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ARTICLE

Influence of Environmental Variables and Species Interactions on Sport Fish Communities in Small Missouri Impoundments

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Abstract

Small impoundments (<400 ha) are numerous and provide close-to-home fishing opportunities for anglers but may not support optimal sport fisheries. Most of these fisheries are managed by harvest regulations, but watershed and impoundment characteristics, poor water quality, or detrimental species interactions can also influence the desirability of fisheries. We examined the relative importance of watershed characteristics, impoundment morphology, water quality, and species interactions in explaining differences in relative abundance, growth, and size structure of five sport fish species (largemouth bass *Micropterus salmoides*, bluegill *Lepomis macrochirus*, redear sunfish *L. microlophus*, white crappie *Pomoxis annularis*, and black crappie *P. nigromaculatus*) among 89 small Missouri impoundments spanning a large fertility gradient. Using regression analysis, we found that variables associated with predation, competition, and lake fertility were most important in explaining variation in sport fish demographics, whereas watershed and impoundment morphology variables were typically less important. Lakes with dense largemouth bass populations commonly contained sunfish and crappie populations with desirable size structure and growth, implying that predation was a strong structuring force. Density-dependent growth was common among all sport fish species. White crappies and black crappies had better growth or size structure in lakes with fewer bluegills, suggesting competition among these species. Lakes containing common carp *Cyprinus carpio* had fewer largemouth bass and slower-growing black crappies than lakes without common carp. The presence of gizzard shad *Dorosoma cepedianum* benefited largemouth bass populations but negatively affected bluegill and black crappie populations. Growth and size structure of sport fishes usually improved with increasing lake fertility. Predation and competition seemed to be most important in structuring sport fish communities in these impoundments provided that lake fertility was adequate to sustain acceptable abundances and growth rates of these fishes.

Small impoundments (<400 ha) are numerous and provide close-to-home fishing opportunities for millions of anglers throughout the United States (Willis et al. 2010). Many agencies in the Midwestern and southern states have constructed and managed small impoundments for the primary purpose of sportfishing. Other impoundments owned by municipalities are similarly managed through cooperative agreements. Some small public impoundments are intensively managed through stocking, fertilization, supplemental feeding, selective or complete prescribed fish kills, water level regulation, and restrictive harvest regulations (Shaner et al. 1996; Olive et al. 2005), but most are managed primarily by harvest regulations and the stocking of channel catfish *Ictalurus punctatus*.

Although these small public impoundments are numerous, many of them do not support optimal sport fisheries, demonstrating poor growth, poor size structure, or both for one or

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more sport fish species. There are probably many causes for these less-than-ideal populations, including overharvest, poor water quality and habitat, and deleterious species interactions. Early studies of these systems documented the overharvest of largemouth bass *Micropterus salmoides*, which led to the restriction of angler harvest by imposing minimum length limits (Funk 1974) and various other length restrictions, including slot limits (Anderson 1976; Eder 1984; Novinger 1990). Currently, overharvest of largemouth bass may be relatively uncommon because of these length limits and the common practice of catch and release (Quinn 1996; Siepker et al. 2007; Myers et al. 2008). High angler exploitation of other common species, such as the bluegill *Lepomis macrochirus*, black crappie *Pomoxis nigromaculatus*, and white crappie *Pomoxis annularis* (Coble 1988; Eder 1990; Bister 2002), can result in poor fish size structure by directly removing large fish and creating shifts in life history strategies (Beard et al. 1997; Drake et al. 1997). Although length limits have been imposed for some small impoundments, these regulations frequently have not improved fish size structure and have not been well received by anglers (e.g., Bister 2002; Hurley and Jackson 2002; Ott et al. 2003). Poor growth or high natural mortality probably limits the effectiveness of length limits for panfish in many small impoundments (Allen and Miranda 1995; Beard et al. 1997; Crawford and Allen 2006).

Within small impoundments, water quality and habitat as determined by watershed characteristics (e.g., land use, geology, and basin morphometry; Knoll et al. 2003; Jones et al. 2004, 2008a; Bremigan et al. 2008) may also influence fish population dynamics. For example, impoundments in agricultural landscapes typically contain higher nutrient levels than impoundments in forests (Jones et al. 2004). Within either landscape type, impoundments with high flushing rates, which are a function of watershed and impoundment morphometry, tend to have higher nutrient concentrations than those with long water retention (Bremigan et al. 2008; Jones et al. 2008a). Sport fish biomass and harvest tend to increase with lake fertility (Hanson and Leggett 1982; Jones and Hoyer 1982). Growth and size structure of sport fishes are often positively correlated with water fertility (e.g., Tomcko and Pierce 2005; Wagner et al. 2007; Schultz et al. 2008; Hoxmeier et al. 2009), probably because of the greater prey abundance in more fertile waters. However, undesirable fish species are common in highly fertile systems (Bachmann et al. 1996; Egertson and Downing 2004). McInerny and Cross (1999) found that the first-year growth of black crappies increased with chlorophyll concentrations up to a threshold of approximately 100 μg/L, after which growth was reduced. This finding suggests that excessive nutrient concentrations can lead to undesirable growth and size structure of sport fishes, similar to the relationship observed for biomass. Many of these highly fertile systems also suffer from low dissolved oxygen levels and periodic fish kills (Moyle 1949; Mericas and Malone 1984).

