[b]	*Ameiurus catus*	WHCF
White Crappie[b]	*Pomoxis annularis*	WHCR
White Perch[c]	*Morone americana*	WHPH
White Shiner[a]	*Luxilus albeolus*	WHSH
Yellow Bullhead[b]	*Ameiurus natalis*	YLBH
Yellow Perch[c]	*Perca flavescens*	YLPH

Species with fewer than 10 sampled individuals were removed from gear-specific taxonomic analyses.
[a] Species for which < 10 individuals were sampled across all gillnet samples.
[b] Species for which < 10 individuals were sampled across all electrofishing samples.
[c] Species detected in all reservoirs.

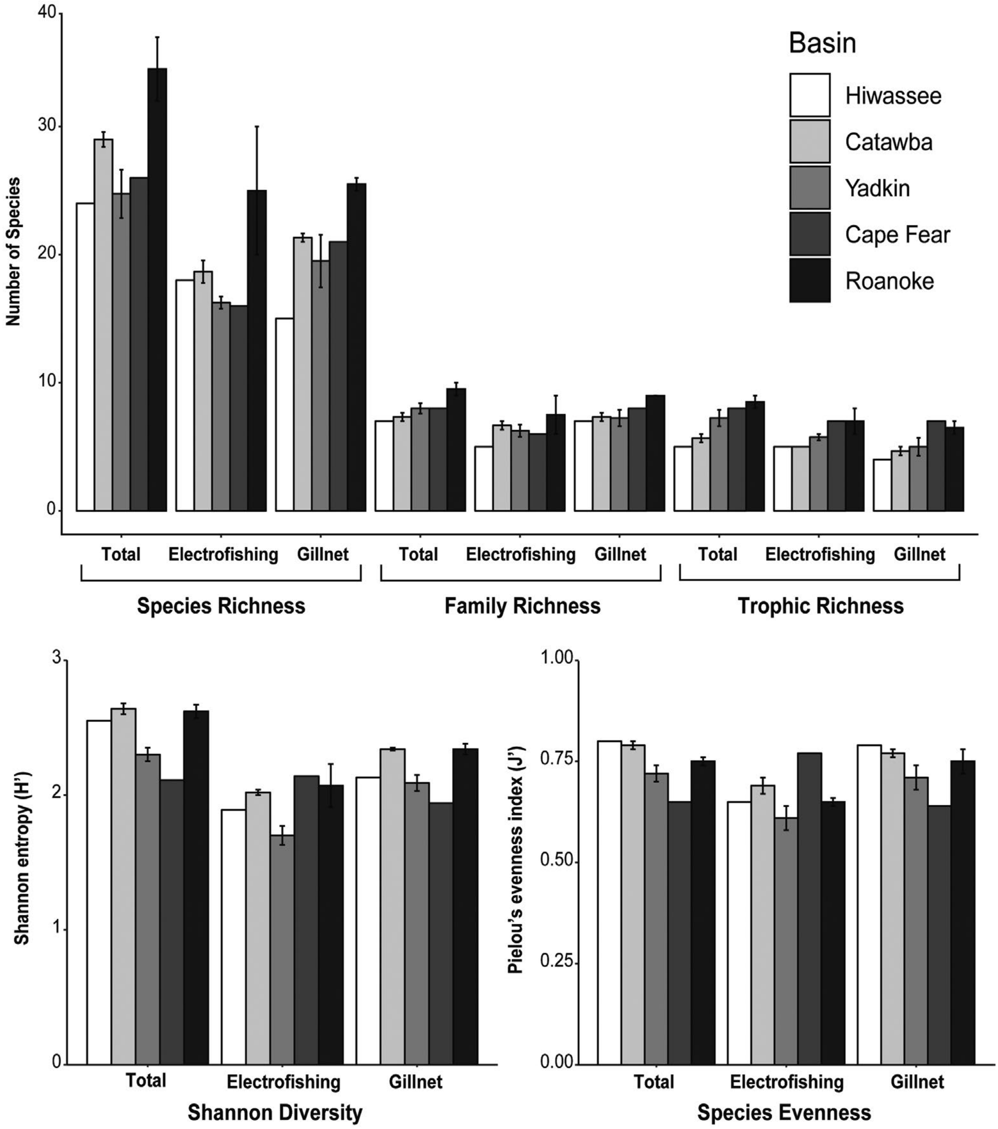

Figure 2. Mean river-basin species, family, and trophic richness (top, left to right), Shannon diversity (bottom left), and Pielou evenness (bottom right) for total sampling (electrofishing and gillnet) in 11 North Carolina, USA reservoirs. Error bars represent 95% confidence intervals around each mean; missing error bars reflect a sample size of one.

method (Table 3). These species represented 81.4% of the total catch and 61.9% of the total sampled biomass. No statistically significant differences were observed in electrofishing or gillnet sampling comparisons of river-basin species, family, and trophic richness or species evenness (Figure 2). Furthermore, using combined data from both sampling methods, hereafter referred to as ‘total sampling’, species richness differed significantly among river basins ($F_{4,6}$ = 6.53; $p = 0.02$). The river-basin Shannon diversity index was significantly different among gillnet samples ($F_{4,6}$ = 15.1; $p = 0.003$), but not among electrofishing samples ($F_{4,6}$ = 4.36; $p = 0.054$; Figure 2).