Abundance, growth, and size structure of sport fishes have been also linked to lake morphometry and aquatic vegetation. Lake morphometric variables, such as water depth (Tomcko and Pierce 2001; Paukert and Willis 2004; Schultz et al. 2008), surface area (Cross and McInerny 2005; Tomcko and Pierce 2005), volume (Shoup et al. 2007), basin slope (Hill 1984), shoreline complexity (Guy and Willis 1995; Schultz et al. 2008), and percent littoral area (Tomcko and Pierce 2001; Shoup et al. 2007), are often correlated with various sport fish demographic variables, sometimes with conflicting results. For example, desirable growth or size structure of bluegills was positively related to water depth in Iowa lakes (Schultz et al. 2008) but negatively related to water depth in Minnesota lakes (Tomcko and Pierce 2001). Similarly, the reported relationships between aquatic macrophyte coverage and sport fish demographics have been inconsistent (Savino et al. 1992; Hoyer and Canfield 1996; Pothoven et al. 1999; Paukert and Willis 2004; Cheruvelil et al. 2005). Dibble et al. (1996) suggested that the growth of sport fishes should be optimized at some intermediate plant density because excessive macrophyte coverage could lead to excessive fish densities and corresponding slow growth, whereas sparse vegetation could result in slow growth because of the depletion of food resources. Others have not detected this unimodal relationship between sport fish growth and plant density (Savino et al. 1992; Cheruvelil et al. 2005).

Fish population dynamics are commonly structured by competitive and predator–prey interactions both among and within species. Intraspecific competition is common in small lakes and impoundments because of density-dependent growth within sport fish species (Guy and Willis 1995; Paukert and Willis 2004; Tomcko and Pierce 2005). Interspecific competition among sport fish species is also common in small impoundments. For example, bluegills may compete with juvenile largemouth bass for food resources (Brenden and Murphy 2004; Aday et al. 2005). Competition from and habitat alterations caused by invasive or introduced species, such as the common carp *Cyprinus carpio* and gizzard shad *Dorosoma cepedianum,* can result in suboptimal sport fish populations (Aday et al. 2003; Michaletz and Bonneau 2005; Weber and Brown 2009; Jackson et al. 2010). Lastly, predation by apex predators, such as largemouth bass, can strongly influence growth and size structure of bluegill and crappie populations (Gabelhouse 1984; Guy and Willis 1990; Olive et al. 2005; Schultz et al. 2008).

Clearly, numerous factors influence sport fish populations in small impoundments, and there is uncertainty about which variables are most important. However, few studies of small Midwestern impoundments have simultaneously examined the relative influences of watershed, lake morphology, water quality, and species interactions on several sport fish species across a relatively large spatial scale and a large range of impoundment fertility levels. Most sport fish populations are managed by harvest restrictions, but these restrictions may be ineffective if watershed or impoundment characteristics are directly shaping population dynamics. Thus, to effectively manage these small impoundments, a better understanding of the relative importance of watershed, impoundment, water quality, and species interaction variables is necessary. Using regression analysis, we examined the relative importance of these variables for 89 small Missouri impoundments. Specifically, our objective was to determine the relative importance of watershed, impoundment, water quality, and species interactions for explaining differences in relative abundance, growth, and size structure of largemouth bass, bluegills, redear sunfish *L. microlophus*, white crappies, and black crappies among small impoundments at a statewide scale.

METHODS

Study sites.—Variables influencing sport fish demographics were examined in 89 small impoundments (hereafter, "lakes") scattered across the state of Missouri. Most of the lakes were located in the Glacial Plains physiographic section of the state ($N = 48$), whereas fewer lakes were situated in the Ozark Border ($N = 6$), Osage Plains ($N = 16$), Ozark Highlands ($N = 18$), and Mississippi Lowlands ($N = 1$) physiographic sections (see locations of physiographic sections in Figure 1 of Jones et al. 2008b). Small lakes were included in our study if (1) at least 3 years of sport fish and water quality data were available, (2) the presence or absence of gizzard shad and common carp was known, and (3) macrophyte coverage was indexed (see below). The study lakes spanned a broad range of conditions that were representative of Missouri's small lakes; lake size ranged from 2 to 408 ha, and trophic state ranged from oligotrophic to hypereutrophic (Table 1). Fish communities consisted primarily of largemouth bass, bluegills, channel catfish, crappies, and other sunfishes *Lepomis* spp., sometimes including redear sunfish. Harvest restrictions varied among lakes, but most included either a 384-mm minimum total length (TL) limit or a 305–384-mm TL slot limit and a daily creel limit of six fish for largemouth bass. Length limits were rare for other species, and harvest of these species was mostly regulated by daily creel limits of 20–30 fish for sunfishes and crappies and 4 fish for catfishes (*Ictalurus* spp. and flathead catfish *Pylodictis olivaris* combined).

Fish demographic data.—Sport fish demographic data were obtained from standardized spring electrofishing surveys that were conducted from 1969 to 2009 by Missouri Department of Conservation (MDC) fisheries management biologists. However, over 98% of the data were collected in 1978 and later years. Surveys were conducted nearly annually in some lakes but only occasionally in others (mean = 13.5 sample years; range = 3–34 sample years). For a sample year, one or more electrofishing surveys were conducted during late April to early June. Electrofishing effort averaged 1.9 h (range = 0.6–11.3 h) per sample year in each lake. Fish that were collected during these surveys were measured for TL (nearest 2.5 mm). Fish ages were estimated from scales collected during some surveys from a subsample of fish (usually 5 fish per 12.7-mm TL group). Although otoliths are preferred structures for determining fish age, scales are likely to be reasonably accurate for fish younger than 5–6 years of age (Maceina et al. 2007). Fish with assigned ages were used to construct an age–length key that was then applied to the entire sample to estimate mean length at age. Sampling was conducted mostly during the daytime in turbid lakes and at night in clear lakes; however, some lakes were sampled during the day in some years and at night in other years.

TABLE 1. Summary statistics describing the environmental variables measured from 89 small Missouri impoundments. For water quality data, four lakes were represented two times each due to changes in the presence or absence of common carp or gizzard shad (see text for details).

Variable	*N*	Mean	SE	Median	Minimum	Maximum
Watershed						
Watershed area (ha)	89	2,194	767	689	20	66,622
Lake morphometry						
Lake surface area (ha)	89	61	8	31	2	408
Dam height (m)	89	13.0	0.6	12.5	4.6	33.6
Volume ($m^3 \times 1{,}000$)	89	3,307	666	1,271	59	34,146
Watershed area : lake surface area ratio	89	36	8	18	4	592
Flushing index (times/year)	87	3.4	1.2	1.0	0.1	87.0
Shoreline development index[a]	89	2.6	0.1	2.4	1.1	6.3
Water quality						
Chlorophyll (μg/L)	93	21	2	17	2	114
Total phosphorus (μg/L)	93	51	4	45	8	188
Total nitrogen (μg/L)	92	783	34	775	185	1,920
Volatile suspended solids (mg/L)	92	3.8	0.2	3.2	0.8	13.8
Nonvolatile suspended solids (mg/L)	93	4.5	0.5	3.1	0.5	35.9
Secchi depth (m)	93	1.1	0.1	0.9	0.2	3.2
Conductivity (μS)	93	197	8	197	40	417

[a] Ratio of shoreline length to the circumference of a circle having the same area as the lake.

The electrofishing data were obtained from management biologists in various forms, including raw field data sheets, output from various software programs, and lake management reports. From these sources, catch per effort (CPE) for stock-size and larger fish (number of fish/h of electrofishing), proportional size distribution (Guy et al. 2007) for quality-size fish (PSD) and preferred-size fish (PSD-P), and mean TL (mm) at age 3 (ML3) were determined for largemouth bass, bluegills, redear sunfish, white crappies, and black crappies. The stock, quality, and preferred sizes (TL) for these species are from Anderson and Gutreuter (1983). Mean TL at age 3 was chosen for our growth variable because it was the standard parameter presented in lake management reports. Not all of the fish variables were available for every lake; data sets for largemouth bass and bluegills were the most complete because these fishes were the primary targets of standardized sampling. Because the number of annual surveys varied greatly among lakes, we averaged sport fish demographic estimates across all years for each lake (see below for some exceptions). For lakes with multiple surveys within a year, we first averaged estimates from these surveys before averaging across all years. Although fish populations can change over time, we consider these averages to be the best representation of sport fish demographics for these lakes.

From MDC management biologists, we also obtained data on the presence (index = 1) or absence (index = 0) of common carp and gizzard shad in the study lakes. We were unable to acquire relative abundance, size structure, or growth information for these species because this information is not routinely collected. For four of the lakes, the presence–absence of common carp or gizzard shad varied over time due to fish invasions or removals. For these lakes, we considered such periods separately in our analysis (see below). Thus, the four lakes were represented twice in the analysis.

Environmental data.—Watershed, lake morphometry, and water quality data (Table 1) were largely from Jones et al. (2004, 2008a, 2008b). Dam height was used as a surrogate for water depth because it was strongly and positively correlated with mean depth (Jones et al. 2004), which was unmeasured for some lakes. Limnological data were sampled seasonally on three or four occasions during May–August from surface waters near the dam of each lake. Data from these collections were averaged to obtain annual means for each variable. Detailed sampling and analytical procedures are described by Jones et al. (2008a, 2008b). Some additional unpublished water quality data were obtained by using these same methods. Limnological data were collected between 1978 and 2009. Shoreline development index was calculated as the ratio of the lake perimeter (determined with GIS software) to the circumference of a circle having the same area as the lake. Aquatic macrophyte coverage (VEG) was indexed as absent, moderate ($<50\%$ of the littoral zone), or abundant ($\geq 50\%$ of the littoral zone) by MDC fisheries management biologists. However, for analysis (see below), we combined the absent and moderate categories of VEG into a single category. Therefore, VEG was indexed as either sparse (index = 0) or abundant (index = 1).

As with fish data, the frequency of annual collections of limnological data varied among lakes, with some lakes being sampled nearly every year and others being sampled less frequently (mean = 7.5 sample years; range = 3–21 sample years). We attempted to match limnological data with fish data that were collected during the same time period. However, when that was not possible ($<20\%$ of cases), we used the long-term average limnological data presented by Jones et al. (2008b). Similar to how we handled the fish data, we averaged the limnological data over all sample years for each lake. For the four lakes where the presence–absence of common carp or gizzard shad varied among years, limnological data were averaged for separate time periods.

Analysis.—Prior to conducting regression analysis, we reduced the number of environmental variables by using principal components analysis (PCA; PRINCOMP procedure in the Statistical Analysis System [SAS] version 9.2). All of the variables (Table 1) were $\log_e(X)$ transformed to normalize the data prior to analysis. The correlation matrix was used as input for the analysis. Following the procedures of Cross and McInerny (2005), environmental variables that were highly correlated to individual principal components (PCs) were used as proxy variables in the regression analysis instead of the PC scores. The use of actual environmental variables allowed for easier interpretation of relationships between environmental and fish variables.

Regression analysis (REG procedure in SAS version 9.2) was used to assess relationships between environmental variables and fish variables. Preliminary analysis indicated that linear regression provided better model fits than regression tree analysis (De'ath and Fabricus 2000; De'ath 2002). Explanatory variables chosen for inclusion in the regression models were (1) the environmental variables identified with the PCA, (2) various sport fish demographic variables (Tables 2, 3), and (3) dummy variables for VEG, common carp, and gizzard shad. We used the $\log_e(X)$-transformed environmental variables as in the PCA. To normalize the fish data, we transformed most of the fish variables by using either $\log_e(X)$ or arcsine ($X^{0.5}$) for proportional data. The ML3 data were normally distributed and were not transformed, and the three dummy variables were also not transformed. Sport fish demographics that could be associated with competition or predation were included as potential explanatory variables. For example, largemouth bass metrics (relative abundance and size structure) were included as explanatory variables for bluegill demographics because largemouth bass predation can structure bluegill populations (Guy and Willis 1990; Olive et al. 2005; Schultz et al. 2008). The intensity of largemouth bass predation is partially determined by their abundance and size. Bluegill CPE was likewise included in largemouth bass demographic models because bluegills can be prey and competitors for largemouth bass (Guy and Willis 1990; Brenden and Murphy 2004; Aday et al. 2005; Olive et al. 2005).