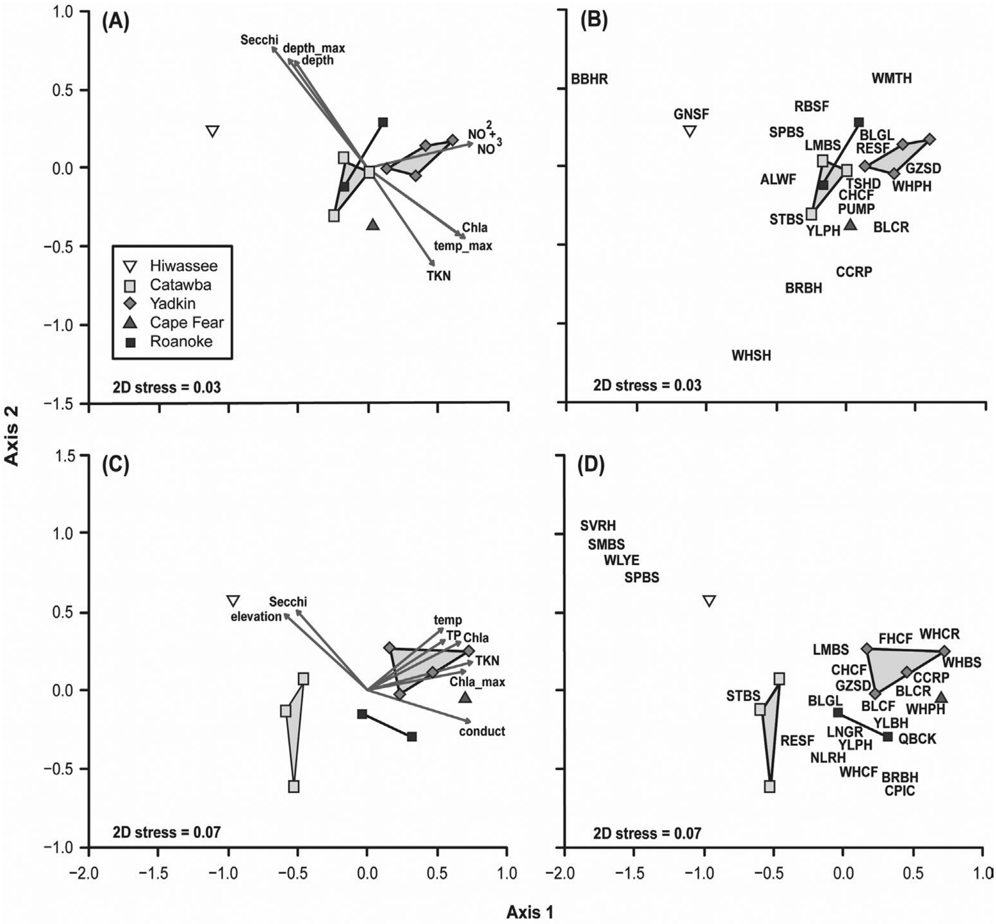

Figure 3. River basin-specific fish assemblage composition nonmetric multidimensional scaling (NMDS) ordinations based on Bray-Curtis dissimilarity of taxonomic catch-per-unit-effort (appendix A) for 11 North Carolina, USA reservoirs. Environmental vectors for (A) electrofishing and (C) gillnet samples indicate the direction and strength of statistically significant ($p \leq 0.05$) correlations within the NMDS ordination for habitat variables with abbreviated codes (Table 1). species-specific ordinations for (B) electrofishing and (D) gillnet samples are presented using species codes (Table 3).

Fish assemblage comparisons

Statistically significant differences in taxonomic fish assemblage composition among river basins were observed (electrofishing [$F_{4,6}$ = 3.69; $p = 0.007$], gillnet [$F_{4,6}$ = 3.44; $p = 0.002$]). Multivariate analyses of taxonomic composition produced low-stress NMDS ordinations for electrofishing (2 axes; stress = 0.03; Figure 3 [A and B]) and gillnet samples (2 axes; stress = 0.07; Figure 3 [C and D]). Taxonomic fish assemblage structure differed among river basins for electrofishing ($r = 0.61$; $p = 0.005$) and gillnet samples ($r = 0.74$; $p = 0.001$). Gillnet samples displayed higher estimates of Bray-Curtis dissimilarity in all pairwise river-basin comparisons (Figure 4). Differences in river-basin taxonomic assemblage structure were greatest in pairwise comparisons with the Hiwassee basin and lowest in Roanoke basin comparisons. Similar environmental vectors were associated with NMDS axes for taxonomic composition among reservoirs (Figure 3). The environmental vectors most commonly associated with assemblage structure from electrofishing and gillnet samples were indicators of reservoir productivity, including Secchi, mean, and maximum depths, conductance, nitrogen, phosphorus, chlorophyll *a*, and temperature (Figure 3; Table 4).