We compared the fit of various combinations of explanatory variables by using the information-theoretic approach (Burnham and Anderson 2002) and Akaike's information criterion corrected for small sample size (AIC_c). All models with an AIC_c

TABLE 2. Summary statistics describing catch per effort (CPE; fish/h of electrofishing) of stock-size and larger fish, proportional size distributions for quality-size (PSD) and preferred-size fish (PSD-P), and mean TL (mm) at age 3 (ML3) for largemouth bass, bluegills, redear sunfish, white crappies, and black crappies in 89 small Missouri impoundments. Four lakes are represented two times due to changes in the presence or absence of common carp or gizzard shad (see text for details).

Variable	*N*	Mean	SE	Median	Minimum	Maximum
			Largemouth bass			
CPE	93	85	3	85	3	159
PSD	93	45	2	44	8	84
PSD-P	93	17	1	15	0	51
ML3	52	278	4	274	210	364
			Bluegill			
CPE	93	135	7	123	41	369
PSD	93	33	1	32	5	70
PSD-P	93	3	1	1	0	40
ML3	56	136	2	134	101	183
			Redear sunfish			
CPE	49	35	4	24	1	143
PSD	49	66	3	70	16	100
PSD-P	49	26	2	25	0	72
ML3	21	168	5	173	121	198
			White crappie			
CPE	59	37	5	24	1	143
PSD	59	49	4	48	0	100
PSD-P	59	17	3	10	0	100
ML3	25	209	6	207	147	251
			Black crappie			
CPE	40	17	2	13	1	78
PSD	40	64	4	67	0	100
PSD-P	40	21	4	14	0	93
ML3	10	228	14	239	145	280

difference ($\Delta\mathrm{AIC}_c$) of 2 or less in comparison with the most parsimonious model (i.e., the model with the lowest AIC_c value) were considered statistically similar. Preliminary analyses indicated that models with more than four explanatory variables did not significantly improve model fit relative to models with four or fewer variables. Thus, to avoid overfitting the models, we restricted the maximum number of explanatory variables to four for all dependent variables except ML3 for redear sunfish (maximum of three explanatory variables), white crappies (maximum of three explanatory variables), and black crappies (maximum of two explanatory variables) due to small sample sizes. Models were only included for consideration if they did not exhibit multicollinearity among the regressors. Models were checked for multicollinearity by using diagnostic tools (options VIF, TOL, and COLLINOINT) within the REG procedure in SAS. For each dependent variable, we sought the simplest models with an $\Delta\mathrm{AIC}_c$ of 2 or less. Models that included the same explanatory variables as a simpler model (i.e., one having fewer variables) with a smaller AIC value are not presented.

RESULTS

The study lakes exhibited a diverse array of environmental and sport fish characteristics. Lakes varied from shallow to deep, from oligotrophic to hypereutrophic, from having simple shorelines to having complex shorelines, and from being void of aquatic macrophytes to being extensively vegetated (Table 1). Likewise, sport fish demographics varied from low to high relative abundance, from small to large fish sizes, and from slow to fast growth (Table 2). Common carp were present in 45 lakes and absent from 42 lakes; in two other lakes, their presence varied over time. Gizzard shad were present in 54 lakes and absent from 31 lakes; in four other lakes, the presence of gizzard shad varied over time.

The number of potential explanatory environmental variables was reduced to six: five proxy variables identified by using PCA and one dummy variable (VEG). The first five PCs (PC1–PC5) explained 94% of the variance in the data set. The sixth PC and subsequent PCs each explained less than 3% of additional variance and were excluded from further consideration. Total phosphorus (TP), total nitrogen, Secchi depth, and

TABLE 3. Sport fish variables that were used as potential explanatory variables in regression models of largemouth bass (LMB), bluegill (BLG), redear sunfish (RED), white crappie (WHC), and black crappie (BLC) demographic response variables for 89 small impoundments. Variables are defined in Table 2.

	Explanatory variable														
Response variable	LMB_CPE	LMB_PSD	LMB_PSD-P	BLG_CPE	BLG_PSD	BLG_PSD-P	RED_CPE	RED_PSD	RED_PSD-P	WHC_CPE	WHC_PSD	WHC_PSD-P	BLC_CPE	BLC_PSD	BLC_PSD-P
LMB_CPE				x											
LMB_PSD	x			x	x										
LMB_PSD-P	x			x	x										
LMB_ML3	x			x	x										
BLG_CPE	x	x	x												
BLG_PSD	x	x	x	x											
BLG_PSD-P	x	x	x	x											
BLG_ML3	x	x	x	x											
RED_CPE	x	x	x	x											
RED_PSD	x	x	x	x			x								
RED_PSD-P	x	x	x	x			x								
RED_ML3	x	x	x	x			x								
WHC_CPE	x	x	x	x											
WHC_PSD	x	x	x	x						x					
WHC_PSD-P	x	x	x	x						x					
WHC_ML3	x	x	x	x						x					
BLC_CPE	x	x	x	x											
BLC_PSD	x	x	x	x									x		
BLC_PSD-P	x	x	x	x									x		
BLC_ML3	x	x	x	x									x		

chlorophyll were most strongly correlated with PC1 (Table 4). We chose TP as the proxy variable for PC1 because TP is strongly correlated with all trophic state metrics in Missouri reservoirs (Jones et al. 2008b). Lake surface area (SA), lake volume, and shoreline development index were most strongly correlated with PC2, and SA was chosen as the proxy variable. Lake volume had a slightly stronger correlation with PC2, but SA was selected because it is more commonly used as a lake size variable. The watershed area : lake surface area ratio (WSA) and the flushing index were most strongly correlated with PC3; the WSA was used as the proxy variable. Conductivity (COND) and nonvolatile suspended solids concentration (NVSS) were used as proxy variables for PC4 and PC5, respectively. Thus, TP, SA, WSA, COND, and NVSS were included as potential environmental variables (along with VEG) in the regression models.