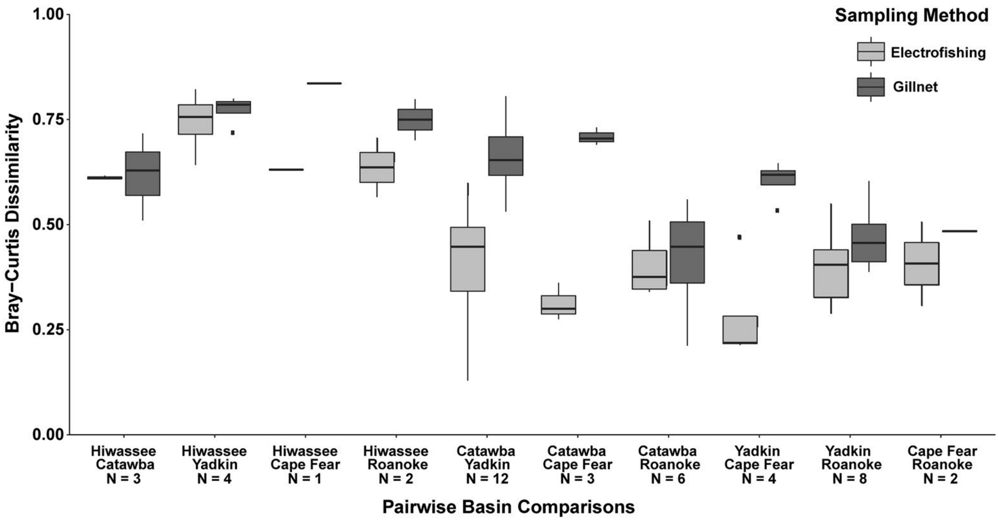

Figure 4. Bray-Curtis dissimilarity of pairwise taxonomic comparisons for five North Carolina, USA river-basin fish assemblages sampled using electrofishing and gillnets. Light grey boxplots represent comparisons of electrofishing-sampled fish assemblages; dark grey denotes fish assemblages collected with gillnets.

Table 4. Environmental vector correlation coefficients for nonmetric multidimensional scaling (NMDS) ordination for electrofishing and gillnet sampling conducted on 11 reservoirs in North Carolina, USA.

	Electrofishing		Gillnet	
Environmental Vectors	r^2	p	r^2	p
Surface area (km^2)	0.19	0.42	0.20	0.43
Drainage area (km^2)	0.23	0.35	0.25	0.32
Volume (km^3)	0.49	0.09	0.24	0.35
Shoreline Development Index	0.46	0.10	0.33	0.21
Elevation (m a.s.l.)	0.46	0.09	**0.73**	**0.01**
Depth (m)	**0.66**	**0.03**	0.54	0.08
Maximum depth (m)	**0.72**	**0.02**	0.49	0.10
Secchi depth (m)	**0.95**	**<0.01**	**0.64**	**0.05**
Turbidity (NTU)	0.46	0.09	0.47	0.07
Temperature (°C)	0.10	0.67	**0.55**	**0.02**
Maximum temperature (°C)	**0.62**	**0.01**	0.43	0.10
Dissolved oxygen (mg/L)	0.00	0.99	0.06	0.76
Minimum dissolved oxygen (mg/L)	0.25	0.33	0.43	0.12
Conductance (μmhos/cm)	0.40	0.14	**0.72**	**0.01**
Chlorophyll *a* (μg/L)	**0.56**	**0.03**	**0.67**	**0.01**
Maximum chlorophyll *a* (μg/L)	0.49	0.08	**0.63**	**0.02**
Total phosphorus (mg/L)	0.40	0.13	**0.51**	**0.05**
Ammonia (mg/L)	0.22	0.34	0.33	0.22
Nitrites and nitrates (mg/L)	**0.53**	**0.05**	0.35	0.17
Total Kjeldahl nitrogen (mg/L)	**0.55**	**0.05**	**0.74**	**<0.01**

NMDS ordinations reflect taxonomic classifications (Figure 3 [a and C]). statistically significant ($p \leq 0.05$) vector correlations for variables in Table 1 are bold.

Several measures of abundance and diversity were correlated with environmental variables. Drainage area was positively correlated with biomass from electrofishing (r_s = 0.63; $p = 0.04$) and gillnet samples (r_s = 0.65, $p = 0.03$), as well as two richness indices (i.e. total family, gillnet species). Electrofishing biomass also positively correlated with water temperature (r_s = 0.68; $p = 0.03$), chlorophyll *a* (r_s = 0.72; $p = 0.02$), maximum chlorophyll *a* (r_s = 0.69; $p = 0.02$), total phosphorus (r_s = 0.65; $p = 0.03$), $NO_2 + NO_3$ (r_s = 0.75; $p = 0.01$), and total Kjeldahl nitrogen (r_s = 0.83; $p = 0.003$), and negatively correlated with minimum DO (r_s = −0.70; $p = 0.02$). Additionally, gillnet biomass correlated with surface area (r_s = 0.69; $p = 0.02$), water temperature (r_s = 0.66; $p = 0.03$), conductance (r_s = 0.65; $p = 0.03$), and lower elevation (r_s = −0.64; $p = 0.04$).

Four species accounted for the greatest Bray-Curtis dissimilarity across all comparisons: bluegill (*Lepomis macrochirus*; 23%) and gizzard shad (*Dorosoma cepedianum*; 21%) in electrofishing samples, and black crappie (*Pomoxis nigromaculatus*; 18.7%) and white perch (*Morone americana*; 13.9%) in gillnet samples (Figure 5). Gear-specific catch rates for gizzard shad, black crappie, and white perch were all positively correlated with water temperature, chlorophyll *a*, maximum chlorophyll *a*, and total Kjeldahl nitrogen (Table 5). Additionally, black crappie and white perch catch rates were negatively correlated with greater mean depth and minimum DO and positively correlated with conductance. Gizzard shad and black crappie catch rates were positively correlated with higher levels of total phosphorus and decreased with greater Secchi depth. Bluegill and gizzard shad catch rates were positively correlated with elevated nitrogen levels, as were overall electrofishing catch rates (r_s = 0.65; $p = 0.03$). High white perch CPUE was observed in areas of high turbidity, and black crappie CPUE was positively correlated with warmer water temperatures.

Discussion

Synopsis

We found that differences among reservoirs in fish assemblage structure were driven primarily by productivity gradients that were consistent within river basins. Additional gradients influencing assemblage composition were associated with reservoir size and geography. Certain species (bluegill, gizzard shad, black crappie, white perch) contributed disproportionately to river-basin differences, and their patterns of relative abundance were positively associated with primary productivity. On an individual species level, these fish are important both recreationally (Spotte 2007) and ecologically (Mills et al. 1994; Schaus and Vanni 2000), but together could serve as indicators of productivity, anthropogenic influence, and fish assemblage structure in reservoirs.

Group comparisons of reservoir environmental variables

Reservoirs differed across individual morphometric and physicochemical gradients but were more similar within than among river basins. River-basin similarity was further supported by ordinations of reservoir taxonomic fish assemblages, in which reservoirs within the same basin were positioned closer together, with minimal overlap among basins. Our findings indicate that basin-wide analyses can yield ecological insights on fish populations, assemblages, and habitats that reservoir-specific analyses do not. Including river basin in analyses emphasizes the natural landscape and accounts for reservoir connectivity (or lack thereof). Similarly, Kratz et al. (1997) provided examples of how landscape position of Wisconsin lakes related to gradients of primary production, lake area, and species richness, likening their observations to the river continuum concept (Vannote et al. 1980).

Catch summary

Species richness, diversity, and evenness variation were primarily associated with eutrophic system physiochemical variables. Eutrophication accelerated by anthropogenic activity (e.g. cultural eutrophication) can cause structural changes in freshwater ecosystems