Largemouth Bass Demographics

Variations in largemouth bass demographics were primarily explained by lake fertility (i.e., TP) and fish variables (Table 5). Relative abundance of largemouth bass was greatest in lakes with large numbers of bluegills, low TP, low WSA, low NVSS, and an absence of common carp. Bluegill CPE accounted for about one-half of the variance explained by the models. The negative relationship between largemouth bass CPE and TP was apparently driven by data from one hypereutrophic lake in which TP exceeded 150 μg/L, as there was little relationship between TP and largemouth bass CPE for the other lakes (Figure 1). Largemouth bass populations typically exhibited faster growth and contained a higher proportion of large individuals

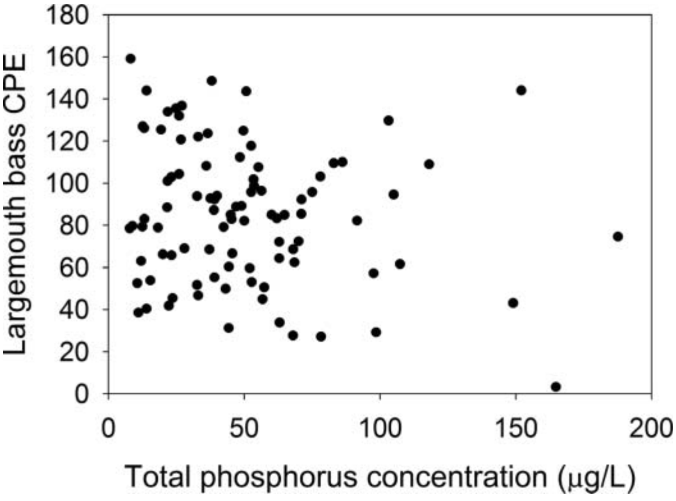

FIGURE 1. Scatter plot relating largemouth bass catch per effort (CPE; fish/h of electrofishing) with total phosphorus concentration in 89 small Missouri impoundments.

TABLE 4. Principal component (PC) loadings (correlation coefficients) and the percentage of variation explained by the first five PCs (PC1–PC5) on environmental variables for 89 small impoundments. Loadings in bold italics indicate the variables that were selected for inclusion in regression analyses. Units for the variables are provided in Table 1.

Variable	PC1	PC2	PC3	PC4	PC5
Watershed area	0.055	0.392	0.352	−0.207	0.064
Lake surface area	0.081	***0.450***	−0.037	−0.253	−0.053
Dam height	−0.064	0.401	−0.139	0.126	0.203
Volume	0.027	0.465	−0.095	−0.178	0.011
Watershed area : lake surface area ratio	−0.016	0.041	***0.634***	0.014	0.177
Flushing index	−0.051	−0.129	0.602	−0.220	0.054
Shoreline development index	0.047	0.425	−0.059	−0.021	−0.062
Chlorophyll	0.390	−0.064	−0.084	−0.124	0.474
Total phosphorus	***0.429***	−0.047	0.056	−0.043	0.004
Total nitrogen	0.412	−0.051	−0.103	−0.029	0.145
Volatile suspended solids	0.408	−0.086	−0.057	−0.033	0.325
Nonvolatile suspended solids	0.354	0.066	0.103	0.140	***−0.641***
Secchi depth	−0.408	0.047	−0.086	0.077	0.363
Conductivity	0.125	0.208	0.191	***0.867***	0.139
Explained variation (%)	36.7	30.2	16.5	5.8	4.7

in larger, fertile lakes with a high abundance of small bluegills, the presence of gizzard shad, and a low abundance of largemouth bass. Largemouth bass populations in turbid lakes (high NVSS) usually had slower growth but higher PSD-P values than populations in clearer lakes.

Bluegill Demographics

The demographics of bluegill populations were most strongly associated with largemouth bass variables and the presence–absence of gizzard shad (Table 6). Bluegills were most abundant in lakes with an abundance of large-size largemouth bass, high

TABLE 5. Regression models explaining variation in catch per effort (CPE; fish/h of electrofishing), proportional size distribution for quality-size fish (PSD) and preferred-size fish (PSD-P), and mean TL (mm) at age 3 (ML3) for largemouth bass (LMB) in small Missouri impoundments (*N* = number of lakes). Explanatory variables are macrophyte coverage (VEG), gizzard shad presence or absence (GIZ), common carp presence or absence (CARP), total phosphorus (TP), lake surface area (SA), watershed area : lake surface area ratio (WSA), conductivity (COND), nonvolatile suspended solids concentration (NVSS), and various fish variables (LMB; BLG = bluegill; RED = redear sunfish; WHC = white crappie; BLC = black crappie). Explanatory variables are listed in order of importance based on partial correlation coefficients. The signs of the regression coefficients for the explanatory variables are shown in parentheses. Models were compared by use of Akaike's information criterion corrected for small sample size (AIC$_c$); ΔAIC$_c$ is the difference in AIC$_c$ values between the candidate model and the model with the lowest AIC$_c$ value.