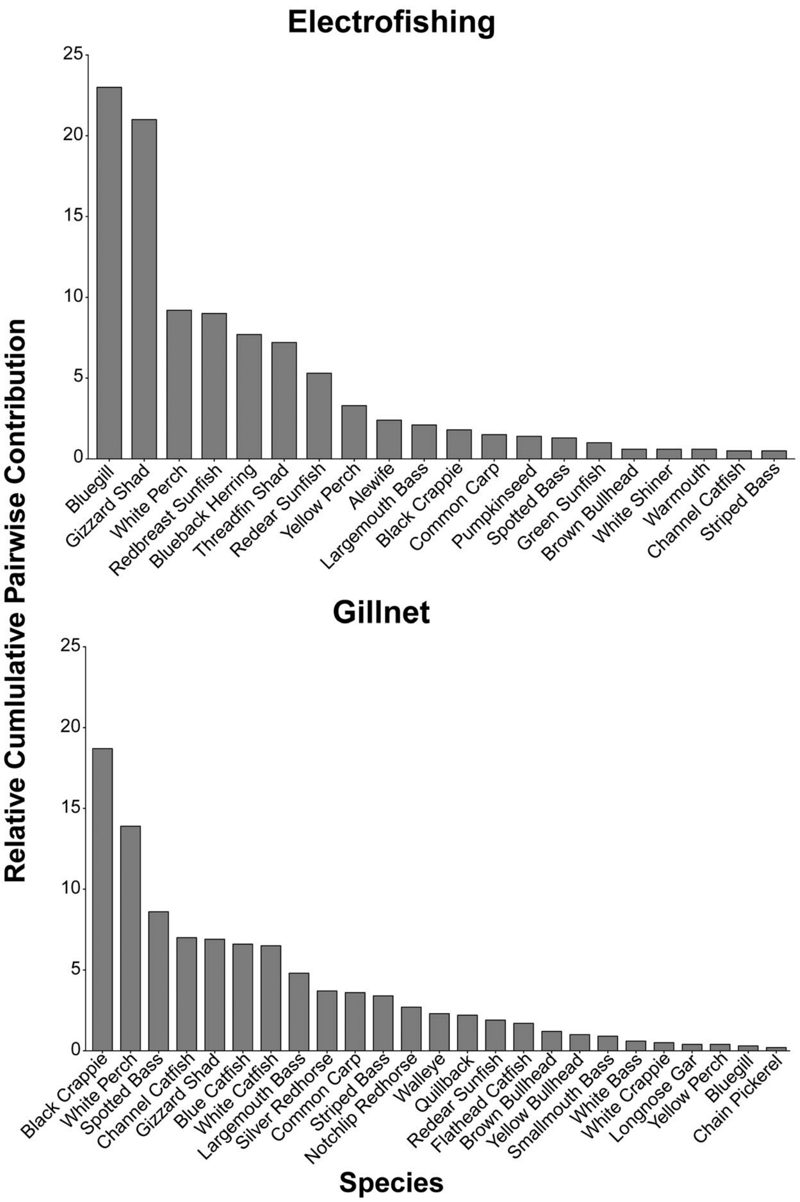

Figure 5. Rank order cumulative contribution of reservoir species from electrofishing (top) and gillnet (bottom) samples to pairwise Bray-Curtis dissimilarities among river basins in North Carolina, USA. Cumulative species contributions to reservoir fish assemblage dissimilarities are relative as a 10% cumulative contribution is equivalent to all Bray-Curtis dissimilarity contained in a single pairwise comparison of two of the eleven sampled reservoirs.

including harmful algal blooms and mortality of aquatic organisms from hypoxic events (e.g. agricultural runoff, wastewater disposal; Schindler and Vallentyne 2008; Schindler 2012). Reservoirs, by definition, are an example of environmental manipulation and are more susceptible to anthropogenic disturbances, such as eutrophication and water fluctuation, than natural lakes (Wetzel 1990; Havel et al. 2005). The annual cost of eutrophication in U.S. freshwater systems has been estimated at $2.2 billion through economic losses

Table 5. Spearman rank correlation coefficients between sampling gear-specific catch rates of bluegill, gizzard shad, black crappie, and white perch and river-basin habitat variables of 11 North Carolina, USA reservoirs.

	Electrofishing				Gillnet			
	Bluegill		Gizzard Shad		Black Crappie		White Perch	
Variable	r_s	p	r_s	p	r_s	p	r_s	p
Surface area (km^2)	0.24	0.49	0.11	0.75	0.35	0.29	0.16	0.63
Drainage area (km^2)	0.57	0.07	0.27	0.42	0.47	0.15	**0.61**	**0.05**
Volume (km^3)	0.13	0.71	−0.08	0.82	0.05	0.88	−0.15	0.67
Shoreline Development Index	0.28	0.40	0.17	0.61	0.18	0.60	−0.05	0.88
Elevation (m a.s.l.)	−0.26	0.43	−0.13	0.71	−0.56	0.08	−0.59	0.06
Depth (m)	−0.02	0.96	−0.34	0.31	**−0.61**	**0.05**	**−0.65**	**0.03**
Maximum depth (m)	−0.15	0.67	−0.49	0.12	−0.47	0.15	−0.32	0.33
Secchi depth (m)	−0.20	0.56	**−0.65**	**0.03**	**−0.69**	**0.02**	−0.52	0.11
Turbidity (NTU)	0.25	0.45	0.48	0.14	**0.61**	**0.05**	**0.67**	**0.03**
Temperature (°C)	0.17	0.61	0.41	0.21	**0.68**	**0.03**	0.54	0.09
Maximum temperature (°C)	0.44	0.17	**0.82**	**<0.01**	**0.68**	**0.03**	**0.62**	**0.05**
Dissolved oxygen (mg/L)	0.17	0.61	0.23	0.50	−0.20	0.56	−0.36	0.27
Minimum dissolved oxygen (mg/L)	−0.42	0.20	−0.40	0.23	**−0.71**	**0.02**	**−0.69**	**0.02**
Conductance (μmhos/cm)	0.25	0.47	0.29	0.39	**0.76**	**0.01**	**0.74**	**0.01**
Chlorophyll *a* (μg/L)	0.45	0.16	**0.79**	**0.01**	**0.84**	**<0.01**	**0.65**	**0.04**
Maximum chlorophyll *a* (μg/L)	0.33	0.33	**0.74**	**0.01**	**0.85**	**<0.01**	**0.66**	**0.03**
Total phosphorus (mg/L)	0.35	0.29	**0.80**	**0.01**	**0.74**	**0.01**	0.59	0.06
Ammonia (mg/L)	0.28	0.40	0.39	0.23	**0.60**	**0.05**	0.44	0.18
Nitrites and nitrates (mg/L)	**0.63**	**0.04**	**0.84**	**<0.01**	0.55	0.08	0.52	0.11
Total Kjeldahl nitrogen (mg/L)	0.43	0.19	**0.78**	**0.01**	**0.92**	**<0.01**	**0.75**	**0.01**

Correlation coefficients with $p \leq 0.05$ are indicated in bold.

in drinking water, biodiversity recovery, lake closure to recreational use, and property value (Dodds et al. 2009). These anthropogenic effects will likely increase globally, as the world's population is expected to grow by over 40% between 2003 and 2050 (Cohen 2003). Therefore, gradients in productivity and trophic state, which separated reservoirs herein, may change over time as anthropogenic influences continue to alter these and other reservoirs.

Carol et al. (2006) used boat electrofishing and gillnets to sample 14 Spanish reservoirs and found that trophic state (i.e. chlorophyll *a*, total nitrogen, and total phosphorus) and altitude explained most of the fish assemblage variation. In our study, all significant predictors of species richness, diversity, and evenness were inversely associated with productivity. A gradient of productivity was observed by environmental vector coefficients in fish assemblage ordinations for all taxonomic sampling data. Additionally, drainage area and water clarity were the only indicators of increases in species richness. Species richness of lentic fish assemblages is known to be positively correlated with water body size (Irz et al. 2007; Miranda et al. 2008), total phosphorus (Olin et al. 2002), habitat complexity (Fischer and Quist 2019), and mean depth (Irz et al. 2002). In these studies, physicochemical variables associated with productivity explained the most fish-assemblage variation among systems, similar to reservoir fish assemblages evaluated herein.

Fish assemblage comparisons

Physicochemical variables associated with eutrophic systems explained most of the overall fish-assemblage variation. Associations between primary productivity (e.g. chlorophyll *a*, total phosphorus, lake depth) and fish yield (i.e. fish abundance or biomass) are well-documented (Oglesby 1977; Downing et al. 1990; Downing and Plante 1993). Gizzard shad, typically the predominant forage fish by biomass in southern reservoirs (Noble

1981), may benefit most from greater productivity as their abundance across lengths and ages tends to increase with reservoir trophic state (DiCenzo et al. 1996; Bremigan and Stein 1999; Bremigan and Stein 2001). Specifically, Bremigan and Stein (2001) found that hatch abundance and survival of larval gizzard shad was positively correlated with total phosphorus concentrations in Ohio reservoirs. We observed the same relationship, as gizzard shad CPUE was positively correlated with most productivity measures. However, turbidity was not a suitable predictor of gizzard shad CPUE, in contrast to Aday et al. (2003). The large observed contribution of gizzard shad CPUE to reservoir dissimilarity is predictable because gizzard shad are seldom found in oligotrophic systems and have the potential to be the greatest contributor to overall biomass in hypereutrophic systems (Bachmann et al. 1996). The success of gizzard shad populations in productive reservoirs can likely be attributed to beneficial life history traits such as rapid growth rates, omnivory, and high fecundity (Bremigan and Stein 1999; Schaus and Vanni 2000, Bremigan and Stein 2001). As organisms with the potential to foster eutrophication by consuming detritus, translocating phosphorus and nitrogen in the water column (Schaus et al. 1997; Vanni et al. 2005), and increasing phytoplankton biomass (Aday et al. 2003), gizzard shad populations can have adverse effects on other species.

Clupeids and lepomids, considered ubiquitous fish in many reservoir systems, are important to fish community structure because they can account for most of all prey fishes consumed in reservoirs (e.g. 80%; Raborn et al. 2007). These taxa were represented by two species—gizzard shad and bluegill—with the highest observed relative contributions to fish assemblage dissimilarity in this study. The effects of gizzard shad on reservoir fish assemblages, especially bluegill populations, are well documented. Gizzard shad and bluegill abundances can be negatively correlated (Garvey and Stein 1998), and gizzard shad removal has been associated with short-term increases in bluegill abundance and more consistent spawning (Kirk et al. 1986). Aday et al. (2003) found that gizzard shad presence in Illinois reservoirs was associated with reduced bluegill growth rates and maximum adult length, suggesting that larval competition could negatively affect bluegill size structure. However, Neely et al. (2018) found no significant trend in bluegill abundance following the near eradication of gizzard shad in a Kansas impoundment, suggesting a greater role of bluegill intraspecific density dependence than was observed in similar studies. Like gizzard shad, bluegills may also contribute to eutrophication; Nowlin and Drenner (2000) found that bluegills increased turbidity, chlorophyll *a*, total nitrogen, and total phosphorus in mesocosm fish assemblages.