Explanatory variables	R^2	ΔAIC$_c$
LMB_CPE (*N* = 93)		
BLG_CPE (+), TP (−), WSA (−)	0.285	0
BLG_CPE (+), NVSS (−), WSA (−)	0.272	1.63
BLG_CPE (+), TP (−), CARP (−)	0.270	1.88
LMB_PSD (*N* = 93)		
TP (+), SA (+), COND (+), BLG_PSD (−)	0.498	0
TP (+), GIZ (+), COND (+), BLG_PSD (−)	0.497	0.24
LMB_PSD-P (*N* = 93)		
BLG_CPE (+), GIZ (+), LMB_CPE (−), NVSS (+)	0.519	0
TP (+), SA (+), BLG_PSD (−), COND (+)	0.512	1.33
BLG_CPE (+), GIZ (+), LMB_CPE (−), COND (+)	0.510	1.57
BLG_CPE (+), NVSS (+), SA (+), LMB_CPE (−)	0.510	1.57
LMB_ML3 (*N* = 52)		
SA (+), NVSS (−), TP (+)	0.290	0

TABLE 6. Regression models explaining variation in catch per effort (CPE; fish/h of electrofishing), proportional size distribution for quality-size fish (PSD) and preferred-size fish (PSD-P), and mean TL (mm) at age 3 (ML3) for bluegills (BLG) in small Missouri impoundments (N = number of lakes; ΔAIC_c is defined in Table 5). Explanatory variables are defined in Table 5 and are listed in order of importance based on partial correlation coefficients. The signs of the regression coefficients for the explanatory variables are shown in parentheses.

Explanatory variables	R^2	ΔAIC_c
BLG_CPE (N = 93)		
LMB_PSD-P (+), LMB_CPE (+), NVSS (−), TP (+)	0.433	0
LMB_PSD-P (+), LMB_CPE (+), TP (+), GIZ (−)	0.430	0.64
BLG_PSD (N = 93)		
LMB_CPE (+), COND (+), LMB_PSD-P (−), TP (+)	0.345	0
LMB_CPE (+), COND (+), LMB_PSD-P (−)	0.318	1.55
BLG_PSD-P (N = 93)		
LMB_CPE (+), GIZ (−), BLG_CPE (−)	0.204	0
LMB_CPE (+), GIZ (−), NVSS (−)	0.203	0.10
LMB_CPE (+), NVSS (−), COND (+)	0.203	0.13
LMB_CPE (+), NVSS (−)	0.177	0.90
BLG_ML3 (N = 56)		
LMB_PSD-P (−), NVSS (−), COND (+), TP (+)	0.321	0
LMB_PSD-P (−), GIZ (−), NVSS (−), TP (+)	0.315	0.52
LMB_PSD-P (−), GIZ (−), CARP (+)	0.270	1.61
LMB_PSD-P (−), GIZ (−)	0.238	1.69
GIZ (−), NVSS (−), TP (+)	0.266	1.97

TP, and low NVSS. Bluegill populations exhibited the fastest growth and contained the highest proportion of large individuals in lakes with a high abundance of small largemouth bass, an absence of gizzard shad, high fertility, low NVSS, and a low abundance of bluegills.

Redear Sunfish Demographics

Redear sunfish demographics were mostly associated with fish, lake fertility, and lake size variables (Table 7). Smaller lakes containing small largemouth bass and large numbers of bluegills exhibited the highest abundances of redear sunfish.

TABLE 7. Regression models explaining variation in catch per effort (CPE; fish/h of electrofishing), proportional size distribution for quality-size fish (PSD) and preferred-size fish (PSD-P), and mean TL (mm) at age 3 (ML3) for redear sunfish (RED) in small Missouri impoundments (N = number of lakes; ΔAIC_c is defined in Table 5). Explanatory variables are defined in Table 5 and are listed in order of importance based on partial correlation coefficients. The signs of the regression coefficients for the explanatory variables are shown in parentheses.

Explanatory variables	R^2	ΔAIC_c
RED_CPE (N = 49)		
LMB_PSD (−), SA (−), BLG_CPE (+)	0.328	0
LMB_PSD-P (−), BLG_CPE (+), SA (−), LMB_CPE (−)	0.347	1.08
LMB_PSD-P (−), BLG_CPE (+), SA (−)	0.302	1.84
RED_PSD (N = 49)		
RED_CPE (−), TP (+), LMB_PSD-P (−)	0.381	0
RED_CPE (−), TP (+), LMB_PSD (−)	0.380	0.13
RED_CPE (−), LMB_PSD (−)	0.344	0.52
RED_CPE (−), LMB_PSD-P (−)	0.343	0.55
RED_CPE (−), WSA (−)	0.336	1.13
RED_PSD-P (N = 49)		
RED_CPE (−), LMB_PSD-P (−)	0.286	0
RED_ML3 (N = 21)		
TP (+), SA (+), LMB_PSD-P (−)	0.507	0
TP (+), SA (+), LMB_PSD (−)	0.502	0.22

TABLE 8. Regression models explaining variation in catch per effort (CPE; fish/h of electrofishing), proportional size distribution for quality-size fish (PSD) and preferred-size fish (PSD-P), and mean TL (mm) at age 3 (ML3) for white crappies (WHC) in small Missouri impoundments (N = number of lakes; ΔAIC_c is defined in Table 5). Explanatory variables are defined in Table 5 and are listed in order of importance based on partial correlation coefficients. The signs of the regression coefficients for the explanatory variables are shown in parentheses.

Explanatory variables	R^2	ΔAIC_c
WHC_CPE (*N* = 59)		
GIZ (+), NVSS (+)	0.211	0
LMB_PSD-P (+), NVSS (+)	0.192	1.45
WHC_PSD (*N* = 59)		
LMB_CPE (+), WHC_CPE (−), SA (+), CARP (−)	0.420	0
LMB_CPE (+), WHC_CPE (−), SA (+), GIZ (−)	0.404	1.59
WHC_PSD-P (*N* = 59)		
SA (+), BLG_CPE (−), WHC_CPE (−), LMB_CPE (+)	0.347	0
SA (+), WHC_CPE (−), CARP (−)	0.303	1.50
WHC_ML3 (*N* = 25)		
WHC_CPE (−)	0.377	0

Populations of redear sunfish with the fastest growth and the highest proportion of large individuals were found in larger, fertile lakes characterized by (1) low abundances of redear sunfish and (2) largemouth bass populations consisting of small individuals.