Bluegill CPUE was positively related to all measures of productivity, but it was only significantly correlated with nitrogen ($NO_2 + NO_3$) despite its high contribution to reservoir fish assemblage dissimilarity and the strong gradient of productivity observed throughout our study. Other studies have documented positive relationships between bluegill growth and total phosphorus (Sundmark and Jennings 2017), and bluegill abundance and turbidity (Bevil and Weber 2018). Bluegills may also benefit from greater productivity, as increases in turbidity may lower predation risk (Miner and Stein 1996). Future research investigating how bluegill populations are affected by biotic and abiotic variables is important due to the complexity of these relationships (e.g. Carlson and Hoyer 2023), particularly their context dependence relative to habitat and fish assemblage alteration, and the role of bluegills as indicators of reservoir fish assemblage differences, as observed herein.

Black crappies also contributed substantially to driving reservoir fish assemblage differences and were positively associated with factors reflecting increasing eutrophic conditions. Rapid growth rates of black crappies have been observed in eutrophic reservoirs (Maceina et al. 1996), and Bachmann et al. (1996) found that black crappie occurrence and standing crop were positively correlated with trophic state. We observed that black crappie CPUE was positively correlated with chlorophyll *a*, which has been positively associated with first-year growth in Minnesota (McInerny and Cross 1999), juvenile abundance in Alabama (Dubuc and DeVries 2002), and probability of occurrence in Florida (Allen et al. 1998). We observed that turbidity-associated variables (e.g. decreased Secchi depth) were positively correlated with black crappie CPUE. Spier and Heidinger (2002) found similar growth among black crappies stocked in ponds across a range of turbidities, suggesting that they can locate prey in turbid water. Our results were consistent with this conclusion, as we observed a moderate, positive correlation between black crappie CPUE and reservoir turbidity. Recruitment variability among black crappie populations in South Dakota waters was best described by shoreline development and reservoir size (Guy and Willis 1995), neither of which influenced black crappie CPUE in our study.

The effects of altered hydrology and watershed disturbance on reservoirs may make them more susceptible to nonnative fish invasions (Marchetti et al. 2004; Havel et al. 2005). White perch are a common freshwater invader (Hergenrader and Bliss 1971; Boileau 1985; Prout et al. 1990; Mills et al. 1994; Feiner et al. 2012) and produce viable populations outside of their native range due to favorable life history traits that include reproductive flexibility (Sheri and Power 1968; Feiner et al. 2012) and opportunistic feeding (Reid 1972; Couture and Watzin 2008). Newly introduced white perch populations often have high growth rates, high fecundity, and early age at maturity, all of which facilitate population establishment (Feiner et al. 2012). Rapid increases in white perch abundance may be associated with declining populations of black crappie and bluegill due to feeding competition (Hurley and Christie 1977; Feiner et al. 2013, 2019). Our findings are concordant with previous research, as white perch were more abundant across our study sites in relatively shallow reservoirs with high nutrient concentrations, high turbidity, and high conductivity, similar to Hawes and Parrish (2003).

Management implications

Among the reservoirs that we sampled, bluegill, gizzard shad, black crappie, and white perch disproportionately explained reservoir fish assemblage dissimilarity, and these species were strongly correlated with variables related to greater productivity. Together, at the assemblage level, these species may merit increased monitoring within the localized environmental context of each reservoir because they are potential indicators of assemblage structure and ecological changes associated with increasing anthropogenic influences in their geographical ranges. Sampling protocols designed to target these four species could be incorporated into fisheries management programs to enhance understanding of their population dynamics and promote informed environmental decision making. However, our results do not support a shift from assemblage-level monitoring to species-specific sampling and, in fact, reinforce the contrary. Indeed, our findings illustrate how simultaneous collection of assemblage- and population-level fisheries data may generate both ecological and management insights. Success in incorporating this framework hinges on consistent monitoring of fish assemblages through standardized sampling, opportunistic data collection on important non-game species, and integration of environmental and fisheries data. Overall, future research on reservoir fish assemblages in relation to biotic and abiotic conditions may be helpful for advancing fish ecology and management alike.

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Disclosure statement

No potential conflict of interest was reported by the authors.

Data deposition

Data supporting the findings of this study are openly available in GitHub: https://github.com/tscoleman3/nc_reservoir_fish_assemblage. Please contact Stephen Parker (stephen.parker@ufl.edu) for data-related questions.

Author contributions

Stephen W. Parker: Methodology, Investigation, Conceptualization, Visualization, Data curation, Software, Writing-original draft preparation, Validation. Tyler Steven Coleman: Conceptualization, Visualization, Writing-reviewing, editing, and formatting, Validation. Andrew K. Carlson: Conceptualization, Writing-reviewing and editing, Supervision, Resources. Jesse R. Fischer: Writing-funded proposal and original draft preparation, Methodology, Conceptualization, Data curation, Supervision, Resources.

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Appendix A

Estimated catch-per-unit-effort (CPUE) for all species individually was calculated as the mean number of individuals per hour of electrofishing and the mean number of individuals per net-night for gillnets. Mean and standard error (SE), minimum (Min), and maximum (Max) CPUE are reported for all species identified in each sampling gear from 11 reservoirs in North Carolina, USA.