White Crappie Demographics

White crappie demographics were primarily associated with fish variables, NVSS, and SA (Table 8). White crappies were typically most abundant in turbid lakes containing largemouth bass populations with high PSD-P and the presence of gizzard shad. Larger lakes with greater abundances of largemouth bass and lesser abundances of white crappies and bluegills usually contained white crappie populations with the fastest growth and highest proportions of large individuals. The presence of common carp and gizzard shad also seemed to have a negative influence on the growth and size structure of white crappies.

Black Crappie Demographics

The demographics of black crappies were mostly associated with fish variables (Table 9). Models explaining black crappie CPE were weak but suggested that black crappies were most abundant in lakes with low COND and with largemouth bass populations composed of a high proportion of large individuals. A variety of variables was included in models explaining variation in growth and size structure of black crappies. However, the most important variables for promoting black crappie populations with fast growth and a high proportion of large individuals were low abundances of black crappies and bluegills, a high abundance of largemouth bass, abundant vegetation (i.e., high VEG), low NVSS, and an absence of common carp and gizzard shad.

TABLE 9. Regression models explaining variation in catch per effort (CPE; fish/h of electrofishing), proportional size distribution for quality-size fish (PSD) and preferred-size fish (PSD-P), and mean TL (mm) at age 3 (ML3) for black crappies (BLC) in small Missouri impoundments (N = number of lakes; ΔAIC_c is defined in Table 5). Explanatory variables are defined in Table 5 and are listed in order of importance based on partial correlation coefficients. The signs of the regression coefficients for the explanatory variables are shown in parentheses.

Explanatory variables	R^2	ΔAIC_c
BLC_CPE (*N* = 40)		
LMB_PSD (+), COND (−)	0.185	0
LMB_PSD (+)	0.121	0.68
LMB_PSD-P (+), COND (−)	0.162	1.11
LMB_PSD-P (+)	0.109	1.19
BLC_PSD (*N* = 40)		
BLC_CPE (−), LMB_CPE (+), WSA (−)	0.246	0
BLC_CPE (−), LMB_CPE (+), VEG (+)	0.242	0.22
BLC_CPE (−), VEG (+)	0.188	0.53
BLC_CPE (−), LMB_CPE (+), SA (+)	0.233	0.72
BLC_CPE (−), LMB_CPE (+)	0.178	0.98
BLC_CPE (−), WSA (−)	0.164	1.67
BLC_PSD-P (*N* = 40)		
GIZ (−), NVSS (−)	0.244	0
NVSS (−), BLC_CPE (−)	0.209	1.77
NVSS (−)	0.158	1.94
BLC_ML3 (*N* = 10)		
CARP (−), BLG_CPE (−)	0.736	0
COND (−), WSA (+)	0.722	0.50
CARP (−), SA (−)	0.714	0.77
SA (−), WSA (+)	0.692	1.52
SA (−)	0.524	1.60
GIZ (−), BLG_CPE (−)	0.688	1.66

DISCUSSION

Our broad-scale analysis of factors affecting sport fish communities in small Missouri lakes revealed that variables associated with predation, competition, and lake fertility were the most important in explaining variation in sport fish demographics. Our results are congruent with those of previous studies that have recognized the importance of predation and competition in structuring fish communities. There was evidence for competition both within and among species, and density-dependent growth was observed for each of the sport fish species we examined. As was previously observed (Novinger and Dillard 1978; Gabelhouse 1984; Guy and Willis 1990; Olive et al. 2005), largemouth bass predation was a strong force in structuring sunfish and crappie populations. Lakes with dense largemouth bass populations typically contained sunfish and crappie populations with desirable size structure and growth, but the largemouth bass were mostly small individuals owing to density-dependent growth (Reynolds and Babb 1978; Paukert and Willis 2004). As has been reported by others (Guy and Willis 1995; Pope et al. 2004; Tomcko and Pierce 2005), size structure and growth within a given species were poorer as density increased. Interspecific competition may also structure sport fish populations in these small lakes. The size structure of white crappies and the growth of black crappies declined with increasing bluegill abundance, suggesting competition for prey resources. Similar to our findings, Cichra et al. (1983) found that lakes dominated by intermediate-size bluegills (100–159 mm TL) contained stunted white crappie populations. Gabelhouse (1984) found a positive relationship between crappie PSD and bluegill PSD, possibly because bluegill abundance was lower in lakes with a higher bluegill PSD. Interestingly, bluegill CPE was positively correlated with largemouth bass CPE and redear sunfish CPE. Although juvenile largemouth bass and bluegills may compete for food resources (Brenden and Murphy 2004; Aday et al. 2005), the correlated abundances of stock-size and larger fish may simply indicate that the conditions suitable for recruitment are similar between these species.

Common carp and gizzard shad exhibited variable effects on sport fish populations. Lakes containing common carp had lower abundances of largemouth bass, poorer size structure of white crappies, and slower growth of black crappies; however, few other negative effects on sport fish species were found. Negative effects on sport fish seem to occur when common carp reach an abundance threshold, beyond which the abundances of sport fishes are reduced (Jackson et al. 2010; Weber and Brown 2011). Unfortunately, we lacked the necessary data for examining these relationships in our study lakes. Common carp are known to destroy aquatic macrophytes (Parkos et al. 2003; Weber and Brown 2009); such destruction would reduce nursery areas for juvenile fishes, thereby potentially reducing sport fish recruitment. Furthermore, aquatic macrophyte elimination and benthic foraging by common carp may also reduce macroinvertebrate densities, which in turn could reduce the growth of fishes that feed on macroinvertebrate prey (Parkos et al. 2003; Wahl et al. 2011). The growth of black crappies, which are known to feed on macroinvertebrates (Ball and Kilambi 1973; Ellison 1984; Tuten et al. 2008), may have suffered in lakes containing common carp because of lower prey resources. Lakes that contained gizzard shad usually had poorer growth and size structure of bluegills and black crappies but a better size structure of largemouth bass than lakes that lacked gizzard shad. Although the actual mechanisms are unknown, negative effects of gizzard shad on bluegills have been commonly reported (Aday et al. 2003; Michaletz and Bonneau 2005; Porath and Hurley 2005). Conversely, gizzard shad constitute an important prey resource for largemouth bass and may improve growth of this predator species (Storck 1986; Michaletz 1997).

Increases in lake fertility (as measured by TP) generally enhanced the growth and size structure of sport fishes in the study lakes. The TP variable was positively associated with growth and size structure of largemouth bass, bluegills, and redear sunfish. The slight negative relationship between TP and largemouth bass CPE appeared to be driven by data from one lake, and TP did not explain more than 10% of the variation in largemouth bass CPE. Relationships between sport fish demographics and lake fertility variables are probably nonlinear (Kautz 1982; McInerny and Cross 1999; Egertson and Downing 2004), but apparently few of our study lakes contained nutrient levels that were high enough to allow the detection of negative effects on sport fish populations.

Other variables were occasionally important in explaining variation in sport fish demographics. The NVSS variable was usually negatively associated with sport fish demographic variables except for a positive association with white crappie CPE. Turbidity caused by inorganic suspended solids can reduce foraging and reproductive success of fishes (Miner and Stein 1996; Trebitz et al. 2007; Shoup and Wahl 2009). However, white crappies seem to be more tolerant of turbidity than other centrarchids and can exist in turbid lakes at high densities (Ellison 1984; Muoneke et al. 1992). White crappies in these dense populations are typically slow growing, and most do not reach large sizes (Ellison 1984; Muoneke et al. 1992; present study). The COND variable had a positive influence on the growth and size structure of largemouth bass and bluegills but a negative influence on the growth and abundance of black crappies. Conductivity is closely associated with total dissolved solids, which in turn have been positively related to fish yield (Ryder 1982). Black crappie PSD was positively associated with the VEG index. Black crappies may have benefited from the macroinvertebrates associated with macrophytes (McDonough and Buchanan 1991; Martin et al. 1992). Large lakes tended to contain largemouth bass, redear sunfish, and white crappies that exhibited faster growth or better size structure. Consistent with our findings, largemouth bass grew faster in larger Nebraska lakes (Paukert and Willis 2004). Cross and McInerny (2005) found that bluegills fared better in smaller Minnesota lakes, but we found no significant relationships between bluegill demographics and SA. Finally, WSA was sometimes included in models and was negatively associated with fish variables except for black crappie growth. Black crappies seemed to grow faster in lakes with a larger WSA, perhaps because these lakes tended to be more fertile owing to higher flushing rates (Bremigan et al. 2008; Jones et al. 2008a). However, sample size was small and other models that did not include WSA explained as much or more of the variation in black crappie growth, indicating uncertainty in the relationship between WSA and growth of this species.

Although most of the models explained less than half of the variation in sport fish demographics, they provide information that will be useful to fisheries managers. Many small lakes are managed primarily by restricting angler harvest, especially the harvest of largemouth bass. Our study confirms the importance of manipulating largemouth bass densities to improve largemouth bass or panfish populations. Provided that lake fertility is adequate, the manipulation of largemouth bass densities may be the most important management strategy for many of these small lakes. Acceptable sport fisheries for both largemouth bass and panfish can be achieved by maintaining moderate densities and size structure of largemouth bass (Swingle 1950; Novinger and Legler 1978). Creation of a panfish population with many large individuals may require elevated densities of largemouth bass, thus sacrificing the growth and size structure of these predators (Gabelhouse 1984; Willis et al. 2010). High-quality bluegill populations will probably only be achieved in productive lakes that have high densities of largemouth bass and no gizzard shad. Conversely, high-quality largemouth bass populations will most likely occur in lakes that are characterized by low densities of largemouth bass, moderate to high densities of small bluegills, and the presence of gizzard shad (Willis et al. 2010). Consequently, lakes containing gizzard shad may be best managed for large-size largemouth bass instead of large bluegills because the selective removal of gizzard shad is costly and unlikely to achieve long-term positive results (DeVries and Stein 1990; Kim and DeVries 2000). Intense largemouth bass predation and lower abundances of bluegills seem necessary for desirable redear sunfish and crappie populations. Additionally, eradication of common carp may benefit sport fish populations, but the abundance at which common carp harm sport fish populations in these small lakes is unknown.

Management efforts within watersheds have become more common with the increased recognition of the importance of watershed characteristics for lake sport fisheries (Miranda 2008; Schultz et al. 2008; Willis et al. 2010). Many of these efforts have been directed toward reducing nutrient and sediment input into lakes. Such efforts have benefited sport fisheries in lakes that formerly received large amounts of nutrients and sediments from their watersheds (Schultz et al. 2008). Our results indicate that reducing sediment loads into lakes could benefit sport fisheries and would increase the life span of the lakes. Inorganic suspended solid concentrations generally had a negative effect on sport fish populations. However, caution should be used in attempting to reduce nutrient input into lakes, as moderate levels of nutrients are necessary to support sport fish communities. Substantial reductions in nutrient inputs have led to declines in sport fisheries in some lakes (Yurk and Ney 1989; Ney 1996). Our data suggest that the potential for harmful effects of high nutrient concentrations on warmwater sport fish populations occurs only in hypereutrophic lakes.

Diurnal timing of sampling could have affected our estimates of sport fish demographics. Electrofishing catch rates of bluegills or largemouth bass can sometimes be greater at night than during the day, especially in clear lakes (Dumont and Dennis 1997; McInerny and Cross 2000; Pierce et al. 2001). In some waters, no differences in daytime and nighttime catch rates were found for largemouth bass (Malvestuto and Sonski 1990; Dumont and Dennis 1997). Size structure estimates for largemouth bass and bluegills do not seem to vary between daytime and nighttime electrofishing samples (Dumont and Dennis 1997; Pierce et al. 2001). We acknowledge that diurnal differences in sampling could have affected our catch rate estimates, but this potential bias is relatively minor given the large range in catch rates among the study lakes (Table 2).

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