		Gillnet		Electrofishing	
Common name	Scientific name	Mean (SE)	Min;Max	Mean (SE)	Min;Max
Alewife[a]	*Alosa pseudoharengus*			5.45 (3.71)	0;42
American Eel[ab]	*Anguilla rostrata*			0.05 (0.05)	0;0.6
Black Bullhead[ab]	*Ameiurus melas*	0.007 (<0.01)	0;0.05		
Blue Catfish[b]	*Ictalurus furcatus*	1.71 (0.61)	0;6.2	0.05 (0.05)	0;0.6
Blueback Herring[a]	*Alosa aestivalis*			8.56 (7.01)	0;78.6
Bowfin[ab]	*Amia calva*	0.002 (<0.01)	0;0.03		
Brassy Jumprock[ab]	*Moxostoma sp.*	0.005 (<0.01)	0;0.05	0.05 (0.05)	0;0.6
Brown Bullhead	*Ameiurus nebulosus*	0.18 (0.17)	0;1.88	0.71 (0.46)	0;4.8
Chain Pickerel[b]	*Esox niger*	0.03 (0.03)	0;0.28	0.38 (0.38)	0;4.2
Channel Catfish	*Ictalurus punctatus*	2.62 (0.7)	0.58;8.48	2.18 (0.48)	0;5.4
Common Carp	*Cyprinus carpio*	0.73 (0.28)	0;2.88	2.29 (1.04)	0;10.8
Eastern Creek Chubsucker[ab]	*Erimyzon oblongus*	0.005 (<0.01)	0;0.05	0.27 (0.17)	0;1.8
Eastern Silvery Minnow[ab]	*Hybognathus regius*			0.11 (0.11)	0;1.2
Flathead Catfish[b]	*Pylodictis olivaris*	0.53 (0.27)	0;3.1	0.11 (0.11)	0;1.2
Gizzard Shad	*Dorosoma cepedianum*	2.25 (0.50)	0.45;5.48	119.29 (28.72)	3.6;330
Golden Redhorse[ab]	*Moxostoma erythrurum*	0.002 (<0.01)	0;0.03	0.05 (0.05)	0;0.6
Golden Shiner[ab]	*Notemigonus crysoleucas*			0.38 (0.17)	0;1.8
Grass Carp[ab]	*Ctenopharyngodon idella*	0.005 (<0.01)	0;0.03	0.11 (0.11)	0;1.2
Longnose Gar[b]	*Lepisosteus osseus*	0.06 (0.03)	0;0.35		
Northern Hog Sucker[ab]	*Hypentelium nigricans*	0.009 (0.01)	0;0.08	0.33 (0.27)	0;3
Notchlip Redhorse[b]	*Moxostoma collapsum*	0.55 (0.27)	0;2.75	0.27 (0.22)	0;2.4
Quillback[b]	*Carpiodes cyprinus*	0.44 (0.25)	0;2.63	0.05 (0.05)	0;0.6
Satinfin Shiner[ab]	*Cyprinella analostana*			0.05 (0.05)	0;0.6
Shorthead Redhorse[ab]	*Moxostoma macrolepidotum*	0.007 (<0.01)	0;0.05		
Sicklefin Redhorse[ab]	*Moxostoma sp.*	0.02 (0.02)	0;0.18		
Silver Redhorse[b]	*Moxostoma anisurum*	0.28 (0.28)	0;3.05	0.27 (0.27)	0;3
Striped Bass	*Morone saxatilis*	1.16 (0.28)	0.2;2.55	0.98 (0.37)	0;3.6
Swallowtail Shiner[ab]	*Notropis procne*			0.16 (0.16)	0;1.8
Threadfin Shad[a]	*Dorosoma petenense*			42.16 (5.79)	0;67.2
V-lip Redhorse[ab]	*Moxostoma pappillosum*	0.01 (0.01)	0;0.08		
White × Striped Bass[ab]	*Morone chrysops × M. saxatilis*	0.005 (<0.01)	0;0.05		
White Bass[b]	*Morone chrysops*	0.11 (0.06)	0;0.53		
White Catfish[b]	*Ameiurus catus*	1.27 (0.49)	0;5	0.27 (0.17)	0;1.8
White Perch	*Morone americana*	4.49 (1.12)	0;9.23	47.56 (9.71)	0.6;117.6
White Shiner[a]	*Luxilus albeolus*			1.15 (1.15)	0;12.6
White Sucker[ab]	*Catostomus commersoni*	0.007 (<0.01)	0;0.05	0.44 (0.44)	0;4.8
Yellow Bullhead[b]	*Ameiurus natalis*	0.13 (0.08)	0;0.73	0.16 (0.12)	0;1.2

[a] Species for which < 10 individuals were sampled across all gillnet samples.

[b] Species for which < 10 individuals were sampled across all electrofishing samples.